

Chapter 11

Energetics of Honey/Beeswax Conversion

Abstract By the mid-19th century consideration of the rates and costs of wax production by *A. mellifera* were developed using the balance sheet method. Moreover, it was known that brood, pollen, combs and queens affect wax production. A century later, sugar/wax conversion ratios were defined as the net amount of sugar consumed against wax produced. Taranov (1959) showed that the total amount of wax produced was linearly related to the amount of sugar consumed; others that comb construction was proportional to colony size and to nectar income. The experiments and observations of this period suffered from a failure to separate the costs of colony maintenance vis-à-vis the production of wax. However, two major factors remained in the cost equation: (1) the relative importance of colony age structure in wax production; and (2) the problems of heat production, colony size and the synthesis of wax itself. Subsequently, Hepburn et al. (1984) calculated the rate of sugar consumption (corrected for attrition), and sugar stored in the nascent combs, as well as the rate of comb construction. The real metabolic rate, averaged over time for bees of different ages, showed that a plateau was reached in bees at about 12 days old, figures that included an adjusted metabolic rate as a function of bee age. This trade-off or cost calculation comes into play at both individual and colony levels. Both wax secretion and construction rapidly decline in autumn and virtually cease during winter. It is not yet possible to adequately assess the relationship of wax synthesis and comb construction to the thermal conditions of a colony's nest.

11.1 Introduction

In the days when the great naturalists believed wax to be the product of flowers gathered by bees when foraging, the swineherd and beekeeper knew, as did his lord or abbot, what sort of ratio of honey to wax could be harvested after the skeps were taken off the sulphur pit (Ransome 1937; Galton 1971; Vernon 1979). In the year that Huber (1814) published his observations on bees, we find little in

contemporary works other than yield figures. John Keys (1814) reported that a 2-year-old colony with a nest volume of three pecks (~ 27 l) would yield 25 pounds (~ 11 kg) of honey and not more than 2 pounds (~ 900 g) of wax.

A real interest in the rate of wax production (measured as combs) and the costs of construction (measured as the amount of sugar required) developed in parallel with agricultural chemistry in the 1830–1840 period. This was a time when the balance sheet method of Lavoisier came into widespread use among chemists (Holmes 1985) and was very effectively used to record food input and the corresponding recovery of a plant or animal product. The first experiments were expressly performed to find out how much sugar honeybees consume in the production of wax are given in a tortuous argument in the treatise of Gundelach who used old German units of measure, so that thirty-two loth equalled about half a kilogram (1842). He reported that 2765 bees produced 1.25 Loth of wax (~ 81360 individual wax plates, 18.25 g) requiring 27 Loth of honey (394.2 g) in 6.5 days. He concluded from his experiments, during an autumnal dearth in central Germany, that a colony requires about 20 measures of honey to produce one of wax. The experiments of Dumas and Edwards (1843) on confined bees were far more precise, but were concerned with the proof of fat synthesis and not conversion ratios. In any event, the thoroughness of their data handling using the balance sheet method allows us to calculate that their small colony of 1788 bees produced 17 g of wax in 11 days and consumed 411 g of honey, giving a honey/wax ratio of 24:1.

The next conceptual advance is contained in a note by Dönhoff (1854), entitled “*Kostet der Wabenbau Honig?*”, who attempted to separate the cost of wax production from the energy necessary to support the other activities of bees. In the days when a sample size of one was acceptable experimental currency, Dönhoff (1854) arranged three skeps in his apiary one October. One skep was completely empty, in the next a large amount of comb was cut away, and the last contained fully drawn combs. Each contained a caged queen (to prevent egg-laying and brood care costs) and about 8000 bees. The bees of each skep were fed unspecified, but presumably equal, amounts of honey. After a week, Dönhoff (1854) determined that the bees of both wax-bearing skeps had built no additional comb but each had stored 1.25 kg of honey. The bees of the initially waxless skep had constructed 42 g of comb and stored 864 g of honey. The 344 g difference in honey stores was attributed to the cost of production, the rate of which would be 750 μg per bee per day with a honey/wax conversion ratio of about 8:1. He repeated the same basic experiments using Dzierzon hives instead of skeps, and obtained figures of 23:1 and 15:1, which is within the range of Gundelach (1842).

During the same period, recognition of other factors that could influence conversion ratios began to appear in the literature. For example, the renowned Dzierzon (1861), discussing the biology of wax production, suggested that pollen might well influence the amount of wax produced, although he did not advance any evidence to support this (correct) view. Over the next hundred years or so, numerous experiments were performed under a variety of circumstances and a number of variables that might affect wax production began to emerge. Thus, the presence or absence of brood, pollen, combs and queens were gradually recognised as having a direct affect

on wax production. Even so, curiously enough, it is implicit in the literature for the period 1840–1940 that, ultimately, a faultless solution would emerge. That is, that the definitive experiment could be done to provide *the* answer to the real cost of converting sugar into wax Hepburn (1986). Yet, conversion ratios ranging from 1.8:1 to 104:1 have been obtained experimentally (Table 11.1).

11.2 Cumulative Ratios

While it is undoubtedly true that these gross conversion ratios reflect real values obtained under varying conditions, the experiments of the various authors cannot be directly compared nor can an explanation for a particular result always be readily found. This difficulty is illustrated by a comparison of the work of Whitcomb (1946) with that of Tokuda (1955). Whitcomb intermittently fed unmerchantable honey to four queenright colonies over 70 days of summer and gave the bees frames of foundation on which to draw combs. His records show that in the first 10 days the ratio of sugar consumed to wax produced dropped from 104:1 to 7:1 and in the ensuing two months oscillated irregularly between 3:1 and 15:1. The running cumulative ratio gradually declined to 8.4:1 at the end of his observations.

Tokuda (1955) conducted a series of experiments on 22 queenright colonies during a good spring flow followed by a summer dearth. The control colonies were given empty drawn combs and the experimental ones frames with strips of wax foundation. The bees were allowed to forage and were fed sugar copiously. He measured the amount of sugar consumed and the amount of wax produced. Unfortunately, only three of his experiments had reasonable controls. In the analyses of Whitcomb (1946) and Tokuda (1955) the conversion ratios were simply defined as the net amount of sugar consumed against wax production. As such, their reports merely indicate the extent of wax production and sugar utilisation by different colonies during periods in which comb was or was not constructed. Their results do however show the extent of natural variation in comb construction, but give no insight as to how the energy assimilated by the bees might have been partitioned in the colony.

The manner in which energy might be related to wax production was further investigated in Moldavia by Taranov (1959) after a summer's flow had ended. He established 16 colonies, equalised for size (500 g) and age, each headed by a mated queen. The bees were given frames of combs from which a portion had been cut away. He fed them 50 % sugar syrup and replaced the combs 18 times over a 59 day period to preclude the rearing of brood. The colonies were grouped in pairs, and each pair was fed differing quantities of sugar-syrup every 24 h for the duration of the experiment. The average wax production obtained in this experiment in relation to the amount of sugar given to the different colonies is depicted in Fig. 11.1.

It can be seen that the total amount of wax produced in Taranov's colonies is linearly related to the amount of sugar consumed. This extremely interesting result

Table 11.1 Chronological and annotated list of studies on food conversion ratios (sugar/wax ratios) in the production of wax

	Author and summary	Sugar/wax ratios
1814	Huber. Three small, confined colonies fed sugar or honey, pollen; assumes all food converted to wax	5.7:1 and 12:1
1842	Gundelach. One small colony, broodless, with queen confined; fed honey in autumn dearth; assumes all sugar converted to wax	20:1
1843	Dumas and Edwards. One small confined colony fed honey, no pollen	24:1 and 36:1
1861	Dönhoff. Average colonies with queen confined; fed honey and allowed to forage in fall dearth; ratios based on consumption differences between colonies that built and those that did not build combs	8.2:1, 15.2:1 and 22.8:1
1873	von Berlepsch. Small confined colonies fed sugar or honey	No pollen, 19:1 and 20.5:1; with pollen, 13:1
1885	Viallon. Two colonies with drawn combs and two combless; bees allowed to forage; procedure then reversed; assumes differences in stores to be cost of wax	6.7:1
1886	Hasty. One average colony allowed to forage; attempted to measure food consumption through weight changes of colony; assumes all honey consumed converted to wax	2.9:1
1887	De Layens. As in Viallon, but with two broodless colonies in summer dearth	6.3:1
1901	Maupy. Minimal value based on theoretical calculations only	4:1
1905	Brünner. Using normal production colonies fed honey; assumes straight conversion of food into wax	6.8:1
1944	Rosov. Four average colonies allowed to forage in a greenhouse; attempted to separate costs of colony maintenance, brood rearing and comb-building	12.3:1 to 14.2:1
1946	Whitcomb. See text for full discussion	3:1 to 104:1
1955	Tokuda. See text for full discussion	1.8:1 to 8.2:1
1965	Weiss. See text for full discussion	3.3:1 to 13.2:1
1965	Horstmann. Theoretical calculations considering several biochemical pathways, none of which have been shown in bees	2.8:1 to 8:1
1984	Hepburn et al. See text for full discussion	4.3:1 to 26.3:1

is open to several interpretations, especially when it is compared to situations in which the bees were given sugar in sufficient excess that they were able to store it as ‘honey’ (e.g. Whitcomb’s (1946) experiment).

It is very tempting to conclude that there is simply an equal partitioning of the energy towards wax production (see Fig. 11.1) in Taranov’s experiment and that a fixed percentage is allocated for producing wax. Such a conclusion would be consistent with the results of Taber and Owens (1970), who found comb

Fig. 11.1 The average wax production for 500 g colonies over a 59-day period. The amount of food, a 50 % sugar syrup, was fixed between 25 and 1000 g a day (based on data of Taranov 1959)

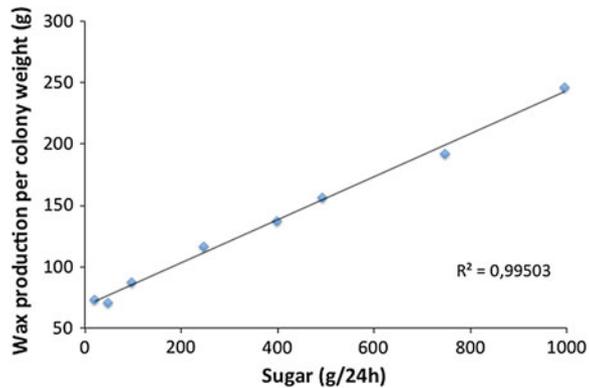
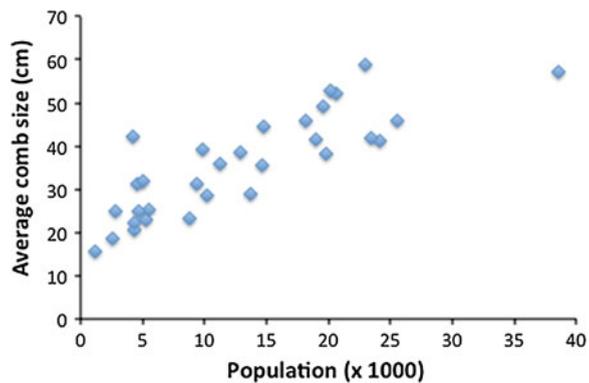


Fig. 11.2 The average size of the comb constructed as related to colony size (after Taber and Owens 1970)



construction to be proportional to colony size (Fig. 11.2), and with those of Florea and Malaiu (1961) that comb building is proportional to nectar income, even though both groups lacked a measure of energy flow in their studies. This would not be contradicted by the wide range of previously noted conversion ratios (Table 11.1), since the latter would reflect experiments in which foodstuffs were available in excess. In any event, although equivocal, the results of Taranov represent a first step towards an experimental solution to the partitioning of foodstuffs in the production of wax.

The experiments and observations during the period 1840–1940 principally suffered from a failure to measure the separate costs of colony maintenance on the one hand, and the production of wax on the other. Nonetheless, this early experimentation has borne much fruit in the recognition of some of the factors that impinge upon the biology of wax, even if the credits and debits for wax production cannot be balanced. The two major approaches used were those in the tradition of Dumas and Edwards (1843) and von Berlepsch (1873—cited from Taranov 1959), who worked, essentially *in vitro*, with confined colonies of bees and on the other hand those of Gundelach (1842) and Dönhoff (1854) whose *in vivo* bees were

allowed to forage away from the nest. Both approaches have their obvious advantages and disadvantages and both continue to be used today. They provide different kinds of information for the development of a general concept of the flow of energy in relation to wax production, which has gained momentum in the past two decades.

Weiss (1965) was the first to attempt a separation of the direct costs of wax production from the other combined activities of a colony under apiary conditions. He performed a series of three experiments on 'nigra' bees (an old local German term for *A. m. mellifera*), kept in field cages during summer. In the first trial he compared two colonies, made by division, each of about 1000 g bees and headed by young mated queens. One colony was given starting strips of foundation, the other fully drawn, but empty comb. For 15 days the bees were allowed to fly in the cage to a feeding site supplied with a 50 % sucrose (w/w) solution. At the beginning of the experiment the youngest bees in the colony were 3 days old. Weiss (1965) measured the amount of sugar consumed by the two colonies and the amount of wax produced by the colony that had been given starting strips of wax foundation. The colony that had been given drawn combs did not construct any additional comb.

Like Dönhoff (1861) before him, Weiss (1965) calculated sugar/wax ratios as the amount of sugar actually needed for wax production, based on the amount of sugar consumed by the experimental colony in excess of that consumed by the control. The analytical refinement made by Weiss (1965) was to compensate for the concentration of the sugar that the building bees had stored in their newly built combs, so that a more accurate measure of sugar consumption could be calculated. In this case, the experimental colony produced 105 g of wax and consumed 1585 g of sugar solution; the controls constructed no combs but consumed 1235 g of sugar. The excess 350 g of sugar divided by 105 g of wax gave a ratio of 3.3:1. In a second experiment using two different colonies (which probably had the same age composition as those in the first experiment), Weiss (1965) obtained a ratio of 3.5:1 over 16 days. These bees were then observed for another 8 days (at the beginning of this second period the youngest bees would have been 18 days old and past their normal wax-secreting prime), and the sugar/wax ratio for this period came to 11.4:1 after his original data were adjusted for production per unit time/day.

The same basic experiment was repeated a third time using Carniolan bees over a longer sampling period. At the outset the youngest bees would have been at least 2 days old; at the end of the experiment they would have been 22 days old and hence past their wax-secreting prime. The results of this experiment are shown in Table 11.2. Even though the relative composition of different age classes is not known, it is tempting to conclude that as the bees grew older the sugar/wax ratio increased; however, Weiss did not adjust for the attrition of bees in these experiments. The problem of attrition was clarified to some extent in a fourth experiment at Erlangen during autumn.

Weiss (1965) gave starting strips of beeswax foundation to five queenright colonies (the experimental group) while another five colonies (the control group) were given fully drawn but empty combs. Portions of the large body of data

Table 11.2 Sugar/wax ratios obtained from caged bees during summer (Weiss 1965)

Experimental period	Sugar consumed (mg/g bees)		Excess consumption (mg/g bees)	Wax (mg/g bees)	Sugar/wax ratio
	Building bees	Control bees			
1. 4 days	239	133	106	20.5	5.2:1
2. 4 days	420	109	311	21	14.8:1
3. 6 days	575	110	465	28.7	16.2:1
4. 4 days	487	113	374	24.7	15.1:1
5. 4 days	587	235	352	25.6	13.8:1

Table 11.3 Sugar/wax ratios in a fall experiment adjusted by attrition, Colony 1 is the same throughout all periods and is matched to the same control colony (Weiss 1965)

Experimental period	Colony number	Sugar consumed (mg/g bees)		Excess consumption (mg/g bees)	Wax (mg/g bees)	Sugar/wax ratio
		Building bees	Control bees			
10 days	1	471	279	192	54.4	3.5:1
	2	736	307	429	611.4	6.4:1
	3	846	296	434	81.9	5.3:1
	4	1031	412	619	86.3	11.2:1
	5	979	438	541	811.3	6.2:1
11 days	1	710	212	498	50.0	10.0:1
	2	1032	269	763	79.3	9.6:1
	3	1195	327	786	93.2	8.4:1
	4	1273	409	864	811.7	9.9:1
	5	1347	401	946	89.4	10.6:1
11 days	1	755	304	451	50.1	9.0:1
	2	1147	370	777	82.6	9.4:1
	3	1133	421	523	102.0	5.1:1
	4	1797	610	1185	89.5	13.2:1
	5	1675	578	1097	85.9	12.8:1

emanating from these experiments are important enough to reproduce in modified form (Table 11.3), because they show the extent of natural variation that can be expected of different colonies. These results also show that sugar consumption per gram of bees is higher in smaller than in larger colonies. Yet two major imponderable factors remain in the cost equation: (1) the relative importance of age structure in wax production; and (2) the problems of heat production as related to age, colony size and the synthesis of wax itself. Among other things, Weiss (1965) suggested that comb construction produces heat, and with it, greater activity in the colony. How should variables like conversion efficiency and foraging time, age structure and colony size, to name a few, should be considered?

11.3 Measures of Conversion Efficiency

Conversion efficiency will obviously depend on a host of factors, among them genetic background (e.g. the subspecies under investigation). This point was brought home very clearly in the comb production studies by Skowronek (1976). He compared four small colonies (about 2000 bees each) of each of three subspecies over three seasons. Pooling his data, we find that the amount of wax produced varied with race: the Caucasians averaged 41.4 mg/bee, the Carniolans 32.5 mg/bee and the native Polish bees 29.8 mg/bee; resulting in combs of 9.8 g of wax per dm^{-2} , 9.7 g dm^{-2} and 8.8 g dm^{-2} respectively. Over the 3 years the Caucasians had produced more wax per bee and had constructed heavier combs than did the other two strains. Similarly, in caged experiments, Jay and Jay (1983) found that American bees of European origin, produced just over twice the amount of wax as did African honeybees.

Combining the balance sheet method of Dumas and Edwards (1843) with the sophisticated instrumentation now available for measuring oxygen consumption and monitoring temperature, Hepburn et al. (1984) studied the relationships between wax and heat production, sugar consumption and metabolic rate, and age and in small queenright colonies (500 bees) of the African honeybee, *A. m. scutellata* (at that stage still called *A. m. adansonii*, only later work identified the populations in northern South Africa as *A. m. scutellata*, cf. Hepburn and Radloff 1998). Their colonies were made up of newly emerged bees from brood frames of several different colonies and which were combined at random to achieve a balanced genetic background to control for potential variability. In all the colonies the bees began the experiment when they were less than 1 day old, and all the variables mentioned were measured, including the daily rate of attrition over a 21 day period. The rate of sugar consumption (corrected for attrition) and sugar stored in the nascent combs, as well as the rate of comb construction, were calculated on a per bee basis at 3-day intervals as shown in Fig. 11.3.

The consumption of sugar increased over the first 12 days and then levelled off, even though the colony size had decreased. Similarly, the metabolic rates of the colonies were found to be parallel to that of sugar consumption. The core temperature of each of the colonies was also measured on an hourly basis over the 21 day period. Even though ambient temperature was kept constant in the environmental chamber, an initial and erratic core temperature was recorded for the first week. This was followed by the development of an extremely regular oscillation in core temperature with a morning low of about 30 °C and an evening high of about 32 °C (these details are discussed in Nijland and Hepburn 1985).

The real metabolic rate, averaged over time for bees of different ages, is shown on the left ordinate of Fig. 11.4 from which it is apparent that a plateau is reached in bees of about 12 days old. The same figure includes an adjusted metabolic rate as a function of bee age on the right ordinate. Since oscillations in metabolic rate did not occur in 3-day-old bees (nor did such bees secrete wax), the metabolic rate measured for these bees was taken as an approximate basal value for subsequently

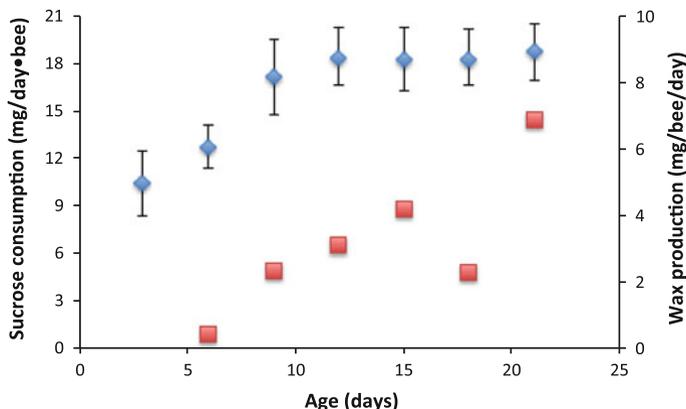


Fig. 11.3 Mean sucrose consumption and standard deviations are shown (*blue diamonds*) and the wax production (*red squares*) of small, queenright colonies of African honeybees (Hepburn et al. 1984)

estimating the cost of wax production. This is not to imply that all the energy expenditure above the ‘basal’ rate was diverted into wax production as such, because some expenditure would have been associated with the production of cluster heat in those bees more than 6 days old. The use of values of metabolic rate from 3-day-old bees thus provides only a partial compensation for energy expenditure in calculating a more exact energy budget for wax production.

Wax production was assessed as the wax which the bees had constructed as combs, as well as those scales which had fallen to the bottoms of the hives. The total wax production for five colonies was determined at the end of the experiment, on the 21st day; single values for the rates of production were obtained at 3-day intervals when five parallel colonies were killed. The total wax production per colony on a given day was the wax produced per bee, corrected for colony size. The value given for wax production per bee of a given age is absolute and independent of the prevailing size on a particular day. The metabolic cost of wax production per bee between the ages of 9 and 21 days was estimated to be about 6 ± 1 mW/g body mass for each milligram of beeswax produced and worked into comb; or in bee terms, about 70 μ g of wax was produced per 420 μ W of bee labour. These figures point to the interrelationships between metabolic rate, sugar consumption and wax production. The correlation coefficient between wax production and adjusted metabolic rate was 0.93 ($P < 0.005$); that between wax production and sugar consumption was also 0.93 ($P < 0.005$). Finally, the correlation between the adjusted metabolic rate and sugar consumption was 0.89 ($P < 0.007$). These relationships are shown in Figs. 11.4 and 11.5.

Just as the ability to thermoregulate develops with age, so does the ability of bees to significantly raise their metabolic rate change with age (Fig. 11.5—Allen 1959). Fine control over metabolic rate and the ability to thermoregulate go hand-in-hand in a mutually interdependent way. Because very young bees, 0 to 3 days

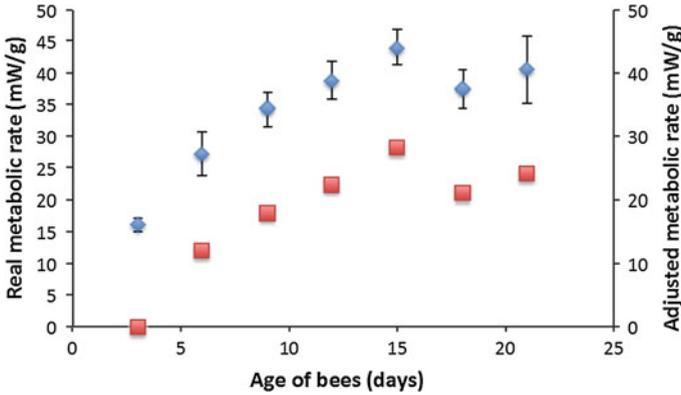


Fig. 11.4 The metabolic rates of African worker bees of different ages. The *blue diamonds* related to the *left* ordinate show the average mean real metabolic rate; *right* ordinate (*red squares*) show an adjusted metabolic rate used to calculate the cost of wax production (Hepburn et al. 1984)

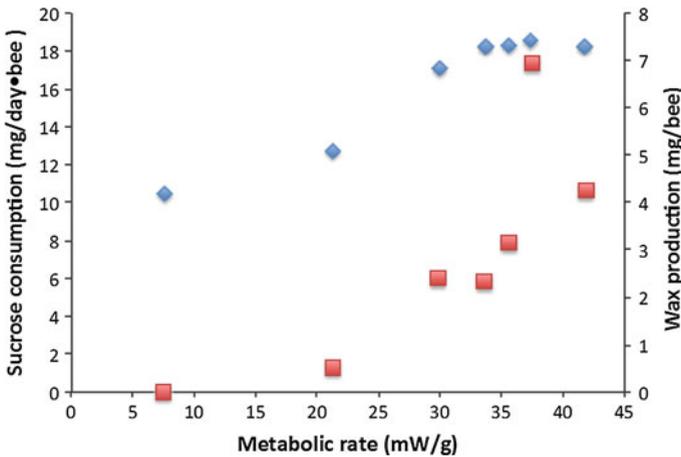
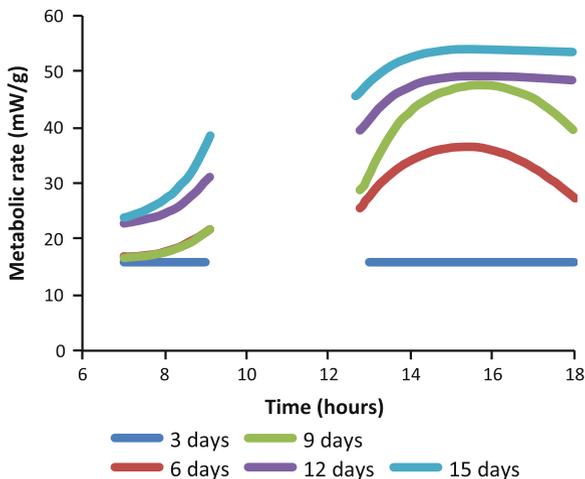


Fig. 11.5 Sucrose consumption (*blue diamonds*) and wax production (*red squares*) for queenright African bees as a function of metabolic rate (Hepburn et al. 1984)

old, have a reduced metabolic rate compared to older bees, they show a steady and unchanging cluster core temperature and do not secrete wax. The metabolic rate of these young bees was taken as basal, and used to approximate maintenance costs in older wax-producing bees. This simplification does not separate the cost of generating heat vis-à-vis production and comb-building per se. However, it is a telling point that the minimal level to which the metabolic rate fell in the older bees at night, was very similar to that of the younger bees which did not secrete wax (Fig. 11.6). It is highly suggestive, but has not as yet been shown, that the elevated temperature somehow facilitates, or is necessary, for wax secretion.

Fig. 11.6 The metabolic rate of queenright clusters of African bees of various ages in the course of a day. The gap indicates the absence of readings (Hepburn et al. 1984)



In trying to estimate the cost of wax production, many other considerations enter the equation. The progression of development in the workers that secrete wax and build comb had been previously observed by Rösch (1927), but the division of labour associated with age can easily be modified by manipulating the age structure of a honeybee colony; workers precluded from taking up a variety of activities, such as foraging, quickly change to other duties (Rösch 1925, 1930; Lindauer 1952). Under the confined conditions of the experiment of Hepburn et al. (1984), in which no foraging was allowed nor was there brood to tend, the metabolic expenditures were solely devoted to self-maintenance, temperature regulation, wax secretion and comb-building.

Among the minor factors affecting wax production is the provision of starting sheets of beeswax foundation. One small strip was attached to the top bar of a frame to define the locality of the cluster with respect to the thermocouple (Hepburn et al. 1984). In consequence, it is possible that the bees produced marginally less wax than they might otherwise have done, because, as Gillete (1900) discovered and Skowronek (1973) confirmed, bees produce marginally less wax when supplied with beeswax foundation than when not. The provision of wax starting strips represents a possible source of systematic error on the conservative side.

A major variable in the biology of wax is the relationship between production rate and colony size, established by Taranov (1959). A regression analysis of his original data showed that the amount of wax produced was directly correlated with the number of young wax-producing bees present in the colony, where the mass of bees ranged from between 0.5 kg (about 5000 bees) to 2.5 kg (about 25,000 bees). In his experiments wax was produced at a daily rate of 3 mg/bee. Extrapolation of the regression curve (for which the correlation coefficient for a straight line was 0.97) back to the size of the small colonies (0.35 kg, or 500 bees) used in the experiments of Hepburn et al. (1984), gave a predicted yield of about 150 mg of wax per day for the relationship to hold. Using 15 days of production time

Hepburn et al. (1984) obtained an experimental value of 3.2 mg per bee per day after adjustments were made for the changes in colony size due to death. The daily production rate of wax was calculated to be 141 mg per colony per day, which was within 5 % of the value expected from the analysis of Taranov's data.

Clearly a full analysis of the cost of wax production in a honeybee colony is exceedingly complex, and is made all the more difficult in the absence of measured rates of production for individual wax-secreting bees. Discounting the many variables which have been excluded by the form of these experiments, the observable differences in the amount and cost of wax produced varied greatly with the changing age structure of the colony. However, a general trend did emerge from the experiments; wax production appears to be a process which, for the honeybee colony, is akin to commercial amortisation. Within defined limits, it becomes cheaper for the bees to produce wax and to build comb as they become older. This trade-off or cost calculation comes into play on the individual level and also on the colony level.

The Asian dwarf honeybees, *Apis florea* and *A. andreniformis*, are the only species which salvage their old nest wax after absconding or migrating to a new nest site, thereby recycling the old wax (Hepburn et al. 2011). Although the recovered wax is of high energetic value, it is not the actual energy of the wax which makes it worth recovering, but rather the fuel costs to cover the distance by the workers to fetch it (Pirk et al. 2011). It is not the value of the resource but the time to recover it that is traded against the foraging time for nectar to replace the wax, explaining why this behaviour is only observed in *Apis florea*, (we do not know what *A. andreniformis* does), if the absconding range is within the foraging range of the new nest site, whereas in *Apis mellifera*, for example the absconding range is more than 6 km and the mean foraging range around 1 km (Hepburn et al. 2011; Pirk et al. 2011).

Colonies of *Apis florea*, which only abscond a short distance, and usually return to salvage old nest wax; but those colonies, and all other honeybee species, which go considerably further, do not. Wax salvage would clearly be counter-productive unless the energy input/energy yield threshold was profitable. There are two possible trade-offs in this scenario, the trade-off between the energy expended to recover the wax (recovering hypothesis), as against that of replacing the wax by new secretions (replacing hypothesis). In order to compare the two hypotheses, the fuel costs involved in salvaging wax on one return trip, the average flower handling time, flight time and relative values for substituting the salvaged wax with nectar were calculated. Moreover, the energy value of the wax was determined. Net energy gains for salvaged wax were calculated. The energy value of the salvaged wax was 42.7 J/mg, thus too high to be the limiting factor since salvaging costs are only 642.76 mJ/mg (recovering hypothesis). The recovery costs (642.76 mJ/mg) only fall below the replacement costs for absconding distances below 115 m, thus supporting the replacing hypothesis. This energetic trade-off between replacing and recycling, plus the limited absconding range of *A. florea* may explain why *A. florea* is probably the only honeybee species known to salvage wax. It parsimoniously explains the underlying reasons why *A. florea* only salvages wax from the old nest if the new nesting site is less than 100–200 m away-energetically, it pays off to recycle.

11.4 Temperature and Wax Production

While honeybees thermoregulate in the absence of a nest, it seems that areas in which workers handle wax have higher temperatures (Pirk et al. 2004) suggesting that they regulate the heat to facilitate wax manipulation. Although colonies did not show any temperature preference for settling in the warmer section of an experimental nest cavity (Taber and Owens 1971), they are able to detect and distinguish small temperature gradients (Heran 1952; Basile et al. 2008). How wax synthesis and comb-building are constrained by thermal conditions is not well understood. There is only indirect evidence that bees cannot or will not sustain the costs of heat and comb production when both are very high. Both wax secretion and construction rapidly decline in autumn and virtually cease during winter. The onset of comb production in spring is well correlated with 11 °C for temperate honeybees and it has been suggested that sustained comb-building in practical apiculture occurs around 16 °C (Brünner 1905). That the production of comb apparently requires a minimum environmental temperature must be considered in juxtaposition to a regulated nest temperature. It has often been claimed (Philipp 1930; Büdel 1948; Weiss 1965), but never shown, that a nest temperature of 35 °C is essential for wax secretion and comb-building.

Indeed, Darchen (1962) recorded a range of temperatures around festoons varying from 30 to 34 °C, while Hepburn et al. (1984) recorded a maximum of just below 33 °C in the core temperatures of clusters of building bees. It is, simply, not yet possible to adequately assess the relationship of wax synthesis and comb construction to the thermal conditions of a colony's nest, much less how the microclimate of the nest is related to environmental conditions.

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