

ORIGINAL ARTICLE

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Optimal timing of comb construction by honeybee (*Apis mellifera*) colonies: a dynamic programming model and experimental tests

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Abstract Honeybee colonies, like organisms, should exhibit optimal design in their temporal pattern of resource allocation to somatic structures. A vital colony structure is the comb which stores honey for overwinter survival. However, the timing of comb construction poses a dilemma to a colony attempting to maximize its honey reserves. On the one hand, plenty of empty comb is needed for efficient exploitation of temporally unpredictable flower blooms. On the other hand, because comb is made from energetically expensive wax, its construction too early or in excessive amounts will reduce the amount of honey available for winter thermoregulation and brood-rearing. A dynamic optimization model concludes that colonies should add new comb only when they have filled their old comb with food and brood above a threshold level. The threshold increases with time until, at the end of the season, building is never an optimal behavior. The temporal pattern of construction predicted by the model – pulses of building coincident with periods of nectar intake and comb fullness – matches that seen in an actual colony observed over the course of an entire foraging season. When nectar sources are rich but temporally clumped, the model also predicts that bees should be sensitive to nectar intake, employing much higher thresholds on days when nectar is not available than on days when it is. Even under poorer and more dispersed nectar regimes, little fitness cost is paid by colonies replacing the optimal strategy with a simpler rule of thumb calling for new construction only when two conditions are met: (1) a fullness threshold has been exceeded, and (2) nectar is currently being collected. Experiments demonstrate that colonies do in fact use such a rule of thumb to control the onset of construction. However, once they have begun building, the bees con-

tinue as long as nectar collection persists, regardless of changes in comb fullness. Thus the onset and duration of comb-building bouts appear to be under partially independent control.

Key words Honeybee · *Apis mellifera* · Nest construction · Dynamic programming · Resource allocation

Introduction

Social insects hold a special place in the study of behavioral evolution because they exhibit adaptive design at a hierarchical level above that of the individual organism. Under conditions that defuse the conflict inherent in the genetic heterogeneity of colony members, natural selection has favored worker phenotypes that enhance efficient group function rather than individual reproductive success (Ratnieks and Reeve 1992). Group-level adaptation is expected not only in the functional design of mature societies, but also in the temporal patterns of colony development. Just as a growing organism must allocate limited resources among somatic organs serving different functions (e.g., acquisition, defense, and maintenance), insect societies must invest in worker castes, nest structures, and food stores (Wilson 1985; Tschinkel 1993). The fitness benefit of allocation to each function is likely to vary with colony age, size, and environmental context. Thus, in societies as in organisms, an optimal investment strategy will be dynamic, with allocation ratios changing as the colony grows (Perrin and Sibly 1993).

This paper explores a resource allocation problem underlying the growth of two crucial “organs” of honeybee colonies: the honey hoard which serves as an energy reserve, and the comb in which this honey is stored. The allocation problem arises from the bees’ unusual life history. Unlike other social insects living in temperate climates, bees overwinter as large colonies and raise

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brood even during the coldest winter periods. They accomplish this by nesting in sheltered cavities and by hoarding large amounts of honey and pollen for overwinter survival. Their honey stores provide them with energy for brood-rearing and for thermoregulation, allowing them to maintain core nest temperatures near 35 °C in ambient temperatures as low as -40 °C (Winston 1987). This effort enables the colony to attain a large population size rapidly, enhancing its likelihood of early reproduction and allowing it to deploy large foraging forces among the ample nectar-bearing flowers available in spring (Seeley 1985). It also poses a major life history challenge, as indicated by the much lower survival probability of colonies in winter than in summer (Seeley 1985). Because overwinter survival depends on an adequate fuel supply, amassing a large honey hoard is a critical goal during the spring and summer, when nectar-bearing flowers are available.

As it gathers nectar, the colony must decide how much energy should be diverted from storage as honey and invested in structures, such as comb, needed for future honey collection. On the one hand, the colony needs an inventory of empty comb in order to exploit rich but temporally unpredictable blooms (nectar flows). Not only does the supply of comb place an upper limit on honey stores, but the lack of sufficient empty comb may reduce foraging efficiency by imposing long delays on bees seeking empty cells in which to place incoming nectar (Seeley 1995). On the other hand, the colony should also minimize expenditure on the energetically expensive wax from which comb is constructed. Because bees do not eat wax, an investment in comb cannot later be redirected to other needs. Comb construction at inappropriate times or in excessive amounts will detract from colony honey stores and so threaten overwinter survival.

How do colonies time their construction activity to solve this dilemma? It is clear that swarms do not simply build a full complement of comb as rapidly as possible when they settle into a nest cavity. Rather, after an initial bout of intense construction, they build new comb in pulses (Hepburn 1986). The available evidence suggests that the timing of these pulses depends on both colony state and environmental conditions. The testimony of generations of apiculturists indicates that bees will build only when they are collecting nectar (Hepburn 1986). Kelley (1991) obtained experimental support for this claim, as well as tentative evidence that a colony builds only when it has filled its available comb with more than a threshold quantity of food and brood. This implies a flexible strategy dependent on at least three conditions: the amount of comb already built, the amount of honey already stored, and the availability of fresh nectar in the field.

Here I present a model exploring the effect of these conditions on the fitness-maximizing building strategy of a colony. Previous models of building by social insects have generally been concerned with the proximate mechanisms yielding complex spatial and temporal patterns (Skarka et al. 1990; Karsai and Péntzes 1993;

Theraulaz and Bonabeau 1995; Franks and Deneubourg 1997). This work instead seeks a description of the optimal timing of new nest construction. To address this, I employed stochastic dynamic programming, an optimization technique with several advantages for studying fitness effects of fine-scale behavioral decisions in the context of animal life history (Mangel and Clark 1988). This approach has previously been used to examine foraging strategies in social insects (Houston et al. 1988; Beauchamp 1992), but not temporal patterns of resource allocation. The building rules and comb growth trajectory predicted by the model were compared with data from actual honeybee colonies.

Methods

Dynamic programming model

The model determines the optimal building behavior of a honeybee colony for each day of a single foraging season of duration T days, and for each possible value of three state variables: $N(t)$, the quantity of nectar which the colony can collect on day t ; $C(t)$, the area of comb in the nest on day t ; and $H(t)$, the mass of honey stored in this comb on day t . A colony has two behavioral options on each day: build an amount of comb C_{day} or build no comb at all. The optimization criterion governing its decision is maximization of the probability of survival through the following winter. Survival probability depends on the quantity of honey stored by the end of the foraging season. Inappropriate building decisions can reduce this quantity in two ways: (1) the colony builds excessive comb, thus wasting energy which could have been stored as honey, and (2) the colony does not build enough comb to handle nectar sources as they become available, thus limiting its storage capacity and foraging efficiency. An additional constraint is the need to avoid starvation during the foraging season when faced with prolonged nectar dearths.

The model applies only to the first year of colony existence (except for the earliest weeks, when comb-building is probably driven by the need for rapid brood-rearing to refresh an aging workforce). No reproductive swarms are produced in this year, and future fitness depends primarily on avoiding a highly probable death by starvation over the first winter (Seeley 1985). This temporal restriction is not severe, however, because colonies build most of their comb in the first year (Lee and Winston 1985).

Three equations describe how the state variables change with time and with colony behavior:

$$N(t+1) = \begin{cases} N_{\text{max}} & \text{with probability } P_{N(t)} \\ 0 & \text{with probability } 1 - P_{N(t)} \end{cases} \quad (1a)$$

$$C(t+1) = C(t) + C_{\text{day}_b} \quad (1b)$$

$$H(t+1) = H(t) - H_{\text{other}} - H_{\text{wax}} \times W \times C_{\text{day}} + I \quad (1c)$$

In Eq. 1a, $N(t)$ gives the amount of nectar a colony can collect on day t if it is working at maximum efficiency. For the sake of computational simplicity, the model ignores variation in the size of nectar flows: $N(t) = N_{\text{max}}$ on good days and zero on bad days (no nectar-bearing flowers are in bloom or inclement weather prevents foraging). Foraging conditions are modeled as a first-order Markov chain; nectar availability on a given day depends only on its availability the previous day, according to the probabilities in a two by two transition matrix:

		Conditions on day $t + 1$		
		0	N_{max}	
Conditions on day t	0	$1 - P_0$	P_0	(2)
	N_{max}	$1 - P_{N_{\text{max}}}$	$P_{N_{\text{max}}}$	

$P_{N(t)}$ is the probability of a nectar flow occurring on day $t + 1$ given nectar condition $N(t)$ on day t .

The colony's comb quantity changes according to Eq. 1b, where C_{day_b} is the amount of comb built during a single day given that the colony has made building decision b . If the bees are idle then C_{day_b} equals zero; if they build, it has a fixed positive value C_{day} , subject to the constraint that $C(t) + C_{\text{day}} \leq C_{\text{max}}$, where C_{max} is the maximum area of comb the nest cavity can hold. Comb is measured in square centimeters of double-sided comb (that is, the two faces of a sheet of comb are not measured separately).

Honey stores change according to Eq. 1c, where H_{other} is the daily metabolic energy spent by the colony on all non-building activities (measured in kilograms of honey); H_{wax} is the metabolic cost of producing 1 kg of comb (in kilograms of honey); W is the mass of wax in 1 cm² of comb; and I is the daily nectar intake of the colony (in kilograms of honey).

Honey stores are limited by the amount of comb available for storage:

$$0 \leq H(t) \leq D \times S \times C(t) \quad (3)$$

where D is the amount of honey stored per unit area of filled honey comb and S is the fraction of total comb area available for honey storage (i.e., not being used for brood-rearing or pollen storage). For most of the foraging season, while the colony is rearing brood, S is assumed to have a constant value less than one. In the last 3 weeks of the season, however, S increases linearly to 1, as brood-rearing tapers off before winter.

H_{other} depends on the population of workers and larvae:

$$H_{\text{other}} = H_{\text{ind}} \cdot \left(B(t) + C(t) \cdot (1 - S) \cdot L \cdot \frac{d_l}{d_b} \right) \quad (4)$$

where H_{ind} is the daily honey consumption of a worker or larva; $B(t)$ is the worker population on day t ; L is the number of cells per square centimeter of comb; and d_l and d_b are the length in days of the larval and total brood periods, respectively. $B(t)$ follows a sinusoidal path from a starting value of 10,000 (about the size of a feral swarm: Fell et al. 1977) to a mid-season peak of 30,000, and back to 10,000 by the fall (Jeffrey 1955).

I depends on the nectar flow in the field but is not equal to it:

$$I = N_{\text{max}} \cdot \left(1 - e^{-\frac{D S_{\text{mean}} - H(t)}{k \cdot D \cdot C_{\text{max}}}} \right) \quad (5)$$

where S_{mean} gives the mean amount of comb available for honey storage on days t and $t + 1$:

$$S_{\text{mean}} = \frac{S \cdot C(t) + S \cdot C(t + 1)}{2} \quad (6)$$

Averaging over 2 days takes into account the fact that comb is built gradually throughout the day. Thus a colony can use some of any new comb built on day t during day t . With increasing amounts of empty comb (given by the numerator of the exponent in Eq. 5), the intake goes up at a steadily diminishing rate, eventually saturating at the peak value N_{max} determined by field conditions. Although intake is always zero when the colony has no empty comb, the degree to which small amounts of empty comb limit intake depends on the parameter k . The value of this parameter is the proportion of empty comb at which the daily intake is equal to $1/e$, or 63%, of N_{max} . Thus, the higher k is, the greater the constraint of storage availability on intake rate.

The dynamic programming algorithm maximizes fitness values given by the following equation:

$$\text{fitness}(n, c, h, t, T) = \max_B \left[(1 - P_n) \cdot \text{fitness}(n', c', h', t + 1, T) + P_n \cdot \text{fitness}(n'', c', h', t + 1, T) \right] \quad (7)$$

where $n = N(t)$, $c = C(t)$, $h = H(t)$, T is the last day of the season and

$$\begin{aligned} n' &= 0 \\ n'' &= N_{\text{max}} \end{aligned}$$

$$\begin{aligned} c' &= c + C_{\text{day}_b} \\ h' &= h - H_{\text{other}} - H_{\text{wax}} \cdot W \cdot C_{\text{day}_b} + I \end{aligned}$$

The left side of Eq. 7 represents the fitness expected at time T (the end of the season) given that the colony has state variables valued h , c , and n at time t . This fitness is found by calculating the bracketed part of the right-hand side for both possible building choices B (build or idle) and taking the higher of the two. The building choice corresponding to this maximum fitness gives the optimal behavioral choice for a colony with state variables valued h , c , and n at time t . The bracketed part of the equation gives the mean of expected fitnesses over the two possible foraging conditions at time $t + 1$, weighted by the probability of those conditions. Because these values must be calculated before fitnesses at time t can be determined, the model proceeds by backward iteration from the last day of the season. Fitnesses for the last day do not depend on behavioral choices, since foraging, building, and nectar flow have all ceased by this time. These values are instead given by a terminal fitness function:

$$\text{fitness}(h, T, T) = \frac{F_0 F_{\text{max}}}{F_0 + (F_{\text{max}} - F_0) \cdot e^{-rh}} \quad (8)$$

This function gives the probability of the colony surviving the winter given that it has stored a quantity of honey h by time T , the end of the season. F_0 and F_{max} give the fitness values, respectively, for zero h and for the maximum possible h (determined by C_{max}). The parameter r gives the rate at which fitness improves with increasing h . The function is sigmoidal, with r chosen to give an inflection point between 20 and 25 kg of stored honey. This range is the best available estimate of the winter honey consumption of an unmanaged colony (Seeley 1985).

Most parameter values could be estimated from published reports (Table 1, Appendix), but some could not be easily assigned a single correct value. In particular, the size and temporal pattern of nectar flows are likely to have been highly variable across the locations and years in which the bees' building strategy has been shaped by natural selection. Hence the program was run using several different nectar conditions, modeled by changing the values in the nectar flow probability transition matrix 2. Because the quality of forage specified by a particular set of transition probabilities is not obvious, two descriptive parameters were derived from them. Mean Duration Off, a measure of temporal variability, is the mean length in days of stretches of time in which no nectar is available. It is calculated by noting that the duration of a period without nectar intake conforms to a geometric distribution with a mean of $(1 - P_0)/P_0$ days. Mean Percent On, a measure of the total amount of nectar available in the field, is the mean percentage of days in the season on which nectar can be found. It is equivalent to the limiting probability $\pi_{N_{\text{max}}}$ of the nectar flow probability transition matrix 2:

$$\pi_{N_{\text{max}}} = \frac{P_0}{1 - P_{N_{\text{max}}} + P_0}$$

Although there is experimental evidence for the existence of a constraint imposed on nectar collection efficiency by the amount of empty comb in the nest (Seeley 1995), there is no basis for specifying its magnitude at different quantities of empty comb. Accordingly, the model was run with several different values of k in Eq. 5.

To limit computational complexity, worker and brood populations were modeled as deterministic functions of time and comb quantity, rather than as resource allocations to be optimized. Workers and brood are important somatic components of the colony, but there is good reason to assume that their dynamics are not especially important in the production of building pulses. Honeybees use the bulk of their nest for food storage, rather than brood-rearing (Seeley and Morse 1976). The nectar flows which determine how much honey can be stored and how much comb will be needed are highly volatile. Brood-rearing, on the other hand, generally follows a regular seasonal cycle, with shorter-term fluctuations which are also largely driven by changes in food intake (Ribbands 1953). Thus, the most demanding and dynamic factors influencing comb construction are likely to relate to food, not brood.

Table 1 Parameters of the optimization model

Symbol	Definition	Value	Reference
H_{wax}	Mass of honey consumed per kilogram wax produced	6.25 kg	Weiss 1965
H_{ind}	Daily honey consumption of a worker or larva	6.7 mg	See Appendix
B	Worker population	10,000–30,000	Jeffrey 1955; Fell et al. 1977
d_b	Duration of brood development	21 days	Winston 1987
d_l	Duration of larval stage	5.5 days	Winston 1987
L	Cells per square centimeter of double-sided comb	8.5	Hepburn 1986
D	Mass of honey stored in 1 cm ² of capped, double-sided comb	3.25 g	See Appendix
C_{day}	Amount of double-sided comb constructed in 1 day of building	200 cm ²	Tokuda 1955; Pratt 1998a
C_{max}	Area of double-sided comb in a completed nest	11,700 cm ²	Seeley and Morse 1976
W	Mass of wax per unit area of double-sided comb	9×10^{-5} kg/cm ²	Tokuda 1955; Skowronek 1976
S	Fraction of comb area available for honey storage	0.65	See Appendix
N_{max}	Maximum possible daily honey intake when nectar flow is on	1.0 kg	See text
P_0	Probability of nectar flow on day $t+1$ given flow $N(t)=0$ on day t	0.5	See text
$P_{N_{\text{max}}}$	Probability of nectar flow on day $t+1$ given flow $N(t)=N_{\text{max}}$ on day t	0.5	See text
T	Duration of foraging season	154 days	Seeley 1985

Suboptimal strategies

To explore the superiority of the best strategy to suboptimal strategies, a variant of the dynamic programming algorithm was run. This method uses the same backward iterative approach described above, but instead of calculating the fitness expected for both behaviors (build and idle) and then choosing the superior behavior, it assigns a building behavior according to a fixed strategy, and then calculates the resulting fitness. The last iteration yields a matrix of expected fitness values, one for each combination of state variables, for the first day of the season. The mean of these values over all state variable values, divided by the corresponding figure for the optimal strategy, gives a measure of the relative fitness of the alternative strategy. Fitness values for comb quantities less than 1000 cm² were excluded, because the model probably does not adequately characterize the building motivation of nascent colonies trying to rapidly initiate brood-rearing.

Comb growth trajectory of simulated colony

With the optimal strategy in hand, it was then possible to calculate a trajectory of building decisions and comb growth over the course of a season. A simulated colony was assumed to begin the foraging season with a small quantity of comb and stored honey. For each succeeding day, the colony and environmental state (comb supply, honey stores, and nectar flow) were updated according to the colony's optimal building decision and the state Eqs. 1a, 1b, and 1c. Iterating through to the end of the season generated time series for construction behavior, nectar flow, and comb conditions.

Comb growth trajectory of observation colony

The comb growth pattern predicted by the model was compared with that of an actual colony observed over the course of an entire foraging season. An artificial swarm weighing 1.15 kg was introduced to a large observation hive (88 × 96 × 4 cm) on 7 June 1994 and allowed to forage and build undisturbed through the following winter. The hive was set up at the Cornell University Liddell Field Station near Ithaca, New York State (42°26' N, 76°30' W). Because the hive was initially empty, the bees were required to build all of their own comb, like a feral swarm moving into a previously unoccupied cavity. The hive dimensions allowed the bees to build only a single large sheet of comb, both sides of which were visible through glass walls. The entrance was fitted into a window opening, giving the bees free access to the surrounding countryside.

Three colony state variables were measured daily.

(1) Total comb area. The outline of the comb was traced daily onto a sheet of glass fitted over one wall of the hive. At the end of the season, this glass was photographed, the image was digitized, and the absolute area of comb built each day was measured with the software package NIH Image (produced by the United States National Institutes of Health and distributed at <http://rsb.info.nih.gov/nih-image/>). The area values reported below are for a double-sided sheet of comb; the two faces of each sheet were not measured separately.

(2) Comb use pattern. Comb use was quantified by measuring the relative number of cells in each usage class: empty, pollen storage, honey storage or brood-rearing. Honey storage cells were further classified as open or capped. Brood-rearing cells were subdivided by brood stage: egg, larva, and last-instar larva or pupa (capped brood cells). At the end of each day, the relative numbers of each cell type were measured by noting the contents of 100 randomly sampled cells.

(3) Nectar intake. The hive was placed on a platform scale (Detecto model 4510KG) and weighed to the nearest 0.05 kg. Because nectar intake is by far the largest contributor to weight gain, these measurements are a good approximation of daily nectar intake. All weighings, as well as measurements of comb use and comb area, were made in the evening after foraging had ceased and all bees had returned to the hive.

Relationships between comb construction, nectar intake and comb fullness (defined as the percentage of cells which were not empty) were examined with cross-correlation analysis. Long-term trends were first removed by regressing the data on day of the season and taking the residuals for subsequent analysis, when significant regression coefficients were found. Where necessary, the data were subjected to arcsine square root or Box-Cox transformation to attain normality (confirmed by Kolmogorov-Smirnov tests; Sokal and Rohlf 1981). Autocorrelations in the data (which can introduce spurious cross-correlations) were removed by fitting an autoregressive integrated moving-average model and taking the residuals for subsequent analysis (Chatfield 1996). All tests were performed with the software package Genstat 5.

Experimental analysis of building rules

The building rules predicted by the model were compared with the behavior of actual colonies. Experiments were performed at Liddell, at the Cranberry Lake Biological Station in Adirondack State Park, New York State (44°09' N, 74°48' W), and at the MacArthur Agro-Ecology Research Center near Lake Placid, Fla. (27°9' N, 81°12' W). Small colonies (4000–6000 workers) of largely Italian stock (*Apis mellifera ligustica*) were housed in three-

frame observation hives kept within laboratory buildings or sheds. The hive entrance was fitted into a wall aperture, allowing foragers access to the outside. Each hive contained one or two combs filled with brood, one comb packed with honey (the storage comb), and one empty frame to provide space for building. The glass wall on one side of the hive was divided into three independently removable parts. This facilitated removal and replacement of individual frames of comb with minimal disturbance to the colony.

The experiments examined the respective roles of nectar intake and comb fullness in determining whether a colony builds. In one experiment, colonies received a constant intake of nectar, but had the amount of empty comb in their hive switched between high and low levels. In another experiment, comb fullness was kept at a consistently high level, but nectar intake was switched on and off. Nectar intake was controlled through a feeder offering 2.5 M sucrose (see Seeley 1995 for feeder design). Nectar intake from other sources was controlled either by working in an area largely free of nectar-bearing flowers and honeybee colonies (Cranberry Lake) or by enclosing colonies in large flight cages [$3.5 \times 6.5 \times 1.8$ m; see Pedersen et al. (1950) for design]. Comb fullness was controlled by replacing the colony storage comb with a full or empty one, as needed, to counteract the effects of honey storage (when nectar was being collected) or honey consumption (when it was not). Throughout each experiment, the amount of nectar eaten by the bees at the feeder, the amount of new comb built and the relative amount of empty comb in the hive were measured daily. Comb areas and comb fullness were measured as described above for the observation colony.

For the experiment manipulating comb fullness, food storage efficiency was also measured in order to determine whether it changes at the start or end of building bouts. Efficiency was assayed as the average time taken for a returning forager to find a food storer bee willing to receive her nectar load. This search time is a reliable measure of the match between the rate at which foragers are bringing nectar into the hive and the rate at which bees within the nest are storing it (Seeley 1989). Following the technique of Seeley (1989), 50–100 foragers were paint-marked and then watched for at the nest entrance. Each forager was followed until she found a bee to whom she regurgitated all or most of her load. The interval between entry and the start of unloading was measured with a stopwatch.

Results

Figure 1 gives the optimal building behaviors predicted for moderately rich and variable nectar conditions (Mean Duration Off = 5 days, Mean Percent On = 50%), with a moderate constraint of empty comb amount on collecting efficiency ($k = 0.05$). A colony working at maximum efficiency under these conditions will collect, on average, Mean Percent On $\times T \times N_{\max}$, or $0.5 \times 154 \times 1.0 = 77$ kg of honey over the season, about enough to cover the yearly energy budget of a colony (Seeley 1985). Fig. 1 shows the optimal choice (build or idle) for each possible combination of the three state variables, N , C , and H , on day 75 of the season (mid-summer). Two features are immediately apparent:

(1) Building is optimal only when the colony has stored greater than a threshold amount of honey. This threshold increases with the amount of comb already built but is always rather low. A colony which has half filled its nest cavity with comb, for example, should build new comb once it has stored more than 5–7 kg of honey, even though its available storage comb is still half empty.

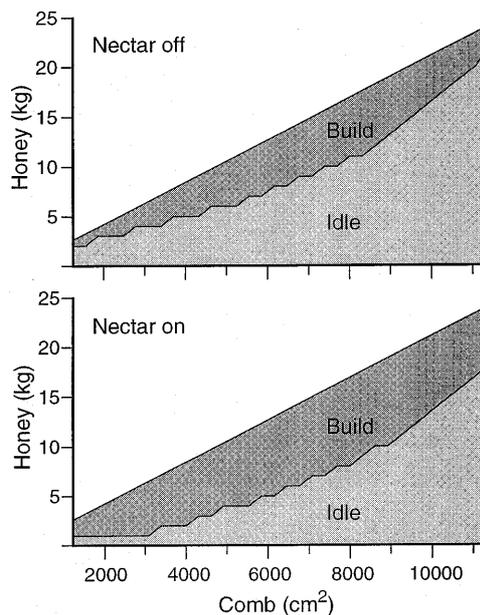


Fig. 1A,B Optimal building behavior as a function of the area of comb in the nest, the mass of stored honey, and the availability of nectar in the field, on day 75 of the nectar-collecting season. For any value of comb area, the optimal strategy switches from idle to build as the quantity of stored honey surpasses a threshold. This threshold is somewhat higher if nectar is not currently being collected. These results assume a moderate mean annual nectar intake, temporally dispersed nectar flows, and a moderate constraint of empty comb quantity on nectar intake (Mean Duration Off = 5, Mean Percent On = 50%, $k = 0.05$). The *diagonal line* in each plot shows the maximum quantity of honey which can be stored in a given amount of comb

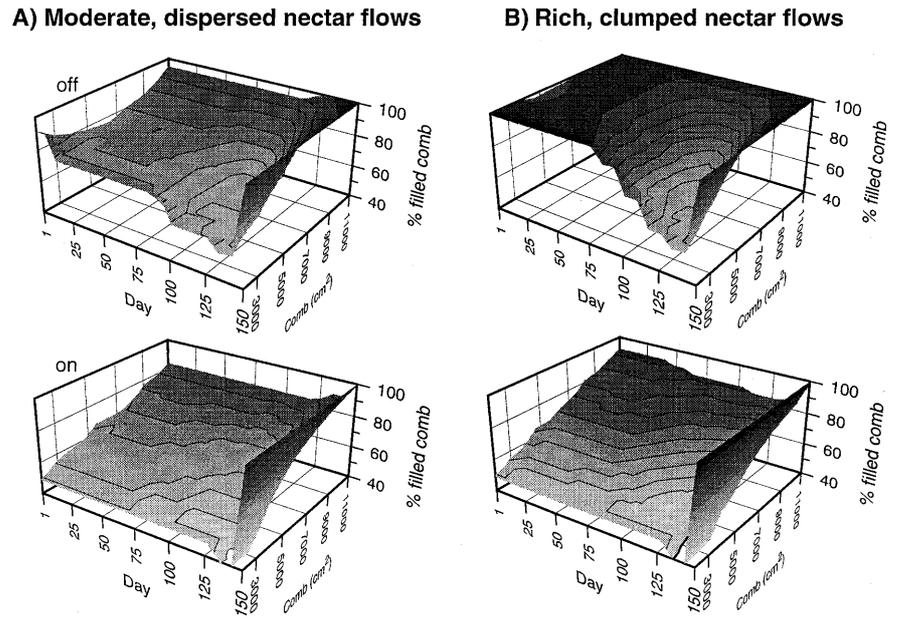
(2) Nectar flow has relatively little influence on the building decision. Although the bees should use a slightly higher building threshold on days when nectar is not available in the field, they should still maintain a large buffer of empty comb. Figure 2A shows the results of the same run of the model, but also depicts the change in optimal strategy over the course of the season. The threshold at which the optimal building strategy switches from idle to build is shown here as the percentage of colony total comb area which is already filled with honey, pollen, or brood. This figure highlights another point:

(3) The building threshold is fairly constant until the final days of the season, when it rapidly increases to 100%.

Growth trajectories of simulated and observation colonies

A typical seasonal growth trajectory produced by these building rules is shown in Figs. 3A and 4A (using the same nectar flow conditions and intake constraints used in Figs. 1, 2A). It is immediately clear from these figures that building bouts are highly correlated with nectar flow and with comb fullness. It is also clear that nectar

Fig. 2 Optimal building strategy under different foraging conditions. **A** Moderate richness and temporal variability of nectar flows (Mean Percent On = 50%, Mean Duration Off = 5). Each three-dimensional plot shows the threshold level of comb fullness at which the optimal building strategy switches from idle to build, for different total amounts of comb already in the nest, and for different days of the nectar-collecting season. The upper and lower plots show these thresholds for days when nectar sources are not and are available, respectively. **B** The same results for very rich and temporally variable foraging conditions (Mean Percent On = 70%, Mean Duration Off = 14). **A, B** There is a moderate constraint of empty comb amount on foraging efficiency ($k = 0.05$)



flow and comb fullness are correlated with one another. The second correlation underlies the first, causing a tight correspondence between construction and nectar flow, even though the optimal policy does not preclude construction in the absence of nectar intake (Figs. 1, 2A). In effect, the colony refrains from building because its comb begins to empty when consumption outpaces collection, quickly falling below the threshold fullness. This indirect dependence on nectar intake, combined with the clumped temporal distribution of nectar flows, causes comb growth to occur in spurts separated by quiescent periods. An optimal colony neither builds at a steady rate throughout the season nor does it build rapidly early on to establish quickly its full complement of comb.

The growth trajectory of the observation colony resembled that predicted by the model (Figs. 3B, 4B), except that the total amount of comb constructed was smaller than for the simulated colony. The bees did not build at a constant rate but rather added new comb in three pulses, separated by pauses in early and late July when the nectar intake decreased and the number of empty cells increased. The rate of building dwindled through late summer, ceasing entirely by the end of September. Regression of daily comb increment on day of the season showed that the oscillations of comb-building were superimposed on a negative seasonal trend (regression coefficient = -1.235 , $n = 72$, $r^2 = 0.18$, $F = 16.1$, $P < 0.001$). Significant positive correlations were found between daily nectar intake and comb construction on the following day ($r = 0.348$, $P < 0.05$), between comb fullness on each day and the amount of comb built on that day ($r = 0.267$, $P < 0.05$), and between comb fullness on each day and nectar intake on that day ($r = 0.4$, $P < 0.05$). (Data taken after 20 August were

excluded, since no measurements were made for many days near the end of the season.).

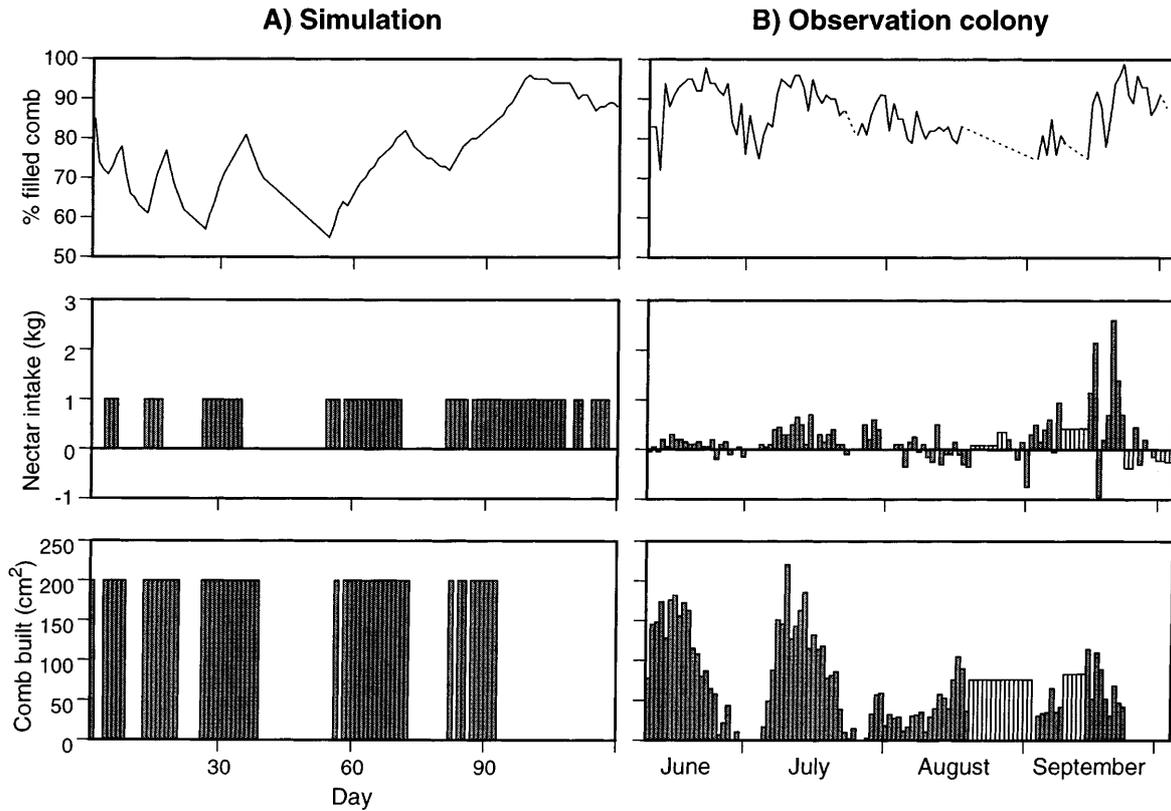
Effects of nectar conditions and intake limit

The effects of nectar conditions and intake constraints on the optimal strategy were measured by running the model repeatedly with different values of Mean Percent On, Mean Duration Off, and k . The results for all combinations of parameter values showed that building is optimal only when the colony has surpassed a fullness threshold and that this threshold increases in size late in the season. However, the size of the threshold varied markedly between runs, as did the dependence of threshold size on nectar availability. Figure 5 gives the mean building threshold over all comb amounts and all days of the season for each combination of the parameters. Two features are apparent from this figure:

(1) There is a strong positive effect of k on the readiness of the colony to build. That is, the stronger the constraint imposed by storage space on collection efficiency, the lower the building threshold.

(2) At any value of k , the higher Mean Duration Off and the higher Mean Percent On, the greater the effect of nectar availability on threshold size. This effect derives both from lower thresholds when nectar is on and higher ones when nectar is off. Thus, as the nectar supply becomes on average richer and more clumped in its temporal distribution, colonies are rewarded for paying attention to nectar conditions when deciding whether to build.

Figure 2 shows the latter effect in more detail by comparing the optimal strategy when nectar flows are temporally clumped and very rich with that predicted



when they are temporally dispersed and only moderately rich.

Suboptimal strategies

The above results predict a dependence of building threshold on nectar intake only under certain nectar regimes. However, the performance of suboptimal strategies suggests why such a dependence might be expected under a wider array of foraging conditions. These strategies were generated by independently varying the size of the building threshold for days when nectar was available and days when it was not. For instance, a colony employing a strategy with a threshold of 0% for nectar on (the On Threshold) and 100% for nectar off (the Off Threshold) builds whenever nectar is available, regardless of its current level of comb fullness, and never builds when nectar is not available. Each threshold was varied from 0% to 100% in increments of 10%, for a total of 121 runs of the model. These were repeated for two sets of foraging conditions (those used in the models of Fig. 2), both with ($k=0.05$) and without ($k=0.0$) an intake constraint. Because the outcome was similar for all four sets of conditions, Fig. 6 shows the results only for one of them. Two principal features are apparent:

(1) For any value of the Off Threshold, fitness falls rapidly as the On Threshold rises above its optimal value. Fitness falls only slightly if the On Threshold is decreased below its optimal value.

Fig. 3 **A** Simulated trajectories of comb construction, honey stores, and comb fullness for a colony following an optimal condition-dependent building policy. The top plot shows the percentage of comb area comprised of cells containing food or brood for each day of a 120-day foraging season (This season length was chosen to match the duration of the foraging season experienced by the colony in **B**). The middle plot shows the nectar available in the field on each day. The lower plot shows the area of new comb constructed each day. The simulation employed the same nectar conditions and intake constraints used in Fig. 2 **A**. **B** Daily measurements of comb fullness, nectar intake, and new comb construction in an observation colony over the course of a nectar-collecting season. The upper and lower plots show the same information as the corresponding plots in **A**. The middle plot shows colony daily weight change, an estimate of its nectar intake. *Dotted lines* in the upper plot and *paler bars* in the lower two plots indicate interpolated values for days on which data were not collected

(2) For any value of the On Threshold, fitness falls rapidly as the Off Threshold decreases below its optimal value. Fitness falls only slightly if the Off Threshold is increased above its optimal value.

In other words, fitness is highly sensitive to failure to build when nectar is available, and to building too much when nectar is not available. It is not as sensitive to overbuilding when nectar is available and to underbuilding when nectar is not available. In particular, there is very little fitness difference between the optimal strategy and a strategy of building with a constant, low threshold if nectar is on and never building when nectar is off.

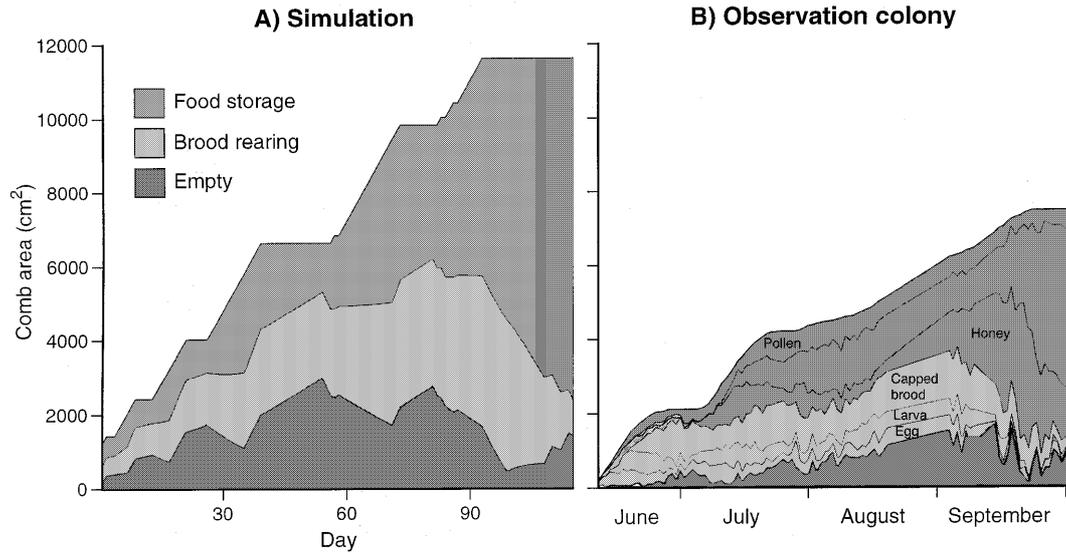


Fig. 4 **A** Growth and change in pattern of comb use for the same simulation depicted in Fig. 3A. **B** Growth and change in pattern of comb use for the observation colony described in Fig. 3B

Experimental analysis of building rules

In fact, the behavior of experimental colonies was consistent with such a strategy. Bees receiving a constant nectar intake built no comb while their comb fullness was maintained at a low level (30–40% of cells completely empty). They began to build only when the percentage of empty cells was allowed to fall to 20–25% (Fig. 7). Likewise, colonies deprived of nectar did not build while their comb was maintained at a high level of fullness (fewer than 15% of cells completely empty), but began only after collecting nectar for several days (Fig. 8). In the second replicate of the latter experiment, a brief bout of comb-building occurred during the first phase, perhaps because these bees had free access to the countryside and any nectar sources it might hold (the colony in the first replicate was caged). Although such sources are typically rare at Cranberry Lake, where this replicate was carried out, the presence of a few dancers in the hive during the building episode suggested that colony foragers had found nectar sources in the surrounding woods.

While the start of building bouts in these experiments depended on both comb fullness and nectar intake, their continuation depended only on nectar intake. The bees ceased building 2–4 days after the feeder was switched off (Fig. 8), but they did not stop building when switched from high to low comb fullness, even after 4 days (Fig. 7). To see whether a still longer delay might eventually result in a decline in construction, an additional experiment was run in which the bees ate heavily from a natural nectar source (goldenrod) and were provided combs filled with brood and honey. They were maintained in these conditions for 2 days, during which they built vigorously. On the third day, their comb fullness was suddenly lowered while they continued to collect large quantities of nectar. They remained in this state for another 6 days, building new comb throughout.

The relationship between comb-building and forager search time differed between the two replicates in which the latter was measured. In the first replicate, search time increased dramatically on the day building began, and remained significantly higher on the following 2 days as construction continued and comb fullness remained high (ANOVA: $F=6.75$, $P<0.0001$) (Fig. 7A). It fell again when comb fullness was reduced, although building continued unabated. In the second replicate, no significant variation in search time across days was observed (ANOVA: $F=1.66$, $P>0.05$; Fig. 7B). This difference between replicates may have been related to the much higher daily nectar intake in the first replicate (approximately 250 ml) than in the second (approximately 50 ml).

Discussion

Comb fullness threshold

The optimization model presented here explored the expected influence of nectar intake and honey storage conditions on the timing of new comb construction by a honeybee colony. Under a variety of parameter values describing foraging conditions and colony state dynamics, the model predicts that colonies should build new comb only when they have filled their currently available comb with food and brood beyond a threshold degree. The size of this threshold varies with the quality of foraging conditions and the strength of the constraint imposed on nectar collection efficiency by the amount of empty comb. However, the threshold is typically rather low, such that a colony should build new comb even

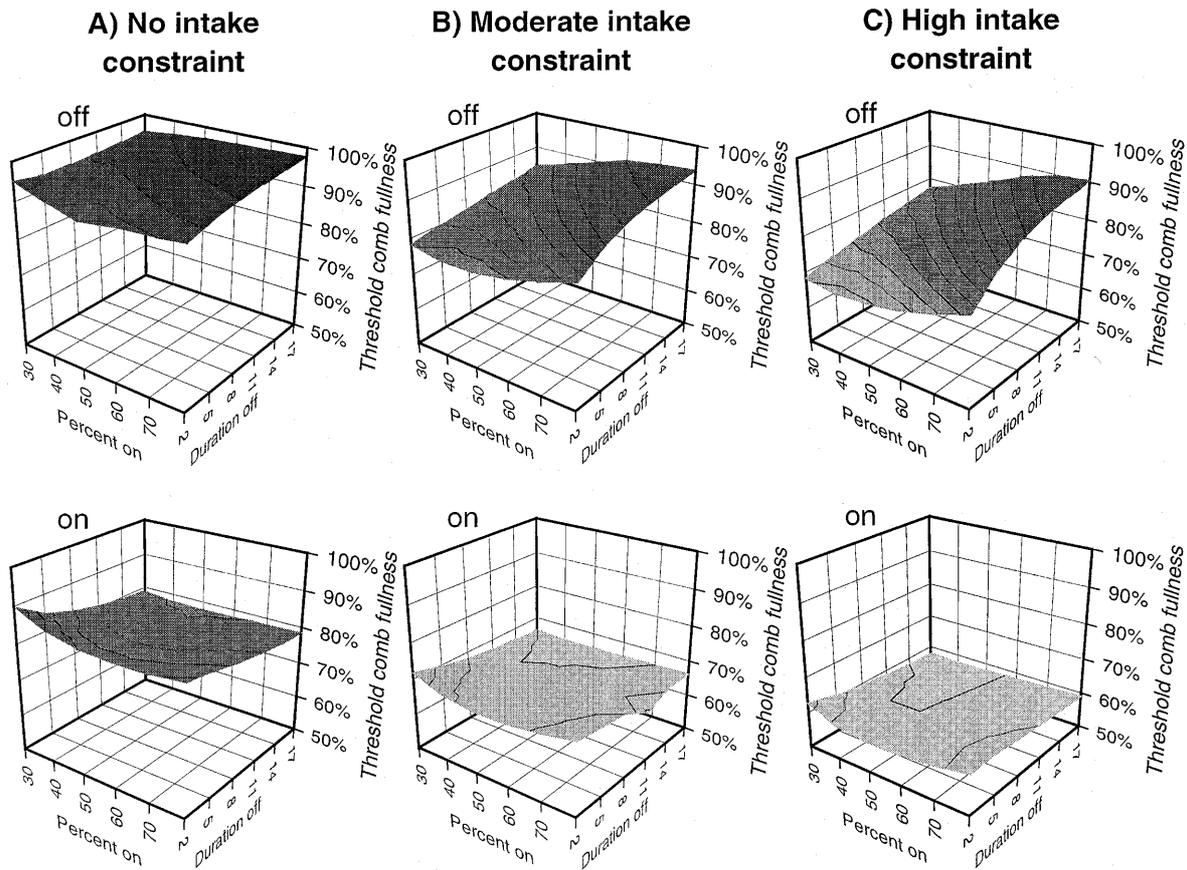


Fig. 5A–C Summary of effects on optimal building strategy of foraging conditions and foraging efficiency constraints. **A** Optimal behavior when bee nectar collection efficiency is not constrained by the amount of empty comb in the nest ($k=0$). The z -axis of each three-dimensional plot shows the mean comb fullness threshold at which colony optimal behavior switches from idle to build, across all days of the nectar-collecting season and all comb amounts. The x - and y -axes show two parameters describing foraging conditions – Mean Percent On and Mean Duration Off (see text for details). The upper and lower plots show the values of these thresholds for days when nectar sources are not or are available, respectively. **B, C** Corresponding data when the constraint of empty comb quantity on foraging efficiency is moderate ($k=0.05$) or high ($k=0.1$), respectively

when it already has enough empty comb to store several kilograms of honey (Figs. 1, 2, and 5). Thus the optimal strategy appears to lean more toward avoiding the opportunity costs of lacking storage space for incoming nectar than toward minimizing the energetic costs of excess comb construction. The behavior of experimental colonies confirms this low threshold, with small colonies building even when they have enough empty comb to hold 1.5 kg of honey.

Importance of nectar intake

The model predictions about the influence of nectar intake on building depend on its assumptions about nec-

tar-foraging conditions. With moderately rich and temporally dispersed nectar flows, the bees' building threshold should fall only slightly on days when nectar is being collected versus days when it is not (Figs. 1, 2A, and 5). However, as the richness and variability of the yearly nectar supply increase, the thresholds for building when nectar is absent become much higher than those when nectar is available (Figure 5). This is intuitively reasonable, since, if nectar is not available on day t , given such conditions, it will probably not be available for some time, and investment in comb will probably be premature. On the other hand, if nectar is available on day t , it will probably persist for many days, and a colony will likely need large amounts of new storage comb.

Examination of suboptimal strategies suggests a reason why bees may build only during a nectar flow, even if their strategy evolved under less rich and variable foraging conditions. The least fit alternative strategies are those which depart from optimality by building too freely when no nectar is available or building too little when a nectar flow is on (Fig. 6). On the other hand, strategies which build too readily during a nectar flow and too reticently or not at all in the absence of a nectar flow incur a much smaller fitness cost. This is true even under nectar regimes which do not predict a high building threshold in the absence of nectar intake. The forward iterations point to a reason for this similarity in fitness payoffs (Fig. 3A). Because of the tight correlation between nectar intake and comb fullness, colonies rarely

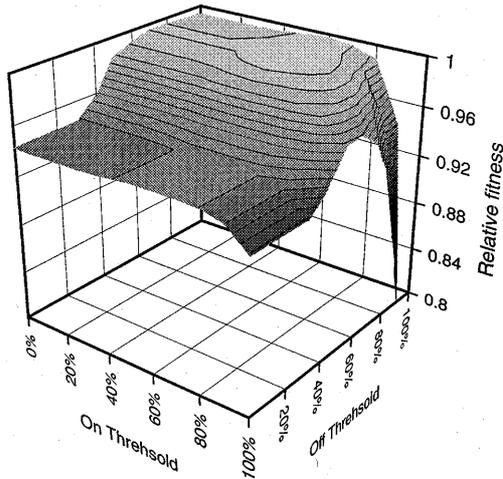


Fig. 6 Fitness of suboptimal building strategies, calculated for the same nectar conditions and intake constraint used in Fig. 2A. The plot shows the relative fitness of strategies which vary in the threshold level of comb fullness at which the colony begins to build. The colony employs the *On* or *Off Threshold* depending on whether nectar is available in the field on the decision day. The fitness of the optimal strategy is 1.0

build on days of no nectar intake, even if they are following an optimal policy which does not rule out building in the absence of a nectar flow. If the bees employ a rule of thumb calling for new construction only during a nectar flow, and only when they have surpassed a low threshold comb fullness, they will do nearly as well as if they followed the optimal strategy.

Experimental data support the conclusion that bees use such a rule. Colonies maintained either at high levels of comb fullness without nectar intake or at high levels of nectar intake without sufficiently full combs did not build until the missing cue was provided. These results confirm and extend Kelley's (1991) findings on the influence of comb fullness and nectar flow on the likelihood of building. They are also consistent with the observations of apiculturists, who have often noted the coincidence of construction and nectar intake, although it has not been clear whether nectar or some correlated factor such as temperature played the main causal role (Hepburn 1986). The present results suggest that nectar is the critical stimulus. Because one of the consequences of nectar collection is comb fullness, building is not only directly dependent on nectar intake, but also indirectly

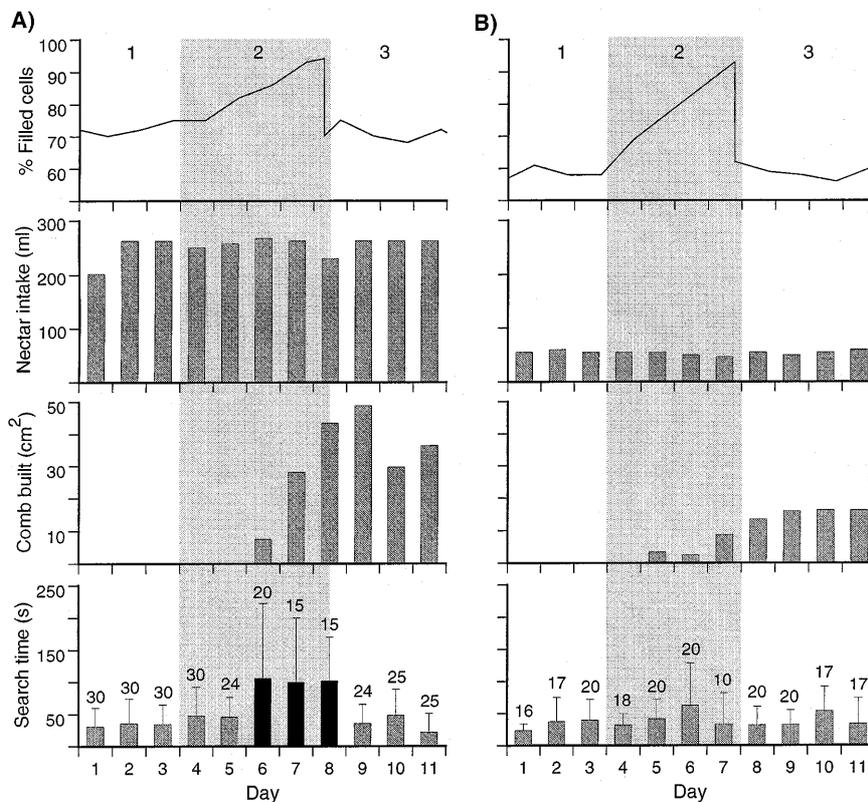


Fig. 7A,B Results of two replicates of an experiment testing the role of comb fullness in a colony's decision to start building new comb. In phase 1, the colony experienced a heavy nectar intake but was maintained at a low level of comb fullness. In phase 2, the nectar intake continued, but the bees were allowed to fill up their comb with honey. In phase 3, the colony was returned to the conditions of phase 1. **A** In replicate 1, the bees built no new comb in phase 1, commencing construction only in phase 2 after the level of comb fullness had markedly increased. The bees did not, however, cease construction when the level of comb fullness was lowered in phase 3. In the lowest plot, *bar height* (+SD) shows the mean search time of returning foragers looking for nest bees to receive their nectar. *Dark bars* are significantly larger than the others (ANOVA: $n = 11$, $F = 6.75$, $P < 0.00001$, followed by Scheffé's test for unplanned contrasts: $P < 0.05$). The number of sampled foragers is shown above each bar. **B** The results of replicate 2 were similar, but the search time of returning foragers did not differ across days (ANOVA: $n = 11$, $F = 1.66$, $P = 0.09$)

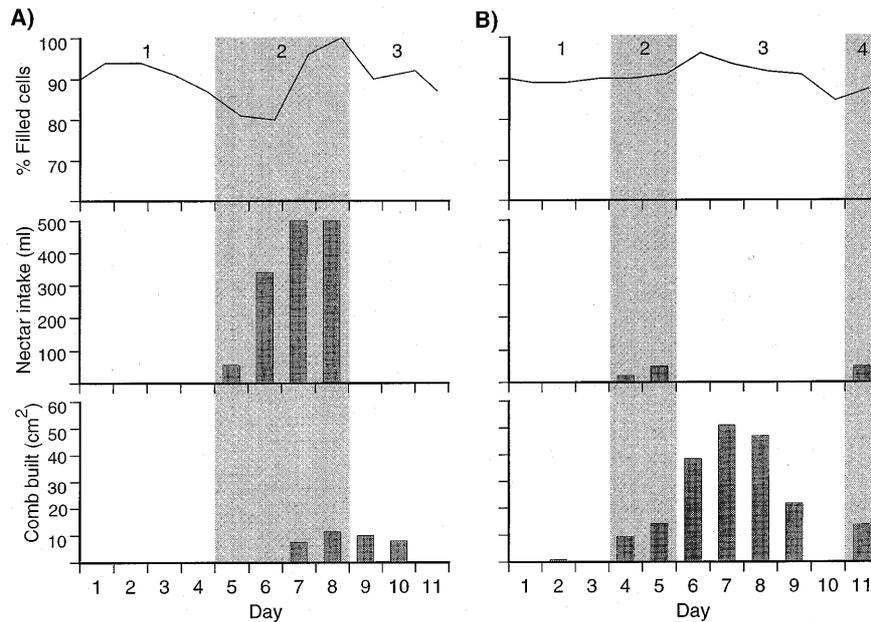


Fig. 8A,B Results of two replicates of an experiment testing the role of nectar intake in the decision of a colony to start building new comb. In phase 1, the colony experienced a high level of comb fullness, but received no nectar whatsoever. In phase 2, the bees were fed a 2.5 M sucrose solution while their level of comb fullness remained high. In phase 3, the colony was returned to the conditions of phase 1. **A** In replicate 1, the bees built no new comb in phase 1, commencing construction only in phase 2 after experiencing 2 days of nectar intake. (Rainy weather reduced nectar intake on day 5, the first day of phase 2.) The bees ceased construction 2 days after nectar intake was cut off in phase 3. **B** The results of replicate 2 were similar, but construction began on the first day of phase 2 and did not cease until 5 days after nectar intake was shut off. In addition, a phase 4 was added in which the colony again received nectar and again began building

dependent through the effects of nectar collection on internal colony conditions.

If the bees are relying on this rule of thumb, they may do so in order to avoid the information-processing demands of adjusting their building threshold to match the magnitude of nectar intake (as called for by the optimal strategy). In general, the costs of acquiring the information necessary to implement an optimal solution may sometimes more than offset the fitness benefits of practising the optimal strategy (Janetos and Cole 1981; Houston and McNamara 1984). These costs arise because the implementation of any optimal policy must rely on physiological and psychological mechanisms of limited capacity, and because the animal must simultaneously optimize solutions to several problems at once: an optimal solution to one problem may impose a sub-optimal solution on another. In cases such as this one, where the benefit of the optimal policy is only slightly greater than that of a simpler rule of thumb, it is not surprising if the rule of thumb is actually observed in nature. Indeed, if the model were expanded to include the physiological or perceptual constraints which make implementation of the optimal strategy so costly, the rule of thumb might well turn out to be the optimal policy (Cheverton et al. 1985). Such refinements would be a useful extension of the present model.

Of course, it is also possible that the apparent sub-optimality of bee behavior derives from an insufficiently accurate modeling of nectar conditions. Perhaps a more realistic model, including variance in size of flows as well

as their timing, would predict an optimum behavior even closer to observations. In addition, allowing the model bees to vary the amount of comb built each day, as they clearly do in nature (Fig. 3B) might also change the predicted optimal strategy.

Winter shutoff

A consistent result of the model is that the building threshold rises during the last part of the foraging season. By the end of the season, building is never the optimal decision, no matter how full the comb. This result is intuitively reasonable since the bees will have little opportunity to make use of comb built late in the season. Also, the reduction in brood-rearing at this stage means comb is opened up for storage even without building new comb. Indeed, a growing reluctance to build is apparent in the behavior of actual bees. During winter, the wax glands of worker bees shrink and become inactive, and the colony builds no new comb until the arrival of spring (Hepburn 1986). The observation colony built no comb in October, even though the nectar flow and comb use conditions were similar to those seen in earlier bouts of building. Indeed, a major shift in comb use patterns was apparent in the final weeks of the season (Fig. 4B). Brood-rearing diminished to near zero and food storage increased dramatically. The number of empty cells shrank, yet little or no new comb was built. In addition, regression of the size of daily comb incre-

ments on day of the season revealed a significant negative trend. This trend was not simply the result of the bees filling the hive with comb. At the time building stopped for good, there was enough empty space to add another 1000 cm² of comb.

Control of the duration of comb construction

Interestingly, once building began, its continuation did not depend on the state of the comb, but only on the persistence of nectar intake. Colonies which were building did not stop if they were suddenly provided with ample empty comb (Fig. 7). This indicates that the control of the timing of comb construction (when to begin a bout of building) is partly independent of the control of the amount built (the duration of a bout of building). In the normal life of a honeybee colony, tracking only the nectar intake after building has begun may be an effective means of matching comb-building with comb need. The sudden evacuation of a large portion of comb during a nectar flow is an event highly unlikely to occur in nature, where a continued nectar flow should reliably indicate a continued demand for comb in which to store it.

Even after nectar intake is shut off, there is a delay before comb construction ceases (Fig. 8). The lag may reflect the time window during which bees collect data to inform their building decision. Alternatively, once the bees decide to build, they may not re-evaluate their decision for several days, so that changing conditions will not alter their behavior immediately. Re-evaluation might be delayed because the decision to begin building involves physiological as well as behavioral changes. Activating and deactivating the abdominal glands which produce the wax used in construction may require more time than simply starting or stopping building behavior.

Proximate mechanisms initiating comb construction

Given that both nectar intake and suprathreshold comb fullness are required for comb construction to begin, how do individual bees monitor these criteria and change their behavior appropriately? One possibility is that food storer bees detect a cue associated with decreased nectar storage efficiency, as the available comb fills with honey during a nectar flow. Pratt (1998b) found no evidence for one version of this hypothesis, but it appears to be supported by the experiment shown in Fig. 7A. The search time of foragers looking for bees to receive their nectar (a measure of how well nectar storage is keeping up with intake) rose and fell in concert with comb construction. However, no such changes were seen in the second replicate of this experiment, when total nectar intake was lower (Fig. 7B). The coincidence of a large nectar flow and dwindling storage space may well reduce nectar storage efficiency, but this loss of efficiency is not a

prerequisite for the start of comb-building. Moreover, in both replicates, the bees began building at remarkably low levels of comb fullness. The dynamic optimization model likewise predicts a low threshold comb fullness, suggesting that bees should follow a strategy of risking premature construction in order to assure adequate storage for large nectar flows. Such a strategy requires a proximate mechanism for triggering construction that does not depend on the colony running short of empty comb for storage. The identity of this mechanism remains a challenge for future study.

Building policy and resource allocation

The building policy discussed above is the means by which a colony arrives at an optimal resource allocation between comb and honey stores. Previous work on resource allocation in social insect colonies has focused on two problems: the timing of investment in reproduction versus somatic growth (Oster and Wilson 1978; Franks et al. 1990), and the temporal pattern of investment in different kinds of colonial soma (i.e., different physical castes of worker: Oster and Wilson 1978; Wilson 1983; Tschinkel 1988). The first problem has obvious fitness implications, but the second problem also indirectly affects fitness, because allocation among somatic tissues will profoundly affect the amount of resources a colony amasses for eventual reproduction, as well as its probability of surviving to reproduce at all. This model expands the scope of the second inquiry by examining nest structures and food stores as somatic “organs” making major contributions to colony fitness.

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Appendix: Determination of parameter values

H_{ind} Mean daily honey consumption of a worker or larva, based on a colony consumption of 35 kg over a 150-day season (Seeley 1985), a mean worker population of 30,000 (Seeley 1985), and a mean larval population of 5000. [Assuming 150,000 bees raised over a 150-day season

(Seeley 1985), and a larval life of 5.5 days (Winston 1987), this is approximately the number of larvae alive each day.] The resulting estimate (6.7 mg) is rough because it assumes a steady-state brood population and equal mean honey consumption of workers and larvae.

- H_{wax} Amount of honey consumed to produce 1 g wax. Estimates vary over two orders of magnitude (reviewed by Hepburn 1986), but the best-controlled study (Weiss 1965), reported a range of 3.5–13.2 g/g and estimated a ratio of 4 or 5 g/g under ideal conditions. Honey is an approximately 80% sugar solution, hence this gives 5 g sugar/g wax \div 0.8 g sugar/g honey = 6.25 g honey/g wax.
- D Mass of honey stored in 1 cm² of capped, double-sided comb. The mean weight of ten standard Langstroth frames (minus the weight of an empty comb and frame) was divided by their area. This figure was corrected for the difference in comb width plus bee space in these hives (3.75 cm) and feral combs (3.55 cm: Taber and Owens 1970) to give 3.25 g/cm².
- S Mean fraction of comb area available for honey storage (that is, not in use for brood-rearing or pollen storage). Approximately 25–27% of total comb area in feral nests and unmanaged hives is devoted to brood (Seeley and Morse 1976; Fewell and Winston 1992). Fewell and Winston (1992) found a mean of 1120 cm² of double-sided comb filled with pollen in their two-hive-body nests. Assuming ten 1600-cm² frames per body, the relative comb area devoted to pollen storage is 1120/(10 \times 1600) = 7%, giving a total for brood and pollen of nearly 35% and leaving about 65% for honey storage.

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