Swarming in Honey Bees

Part I
The Role of the Worker and Queen Bee in Honey Bee Swarming

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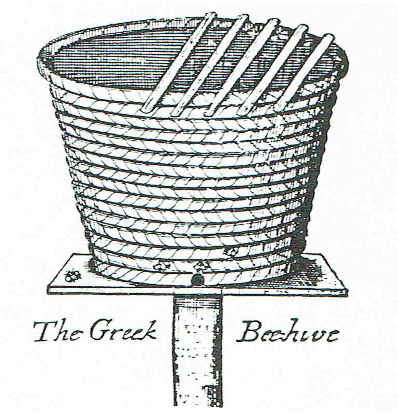
Eva Crane's book *The archaeology of beekeeping* relates Sir George Wheler's 1682 account of manipulation of Greek top-bar hives, the first scientific observation of honey bee swarm control[1]:

> 'The Hives they keep their bees in, are made of Willows, or Osiers, fashioned like our common Dust-Baskets... To increase them in Spring-time, that is, in *March* or *April,* until the beginning of *May,* they divide them; first separating the Sticks, on which the Combs and Bees are fastened, from one another with a Knife: so taking out the first Combs and Bees together, on each side, they put them into another Basket, in the same Order as they were taken out until they have equally divided them. After this, when they are both accommodated with Sticks and Plaister, they set the new Basket in the Place of the old one, and the old one in some new Place. And all this they do in the middle of the day, at such time as the greatest part of the Bees are abroad; who at their coming home, without much difficulty, by this means divide themselves equally. This Device hinders them from swarming, and flying away...'

This is 'the colony split', a well recognised swarm control measure.



Greek top bar hive sketched by Wheler [1651-1724]

However is was to take another 100 years for the Swiss naturalist François Huber[2] [1750-1831] to appear on the scene and to make the first systematic in-hive observations. Letter IX, *On the formation of swarms* describes his 1788-1799 study of the swarming process in exquisite detail:

> 'I can add but a few facts to the information M. de Reamumur has communicated relative to swarms... In the course of spring and summer, the same hive may throw several swarms. The old queen is always at the head of the first colony; the others are conducted by young queens. Such is the fact which I shall now prove; and the peculiarities attending to it shall be related…'

The Reverend Johann Dzierżoń[3] [1811-1906], referred to as the true father of beekeeping[4], became famous for further discoveries including bee parthenogensis, the production of royal jelly and the spacing of frames so they could be easily removed. Amongst his most notable contributions, he pioneered practical principles for transfer of fixed-frame colonies and bees to moveable-frame hives:

> 'It would be superfluous to speak of the season when the occupation should take place if many bee-keepers in their eagerness to introduce these hives into their apiaries did not come to grief by transferring stocks from log or straw-hives in autumn—a time quite unsuitable. They not only thereby do themselves harm, but create prejudice against the new hives, because of the unfavourable result is ascribed to the hives rather than to the unsuitable time when the changes are made.
>
> New hives should be occupied when the bees are naturally ready for moving. There is no need to wait the full arrival of swarming time, as is the case of other empty hives, because we can provide comb for the bees beforehand so that eggs may be laid immediately, and thus hives may, at any rate, be stocked in April.'

The impact on beekeeping of Dzierżoń's and Huber's observations, and those of the Reverend Lorenzo Lorraine Langstroth's 1851 discovery of bee space[5], and of their moveable frame hives[6], were to banish the skeppist approach to keeping bees. Suddenly apiarists reliance on issued and captured swarms was replaced by a strategy of active swarm control and prevention.

Langstroth [1810-1895], it might be said, was the first to clearly articulate the importance of very practical moveable frame hives for modern beekeeping practice. The 1862 Massachusetts advertisement for his Langstroth Hive articulates this momentous leap:

> 'Each comb in this hive is attached to a separate, moveable frame, and in less than five minutes they may all be taken out, without cutting or injuring them, or at all enraging the bees. Weak stocks may be quickly strengthened by helping them to honey and maturing brood from stronger ones; queenless colonies may be rescued from certain ruin by supplying them with the means of obtaining another queen; and the ravages of the moth effectively prevented, as at any time the hive may be readily examined and all the worms and c., removed from the combs. New colonies may be formed in less time than is usually required to hive a natural swarm; or the hive may be used as a non swarmer, or managed on the common swarming plan...'

The chase to discover swarm control measures

Swarm control practices that were to follow ensured that the productive capacity of whole apiaries would no longer fly out the front door. But what was discovered, what were the key swarm control strategies and why do they work? To answer these questions, it is important that we understand the underlying factors signalling the readiness of bees to swarm. It is also instructive to record how and when the swarm control discoveries were made as the findings were those of very astute observers.

Honey bees have a natural proclivity to swarm and defend themselves: they have evolved to reproduce as efficiently as possible and to fend off marauders. However with most honey bee species, other than temperate strains of the Western Honey Bee (*Apis mellifera*) and some races of the Asian Honey Bee (*Apis cerana*), their propensity to swarm is so great that they are not amenable to managed honey production or to controlled provision of pollination services. This does not mean that they are of no practical value. On the contrary, many are hunted for their honey and wax and all, especially species such as *Apis florea* and *Apis dorsata,* are important crop pollinators.

The contemporary beekeeper perspective is usually one of practical swarm minimisation rather than outright prevention. Historically, the late nineteenth and twentieth century beekeeper set out to entirely thwart the natural processes of swarming and defence. This is exemplified by Miller in his 1911 book *Fifty years among the* bees[7] and perhaps by his too often cited adage:

> 'If I were to meet a man perfect in the entire science and art of bee-keeping, and were allowed from him an answer to just one question, I would ask for the best and easiest way to prevent swarming, for one who is anxious to secure the largest crop of comb honey.'

Demaree addressed this dilemma in an 1892 oration to the Ohio State Convention in Kentucky[8] attempting to put Miller's swarming concern to rest:

> 'When your apiary is as large as you want it, what would you give to be able, by a simple, practical manipulation at the beginning of the swarming season, to hold all your colonies in full strength of working and breeding force steadily through the entire honey harvest? You can do it beyond a doubt, by practicing my new system of preventative swarming...'

His method, involving separation of the queen from her brood and forcing establishment of a new brood nest, diverts bees from swarming and keeps all workers well occupied. We will return to the mechanics of the Demaree Plan in Part III of this series.

We might ask what, in principle, we might learn about swarming from George Demaree and from these pioneers. As importantly, we might ask ourselves if we could better learn to work with bees rather than against them.

Swarming as the means of reproductive colonisation

Ecologist Mark Winston's bee-oriented perspective[9] is one of equating swarming to reproductive colonisation. Swarming occurs under a narrow window of near ideal conditions, a combination of intrinsic demographic (colony) and extrinsic (environmental) factors that must coincide to enable successful colony division[10]. Winston and coworkers[11] have demonstrated the importance of queen substance[12] secreted by her mandibular glands[13] in regulating swarming. Their interpretation focuses on nest architecture factors promoting swarming, notably the importance of a crowded brood nest and insufficient nectar storage space.

While many manipulation practices work well to arrest swarming, many of the reasons put forward as to why they actually work are buried in folklore. Most sound theory, however, is based on the notion that a combination of a crowded brood nest and inadequate honey storage space are really important factors in initiating swarming. Strategies involving open brood nest architecture, giving the queen ample room to lay, and the timely supply and arrangement of honey supers and stores certainly delays swarming. However a note of warning needs to be sounded. Providing much more space than bees can comfortably manage, especially in times of dearth or in winter, will either arrest colony development, lead to colony demise or make bees prone to stress-related diseases.

The most successful swarm control measures are those that closely replicate natural swarming, notably the aforementioned hive splitting where the new colony suffers an extended period of broodlessness. There the split off colony (described in detail in follow up Part II) develops an emergency queen and, in most other ways, behaves like an issued swarm. By the time this replacement queen commences laying most brood will have emerged and will be more than ready to nurse brood. Meanwhile the old stay-at-home queen lays into a colony depleted of much of its stores and workforce and closely resembles the parent colony that has swarmed[14]. In the normal course of events the original colony will abandon any attempt to swarm. For the two colonies formed to remain productive they must both recover and reestablish themselves in time for the main honey flow and to survive another winter.

The experienced beekeeper will, if needed, simply reunite the two colonies after almost all risk of swarming has passed and do at the beginning of the main honey flow. As we shall see, the practice of splitting works best where the colony is manipulated before the colony commences preparations to swarm since, under favourable conditions, large unmanaged colonies may swarm many times.

Other successful swarm control measures are focused on queen and, possibly, drone management[15]. A necessary condition of swarming is the presence of an additional gyne, namely a potential replacement queen: queen cell cup eggs, queen larvae, queen cells, virgin queens and, in not infrequent instances, laying workers termed gynaecoid females. Without another gyne, that is without an alternative laying queen – the normal colony condition – a hive cannot swarm successfully. The importance of the queen will be further elaborated on once we have examined the role of the worker bee.

As already intimated, some control strategies are focussed on management practices aimed purely at preventing swarming, working against rather than with the bees.

The worker bee as an agent of swarming

A nuanced approach to controlling swarming requires an understanding of the underlying behaviour of worker bees. This necessitates an appreciation of not only the signs and conditions that signal imminent swarming but also of the ever-changing roles and task orientation of worker bees. You can't just 'Tell the Bees'[16] that their brood nest is crowded or that there is insufficient space to put honey and pollen into storage. However the notion that these intrinsic hive conditions are chemically signalled to worker bees and presage swarming warrants very close attention[17].

Telling the Bees[18]

John Hogg, in reviewing the extensive literature of what is known about swarming, provides a cogent interpretation of the swarming phenomenon[19]. Earlier[20] he reported on the practical findings of Bernard Möbus[21]: Möbus's genius and keen observation of bees, made idle by brood-bee imbalance (too many young emerging nurse bees to be accommodated in the nursery) and too many nectar receivers and wax producers (more than needed to receive incoming nectar) or lacking space to store and ripen nectar, explains the swarming phenomenon remarkably well. Möbus's narrative tells us seemingly most of what we need to know about how swarming is initiated and practiced. His and Hogg's ideas are elaborated in the following.

Hogg has designated idle bees as a temporal swarming caste. Young workers, freed of cell cleaning, brood tending and thermoregulation of the brood nest, and isolated from queen pheromone that suppresses queen and drone cell building and ovarian development[22], take control of swarm preparation. If conditions such as weather change suddenly, as they often do in spring, worker bees in close contact with the queen will tear down queen cells, continue to feed the queen and prevent her departure from the hive. Under favourable conditions, however, this swarming caste not only prepares a colony to swarm, but also orchestrates the actual process of swarming. They first cease feeding the queen, then they eject her from the colony, conduct actual swarming, locate a new nesting cavity and quickly construct comb in the colony budded off and established in a new cavity. These swarm caste workers also appear to micromanage after-swarms and accompanying virgin queens.

Convincing lines of evidence for the existence of idle workers, apart from the practiced eye of overly high bee numbers of newly emerged workers on brood comb or bearding outside hive entrances, is the observation that – as swarming preparations get underway – many bees are 'packed to the gills' with nectar and hang off combs outside the brood nest. These worker bees facing insufficient super storage space are well known to act as repletes, that is – much like honey ants[23] that have a temporal caste that engorges honey stores – act as short-term honey storage vessels. Preparation for swarming is also indicated by a sudden cessation of wax production and comb construction[24].

A regular and a long resident swarm at the same location at Waniassa in the ACT in late October 2016
Photos: Alan Wade

These bees, being no longer actively engaged in receiving and processing incoming nectar, building comb, and processing and storing honey – apart from acting as a living honey repository – are as useful to the mother colony as the idle couch potato. Similarly, very young workers, forced out of the brood nest to facilitate ventilation, and that are surplus to requirements for brood nest duties, will congregate outside the brood nest and are isolated from circulating queen pheromone normally achieved by trophylaxis, that is the regulated exchange of food. Large numbers of emerging workers leads to a bee-age imbalance and this is reflected in their being surfeit to immediate colony requirements.

This theory, explaining the culmination of brood rearing, honey storage, brood bee-balance condition and favourable environmental conditions external to the hive, also explains the success and occasional failure of other 'tried and true' swarm control measures.

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[1] Wheler, G. (1682). *A journey into Greece,* London *in* Crane, E. (1963) in *The archaeology of beekeeping*, *Chapter 9. Towards movable-frame beekeeping,* pp. 196-212. Gerald Duckworth & Co. Ltd, The Old Piano Factory, London.

[2] Huber, F. (1806). *New observations on the natural history of bees*, Volume I by François Huber. Letters to M. Bonnet. These letters written between 1787 and 1791 were not published until 1806. http://www.bushfarms.com/huber.htm

[3] Dzierżoń (1882). *Dzierzon's rational beekeeping or The theory and the practice of Dr. Dzierzon*. Translated by Dirk and Stutterd, Houlston & Sons, Paternoster Square, Southall: Abbott, Bros. https://ia800201.us.archive.org/17/items/dzierzonsration00stutgoog/dzierzonsration00stutgoog.pdf http://bees.library.cornell.edu/cgi/t/text/pageviewer-idx?c=bees&cc=bees&idno=5017629&node=5017629%3A1&frm=frameset&view=image&seq=1

[4] Beesource blog (2016). *Overseas_Beekeeper*; 07-19-2016 at 02:55 PM. http://www.beesource.com/forums/showthread.php?328732-Jan-Dzier%26%23380%3Bo%26%23324%3B-(Johann-Dzierzon)-true-father-of-beekeeping

[5] Stamp, J. (2013). *The secret to the modern beehive is a one-centimeter air gap*. Smithsonian online at http://www.smithsonianmag.com/arts-culture/the-secret-to-the-modern-beehive-is-a-one-centimeter-air-gap-4427011/
Langstroth, L.L. (1878). A Practical Treatise on the Hive and Honey-Bee. http://www.thebeeyard.org/wp-content/uploads/2014/02/The.Hive_.And_.The_.Honey_.Bee_.Langstroth.1853.pdf

[6] Langstroth's claim to the discovery of bee space can be traced back, in most part, to the findings and hive inventions of Dzierżoń and Huber.

[7] Miller, C.C. (1911). *Fifty years among the bees*, p. 210. The A. I. Root Company, Medina, Ohio. http://soilandhealth.org/wp-content/uploads/0302hsted/030208miller/030408miller.PDF

[8] The Demaree swarm control method will be described in follow-up Part III *Conventional swarm control measures.*

[9] Winston, M.L. (1991). *The biology of the honey bee.* Harvard University Press.

[10] Cale, G.H., Banker, R. and Powers, J. (1975). Management for honey production *in The Hive and the Honey Bee,* Dadant & Sons, Hamilton, Illinois, pp. 380-384.

[11] Winston, M.L., Higo, H.A., Colley, S.J., Pankiw, T. and Slessor, K.N. (1991). The role of queen mandibular pheromone and colony congestion in honey bee (*Apis mellifera* L.) reproductive swarming (Hymenoptera: Apidae). *Journal of Insect Behavior* 4**:** 649-660. http://agris.fao.org/agris-search/search.do?recordID=US9188805

[12] Butler, C. (1974). *The World of the Honeybee*. Collins New Naturalist, London. [The key queen mandibular pheromones are 9-keto-2-(E)-decenoic acid, the two stereoisomers of 9-hydroxy-2-(E)-decenoic acid, methyl p-hydroxybenzoate and 4-hydroxy-3-methoxyphenylethanol, a mixture of which being the much feted queen substance.]
Winston, M.L., Slessor, K.N., Willis, L.G., Naumann, K., Higo, H.A., Wyborn, M.H. and Kaminski, L.A. (1989). The influence of queen mandibular pheromones on worker attraction to swarm clusters and inhibition of queen rearing in the honey bee (*Apis mellifera* L.). *Insectes Sociaux* **36(1):** 15–27. The effect of these simple organic compounds is enhanced by coniferyl alcohol, methyl oleate, hexadecane-1-ol and linoleic acid also produced by queen bees. See Bortolotti and Costa (2014, loc. cit.) for a wide-ranging review of bee pheromones.

[13] Butler, C.G. (1959). Queen substance. *Bee World* **40(11):** 269-275. http://tandfonline.com/doi/abs/10.1080/0005772X.1959.11096745

[14] In a swarmed colony, the old queen will depart, at least with the prime swarm, so that in the practice of hive splitting, the swarming condition is not perfectly replicated.

[15] Drones find queens by sensing a single queen mandibular (queen substance) pheromone [Wanner, K.W., Nichols, A.S., Walden, K.O.O., Brockmann, A., Luetje, C.W. and Robertson, H.M. (2007). A honey bee odorant receptor for the queen substance 9-oxo-2-decenoic acid. *Proceedings of the National Academy of Science* **204(4):** 14383–14388. http://www.pnas.org/content/104/36/14383.fulpdf] and as a means of finding each other at mating sites employ 'drone pheromone' of unknown chemical composition. Laying worker colonies probably never swarm.

[16] Drake, S.A. (1901). *Telling the bees. New England Legends and Folk Lore,* pp. 314-315. Boston: Little Brown and Co. ISBN 978-1-58218-443-2. https://archive.org/stream/bookofnewengland00dra#page/314/mode/2up/search/%22telling+the+bees%22

[17] Bortolotti, L. and Costa, C. (2014). Chemical communication in the honey bee society *in* Chapter 5, *Neurobiology of chemical communication*. Mucignat-Caretta C. (ed). Boca Raton (F.L.): CRC Press/Taylor & Francis. https://www.ncbi.nlm.nih.gov/books/NBK200983/

[18] https://upload.wikimedia.org/wikipedia/commons/b/ba/Charles_Napier_Hemy-Telling_the_Bees.jpg

[19] Hogg, J.A. (2006). Colony level honey bee reproduction: The anatomy of reproductive swarming. *American Bee Journal* **146(2):**131-135. http://www.twilightmd.com/Samples/Hogg/Hogg_Halfcomb___Publications/ABJ_2006_February.pdf

[20] Hogg, J.A. (1997) Comb honey III: The swarm. Part III of three parts. *American Bee Journal* **137(12):** 875-883. http://www.twilightmd.com/Samples/Hogg/Hogg_Halfcomb___Publications/ABJ_1997_3December.pdf

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and American Bee Journal **127(5):** 356-362 (May 1987). Part 2. http://poly-hive.co.uk/recourses/mobus-bernard-his-work-on-swarming-and-wintering/the-swarm-dance-and-other-swarm-phenomena-2/

[22] Butler, C.C. (1959). Extraction and purification of 'queen substance' from queen bees. *Nature* **184:** 1871.

[23] Wheeler, W.M. (1908). The polymorphism of ants. *Annals of the Entomological Society of America* **1(1):**38–69. doi:10.1093/aesa/1.1.39. https://archive.org/stream/ants_10548#page/n1/mode/1up

[24] Demuth, G.S. (1921). Swarm Control. *Farmers Bulletin* **1198:**1-45. https://ia601401.us.archive.org/32/items/CAT87202908/farmbul1198.pdf