

Chapter 7

The Significance of Brood

Abstract Differences in colony size among *Apis* species are not equated to the ratio of drones to workers or associated comb construction. Oviposition-related cell inspections reveal that a queen's decision to lay a fertilized egg or not, is determined by a specific stimulus generated on cell inspection. Uncapped or sealed queen cells are correlated to a reduction in the number of new cell constructions, possibly pheromonally mediated. Relative increases in the physiological activity of the wax glands in queenright bees are related to the age of the workers. Capped brood and broodlessness dampen the development of wax glands, while the presence of open brood stimulates their development as under queenright conditions. Queenright bees produce much more comb than queenless bees; while queenless, broodright bees construct more comb than queenless, broodless bees. The amount of wax produced is a linear function of the number of young bees in a colony, but the greatest amount of wax produced/bee, relative to colony size, occurs in small colonies. Bees prevented from brood-rearing produce the same amount of wax as those engaged in both comb-building and brood-rearing. Colonies precluded from comb construction rear no more brood than those engaged both in brood-rearing and comb-building. The proportion of drone comb depends on the amount of drone comb present and the number of adult drones present in a colony, and is positively correlated to the number of workers. The combination of queenright and broodright colonies appears to be a more powerful stimulus than any other for comb-building.

7.1 Introduction

Honeybee brood nests of are obviously essential to the existence and propagation of honeybee species. Firstly, there is the matter of choosing a suitable site for both open-air and cavity-nesting species (cf. [Chap. 2](#)), the subsequent organization of the contents of nests on a cyclical and seasonal basis in which sex ratios of queens, drones and workers vary enormously (cf. [Chap. 3](#)). As noted by Koeniger (2011),

it may be energetically cheaper and more profitable to produce cheap, expendable drones than more expensive queens, although the cost of rearing queens and drones and maintaining them is only slightly different. In *Apis*, the ratio of queens to drones ranges in *A. florea* from 1:57 and about 1:500 in *A. dorsata* (Koeniger 2011), and raises questions, perhaps unanswerable, about a ‘conflict over sex ratios’.

In any event, there are large variations in colony size among *Apis* species, differences which are not equalized by a colony’s decision on its ratio of drones to workers and the corresponding necessary modifications in comb construction. There are two notable exceptions where there are no differences in cell diameter between worker and drone cells, the giant honeybees, *A. dorsata* and *A. laboriosa*. The construction of cells is discussed elsewhere (cf. Chap. 12), but here we review the basic biological traits which go hand-in-hand with the development of brood in relation to cell types: parthenogenesis, the meaning of brood, efficacy of brood, drone brood and brood-rearing in relation to honey storage.

7.2 Parthenogenesis

That queen honeybees lay eggs in worker-sized cells from which female worker adults emerge; and, conversely, that queens lay eggs in drone-sized cells from which drones eventually emerge, was for many centuries an incomprehensible puzzle, a conundrum of great proportions. The eventual solution to this problem involved two important discoveries: (1) honeybee queens were capable of parthenogenesis, and (2) queens could control the release of fertilized or unfertilized eggs during oviposition. The immediate history of these discoveries is a fascinating story of claims and counterclaims that ran through the pages of *Eichstädt Bienenzeitung* for a decade or so in the mid-19th century. In 1845, Jan Dzierzon (Fig. 7.1) published the results of his careful studies on the eggs of honeybees and how they arose. In short, he discovered parthenogenesis. This idea finally became accepted as a reality following collaboration between Dzierzon and von Siebold, a university Professor of Zoology at the Maximilians-Universität in Munich, who unequivocally confirmed the occurrence of parthenogenesis in some butterflies and honeybee queens (Dzierzon 1847; von Siebold 1856).

The above account of parthenogenesis in honeybee queens is based on research on European *A. mellifera*, but applies to all the other species of honeybees, with the exception of Cape honeybee, *A. m. capensis* workers, in which thelytokous parthenogenesis occurs in both queenless and queenright colonies. Aside from the many peculiar traits in the Cape honeybee (Hepburn and Crewe 1991), a cytological analysis of this phenomenon was conducted by Verma and Ruttner (1983), who demonstrated that egg diploidy is restored by the fusion of the two central meiotic products. Thelytoky has been shown to be controlled by a single major gene (Lattorff et al. 2005).

Fig. 7.1 Jan Dzierzon (16 January 1811–26 October 1906), was a pioneering Polish apiarist who discovered parthenogenesis in honeybees, *A. m. mellifera*, and also designed the first, successful movable-frame hive before von Berlepsch and Langstroth developed their hives



The significance of this on comb-building by *A. m. capensis* was the discovery of the following experimental results. Neumann et al. (2000) dequeened and removed all brood from 26 *A. m. capensis* and *A. m. scutellata* colonies and their natural hybrids. Neumann et al. (2000) found that *A. m. capensis* laying workers were thelytokous, and all *A. m. scutellata* arrhenotokous. Of the hybrid colonies 42.1 % produced only female offspring while none produced only male offspring. *A. m. capensis* colonies built only worker cells and *A. m. scutellata* only drone cells. Hybrid colonies produced either both cell types or only worker cells, according to the mode of laying worker reproduction. These results unequivocally demonstrate that the mode of worker reproduction in queenless, broodless colonies holds important consequences for cell construction, even if the mechanisms producing these effects have not yet been demonstrated.

7.3 Oviposition by Queens

The second remaining problem was an explanation for how a queen could control the sex of egg she laid and in which kind of cells. Reaching the answer to this problem was also a protracted one, which has been clearly described and discussed by Gessner and Ruttner (1977) who demonstrated that the spermathecal pump musculature controls the release of spermatozoa or not. Nonetheless it still remained to determine how queens could measure cell sizes. In extended observations on the behaviour of egg-laying queens, Koeniger (1970) noted that during the course of cell inspection, before actually depositing an egg in a cell queens introduce their two forelegs and head into the cells. Under the not entirely natural conditions of an observation hive, the queen lays one egg following two such inspections. No differences in this behaviour were observed between drone or worker cells. It appears that the decision to lay an egg in a cell or not is predicated

on an inspection of the cell. It is equally probable at such a moment that the size of cell (worker or drone) is taken into account by the queen. A method to interfere with these inspections was developed by placing small, square pieces of adhesive tape around the tibiae of the queen's forelegs (Koeniger 1970).

The behaviour of the queen, even with the tape appendages appeared normal in every respect; she continued to oviposit and was fed and groomed by the workers. To assess the effects this method had on the queens' ability to distinguish cells, Koeniger (1970) presented drone cells to three *A. mellifera* control queens, in which drone eggs were laid. Only drone pupae were recovered from the drone cells. Subsequently, adhesive tape squares were attached to the tibiae of the queens' forelegs, and she was given a new set of drone cells. When these drone cells were examined only worker pupae were found. When the tape was removed, the queens laid only drone eggs in the drone-sized cells.

Following this, the role of the possible use of the queen's forelegs in drone cell recognition was further investigated by again taping the tibiae of the forelegs and allowing the queens access to drone cells. In this test 89 % of the eggs laid were worker eggs. Koeniger (1970) then performed a series of gradual amputations of both leg segments through trochanters, femora and tibiae, and found that 78, 18 and 3 % respectively of the pupae found in drone cells were workers. After amputation of one foreleg, only 0.3 % of the pupae developing in drone cells were workers. Koeniger concluded that the queen's decision to lay a fertilized or non-fertilized egg is determined by a specific stimulus generated when the queen inspects the drone cells with her forelegs. So, it is highly probable that queens use their forelegs essentially as a pair of inside calipers and actually measure cell size (Figs. 7.2, 7.3, 7.4).

7.4 The Meaning of Brood

As in many other areas of animal husbandry, the ancient truths of apiculture collect like clichés that grow into aphorisms. Thus, it is widely known that honeybees expand their nests at the onset of spring with warmer temperatures and the abundance of nectar and fresh pollen for brood-rearing (Butler 1609; Koch 1957, 1959, 1961). Unfortunately, this 'old truth' hides a horrible conundrum in which the role of brood as a stimulus for wax production lies hidden among many other complex and interdependent factors. Hence, bees build in response to the queens' need for available cells in which to lay eggs (Huber 1814). Bees never build combs if they lack a queen; or, if queenless, they lack brood from which to rear a new one (Gundelach 1842). Finally, the great Dzierzon (1848, 1861) tells us that as soon as breeding commences, the bees also produce wax; if breeding is interrupted, wax production is discontinued immediately, even under the most favourable conditions.

Against all of these claims, De Layens (1887) actually recommended that comb construction can be enhanced by the removal of brood from colonies for which comb construction is required so as to obviate the shunting of honey and the rearing

Fig. 7.2 An *A. mellifera* queen, having inspected a cell, has placed her abdomen into a recurved position to enter the cell and oviposit (photo courtesy of Niko Koeniger from Koeniger 1970)



Fig. 7.3 An *A. mellifera* queen inspecting a cell with head and forelegs (photo courtesy of Niko Koeniger, from Koeniger 1970)



Fig. 7.4 An *A. mellifera* queen ovipositing in a worker cell (photo courtesy of Niko Koeniger, from Koeniger 1970)



of larvae. It merely implies that 'brood' has different meanings in differing contexts, and that the stimulatory efficacy of brood may well vary with circumstances. This is amply demonstrated, as it so happens, in at least three ways in the experiments on comb construction by Dreischer (1956), Taranov (1958, 1959) and Free (1967), and in an entirely different way, by Fell and Morse (1984) with respect to queen cell construction.

In a study by Fell and Morse (1984) quite clearly there was a rapid decline in the rate of new queen cell construction of (cf. Fig. 6.4). In earlier work on the construction of queen cells, under both swarming and emergency conditions, Fell and Morse (1984) had shown that the presence of queen cells, containing uncapped larvae as well as sealed queen cells, is correlated with a reduction in the number of new cells or comb construction. To this we can add that, while worker bees cut away the apex of a queen cell before her emergence, the cappings of drone or worker cells are left intact. These authors suggested that both a reduction in new queen cell construction and the absence of re-working capped brood cells might both be mediated through a negative feed-back system driven by pheromones. Unfortunately, these intriguing ideas have not been further experimentally investigated.

Dreischer (1956) compared queenright and queenless *A. mellifera* colonies in late summer, usually a time of sparse comb-building. She introduced some marked, newly emerged bees each day into her colonies and subsequently sampled these bees of known age throughout her experiment. The progression of life in a queenless colony was divided into periods of differing social conditions as follows: (1) with both open and closed brood, then, as the brood became capped; (2) with sealed brood only, after the emergence of that brood; (3) entirely broodless; and finally (4) the presence of laying workers coupled with the open brood which they had produced. The daily addition of newly emerged, marked bees allowed for the appearance of bees of comparable age to occur in each of the different social situations defined for queenless bees. The queenright colony contained both open and sealed brood but presumably lacked laying workers. Dreischer then measured the course and extent of development of the ovaries, hypopharyngeal glands, wax gland epithelium and corpora allata for each condition of the colonies.

She found that the relative increase in height (a morphological indication of physiological activity, hence function—Rösch 1927, Boehm 1961, 1965), of the wax gland epithelium in bees of the queenright colony was related to the ages of the bees in just the same way as had been previously shown by Rösch (1927). Considering those bees from the queenless hive, in all four different social conditions, the initial increase in the epithelium progressed just as it did in the queenright bees and there was no significant difference in the height of the epithelium for the 11- to 15-day-old age group (encompassing the normal peak of wax secretion—cf. Chap. 15). However, following the peak height of the epithelium (at roughly 2 weeks of age), two entirely different patterns emerged among the queenless bees during the ensuing 2 weeks of a worker's life.

In the cases where queenless workers had uncapped brood, there was a decline in the epithelium of the wax gland, but at a slower rate of decrease than in the queenright bees (Fig. 7.5a, b). In the queenless bees with only sealed brood, or were

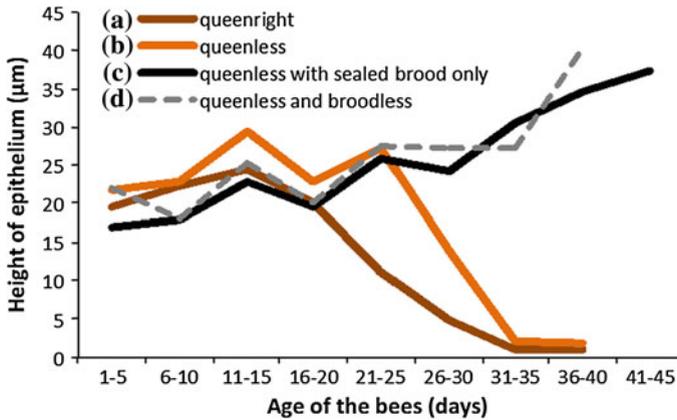


Fig. 7.5 Changes in height of the wax gland epithelium with age in *A. mellifera*: **a** queenright colony; **b** queenless colony with open and capped brood; **c** queenless colony with only capped brood; and **d** queenless and broodless colony (Dreisler 1956)

entirely broodless, the height of the wax gland epithelium did not regress at all; in fact, it slowly increased over the next fortnight to higher levels than those obtained at the normal 11–15-day peak in the queenright bees (Fig. 7.5c, d), the glands possibly remaining active. The same was true of the hypopharyngeal glands; the development of which normally precedes that of the wax glands (Rösch 1927).

A comparison of the bees of the queenless colony with open brood and those of the queenright one, showed the same general trend; the wax gland epithelium of both developed more or less apace and declined in the same way (Fig. 7.5). The same results were obtained in other experiments on queenright but broodless *A. m. scutellata*, colonies (Hepburn et al. 1984). While the significance of a queen is fairly obvious, one is not required for gland development in workers, given open brood. The role of worker brood in the isolated case is shown by comparing curves b, c and d in Fig. 7.5. Capped brood and broodlessness have precisely the same effects on the development of the wax gland (and also on the ovaries, hypopharyngeal gland, and corpora allata), while the presence of open brood stimulates the development of the wax glands in a pattern similar to that obtained under queenright conditions. The discovery of a brood pheromone that is chemically distinct from any of those elaborated by queens (Koeniger and Veith 1984; Le Conte et al. 1990) adds interest, if not clarity, to the observations.

7.5 Efficacy of Open Brood

The efficacy of open brood as a stimulus for wax production has been shown in a different way in some experiments by Free (1967), although his actual intention was to study drone cell production. During a late English summer, Free established

Table 7.1 Effects of the presence or absence of a queen and brood on comb cell production in *A. mellifera* (Free 1967)

	Experiment 1					
	Colony 1		Colony2		Colony3	
	Treatment	Cells built	Treatment	Cells built	Treatment	Cells built
26–28 Aug	Queenright	1921	Queenright	2250	Queenright	4206
28–31 Aug	Queenless	0	Queenless	635	Queenright	3316
31 Aug–3 Sept	Larvae added	1646	Larvae added	4750	Queenless	3737
3–7 Sept					Larvae added	4213
	Experiment 1		Experiment 2			
	Treatment	Cells built	Treatment	Cells built	Treatment	Cells built
	Treatment	Cells built	Treatment	Cells built	Treatment	Cells built
26–28 Aug	Queenright	4206	Queenright	2042	Queenright	2440
28–31 Aug	Queenright	3827	Queenless	1367	Queenless	1921
31 Aug–3 Sept	Queenless	0	Larvae added	1812	Larvae added	3120

an apiary with six colonies, from which all combs had been removed. Each colony was given four test frames as building sites. Every few days the nests were examined and the combs built were photographed so that the number of cells constructed could be counted. Free (1967) managed the colonies as queenright for a few days, then queenless and broodless for a few days, and finally queenless and broodright for a few more days. The results of his experiment are shown in Table 7.1. When queenright, the bees produced more than twice as much comb, on average, as they did when they were queenless. Subsequently, when queenless but broodright the same colonies also constructed more than twice as much comb as they had done when they were queenless and broodless.

In an earlier experiment, Taranov (1959) had shown that the amount of wax produced was a linear function of the number of young bees present in a colony, at least for colonies of less than about 2.5 kg (Fig. 7.6). He also showed that the greatest amount of wax produced, relative to colony size, occurred in small colonies in which wax production went hand-in-hand with brood care (Fig. 7.7). In view of these results, Taranov questioned the inter-dependency of brood-rearing and wax production as competitive activities; does the increased work-load of wax production interfere with the nursing of young larvae, or does an increase in one function go hand-in-hand with the other?

Taranov explored these relationships by setting up three queenright colonies, each with about 10,000 young bees of the same age. The first colony was given empty frames, the second frames of drawn combs, and the third frames of drawn combs from which about one-third of the combs had been cut away. The first colony was kept broodless and could ‘concentrate’ on comb production; the second colony had no space to build additional comb, but enjoyed ample space for brood-rearing; and the third colony had some space for comb construction as well as brood-rearing. The colonies were supplied with pollen and were fed a 60 %

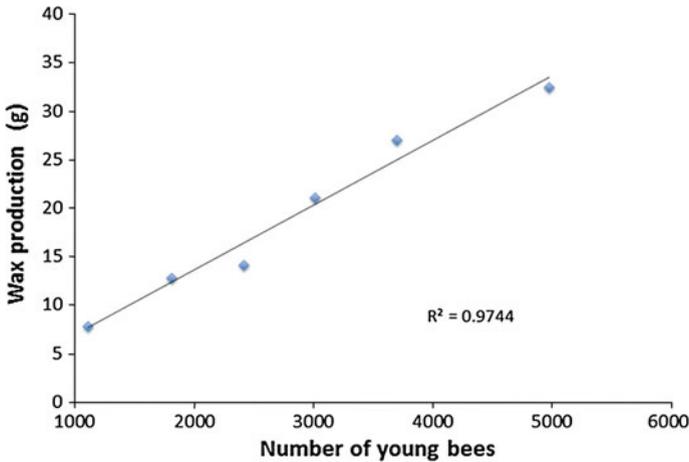


Fig. 7.6 Wax production as a function of the number of young bees in an *A. mellifera* colony is linear for colonies up to 2.5 kg (Taranov 1959)

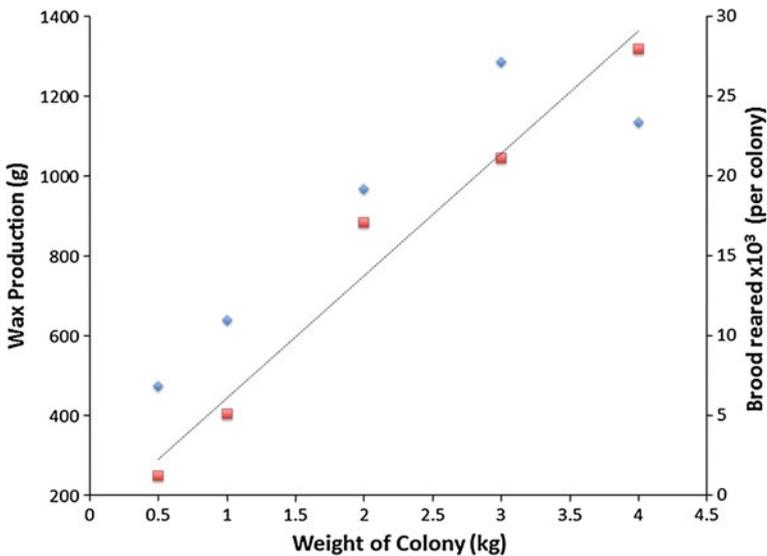


Fig. 7.7 Wax production by *A. mellifera* colonies of different sizes but all brood-rearing. *Solid line* = wax production linear for colonies of up to 3 kg ($r^2 = 0.97$); *broken line* = brood production as a function of colony size (replotted from data as published by Taranov 1959)

honey solution for 2 months. The results of this experiment were quite striking. Those bees prevented from brood-rearing produced the same amount of wax as did the colony engaged in both comb-building and brood-rearing (Table 7.2). Similarly, the colony precluded from comb construction reared no more brood than did

Table 7.2 Wax production and brood-rearing in *A. mellifera* (Taranov 1959)

Colony	Main work of the bees	Experiment 1	Experiment 2	Total
<i>Wax production (g)</i>				
1	Produced wax only	333.2	387.4	711.6
2	Reared brood only	—	—	—
3	Produced wax + reared brood	465.2	336.9	802.1
<i>Brood rearing (No. larvae)</i>				
1	Produced wax only	—	—	—
2	Reared brood only	26,525	1,261	39,135
3	Produced wax + reared brood	25,740	12,675	38,415

Table 7.3 Development of the wax gland epithelium in colonies of *A. mellifera* with 12-day-old bees under differing nest conditions (Taranov 1959)

Nest conditions	Wax gland epithelium height (μm)
1. Comb building	85
2. Brood rearing	76
3. Comb building and brood rearing	103
4. No building, nor brood rearing	40

the bees engaged in both brood-rearing and comb construction. Exclusion of either function did not lead to the accelerated development of the other one.

Taranov also measured the height of the wax gland epithelium in 12-day-old bees from these three colonies and from a fourth which produced neither wax nor had brood to care for, with the results shown in Table 7.3.

7.6 Drone Brood

Some years ago, Allen (1958, 1963), Free (1967) and Free and Williams (1975) investigated factors that determine, at least in part, the rearing and rejection of drones by *A. mellifera* honeybee colonies. The proportion of drone cells built was greatest in May, June and July although colonies continued to build drone comb long after they had ceased to rear drones. The proportion of drone comb built by a colony also depended on the amount of drone comb already present. The amount of drone brood and the number of adult drones present in a colony was positively correlated to the number of workers. Removing drone brood from colonies encouraged drone production; adding drone brood diminished drone production. A large percentage of eggs were sometimes laid in drone cells before the end of April, although few were reared. The proportion of drone brood was at its maximum in May and June. A colony could be forced to evict its drones by preventing the workers from foraging, and in autumn eviction could be greatly delayed by providing additional forage or removing the queen.

7.7 Brood-Rearing and Honey Storage

A final set of experiments elucidates our understanding of brood and wax production, and comes to us somewhat serendipitously. Cerimagic (1969) investigated the possibility of swarm prevention through the elimination of comb-building. He tested ten sister-queenright colonies of about 30,000 bees each over two successive spring seasons in Yugoslavia. In converting Cerimagic's original data into a wax-brood experiment, we have re-designated his 'controls' as the experimental group and vice versa. He gave 12 frames of foundation to one group of five colonies; to another control group of five colonies he gave fully drawn, old combs. In each case, as the brood chambers became filled, he supplied an empty box atop the brood chamber. Thus the experimental colonies were able to both construct combs and rear brood, the controls only the latter. All the colonies were able to forage during the nectar flow.

The trend in the results he obtained was very similar to those of Taranov (Table 7.2). There were no significant differences between the experimental and control colonies with respect to the amount of brood reared or honey stored. However, the experimental colonies produced nearly a kilogram of wax in each season, while the controls constructed no combs. Because all the colonies were headed by sister-queens (nature of matings unknown), genetic variation ought to have been minimal, in which case one would not have expected any large differences in the foraging abilities of the two groups. The combined measurements and experimental observations of Dreischer (1956), Taranov (1959), Free (1967) and Cerimagic (1969) revealed that the role of brood as a stimulus for the development of wax glands and subsequent secretion and comb construction, all juxtaposed against the queen as a stimulus. The data show, rather convincingly, that 'brood' means different things, depending upon the presence of a queen and, if there is no queen, upon whether or not the brood is uncapped or sealed. Similarly, the combination of a colony being queenright and broodright appears to be a more powerful stimulus than any of the other conditions investigated to date. What remains most puzzling about all this experimental data is the likely fate of energy that comes into these various situations.

Brood is a spectacular instance of how a wax production stimulus varies in duration, intensity and quality. The amount of time required for the development of a particular cycle of brood has been experimentally shown to vary with temperature (Milum 1930; Haydak 1970) and, by inference, with season as well. The availability of food is in part a function of season, with the effects that more brood (Nolan 1925) and heavier bees are associated with large influxes of pollen into the summer nest (Levin et al. 1954), but at a lower intensity than in spring (Todd and Bishop 1941). Against this, bees may be heavier in fall than in summer (De Groot 1953), owing to a change in the ratio between those that feed and those that are fed.

The ratio of brood to the adult population varies throughout the year. The production of brood is enhanced during nectar flow (Nelson and Sturtevant 1924), by the quality of the queen (Nolan 1925) and, of course, by the honeybee race.

This seemingly endless flow of variables forms a web of interactions that are not easily encompassed in feed-back loops and which do not clearly explain how the development of brood is related to the activities of the adult work force. Nonetheless, a understanding for this problem emerges from Ribbands (1953) who noted that changes in the proportions of brood and foraging bees are likely to have two combined effects: firstly, the proportion of foragers may be expected to vary inversely with brood, and secondly, brood consumes a substantial quantity of food. When these effects are considered, nectar influx increases sharply with colony size. Both effects undoubtedly influence the secretion of wax and the building of combs, but the ways in which they do so have not as yet been measured.

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