Swarming in Honey Bees

Part II
Swarming across the Honey Bee Genus and Non Reproductive Swarming

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In Part I of this series, we examined the historical origins of swarm control and reviewed the role that both workers and the queen play in orchestrating swarming. We now turn to a broader overview of what is known about swarming and the lessons that may be be learnt from all honey bee species.

Intrinsic factors influencing swarming

There are other genetic and queen-age related factors that affect swarming and these also need to be acknowledged even if they are not yet fully comprehended. Young queens have a higher fecundity – that is, they lay more eggs – and produce more queen pheromone. With the potential of a larger workforce to replace diseased bees and to care for brood, and for old overwintered bees to become foragers and less attendant to early brood rearing, the whole spring buildup strategy is changed. For this reason, autumn requeening is often recommended to facilitate not only late winter brood development but also to reduce the incidence of either queen failure or spring swarming. In any case regular requeening should be regarded as an investment in good beekeeping practice.

The pattern of production of worker bees also varies between honey bee races and species and in response to pollen availability and honey stores. Oliver[1] stresses the importance of bee nutrition, particularly the role of pollen stores. Pollen is converted to the egg yolk protein vitellogenin stored in fatty tissue by diutinus (overwintering or dearth) bees. This protein maximises bee longevity and is important for late winter brood rearing. High levels of vitellogenin are also found in bees preparing to swarm but its role in regulating swarming is not fully understood[2].

Large differences in the propensity of different races to swarm are fairly well known, at least amongst races of European honey bees. For example, the Carniolan Bee (*Apis mellifera carnica*) has a very long-standing reputation[3] of swarming easily and also building up quickly under favourable conditions. But the Western Honey Bee (*Apis mellifera*) comprises not only European honey bees, races of which have been domesticated almost world-wide, but also a genetically removed range of African honey bees also managed for honey production.

The widely cultivated and well studied race of African honey bee, *Apis mellifera scutellata* (from the central eastern region of southern Africa[4]) is reputedly a poor comb builder and this may be a factor in its being a prodigious swarmer. This bee was imported to Sao Paulo, Brazil from South Africa and Tanzania in 1956. The saga of its escaping from the Brazilian research facility, swarming vigorously and supplanting the pure European bee gene pool, and the ensuring media 'killer bee frenzy' in the tropical Americas, is carefully recorded by Winston[5].

Another reproductive anomaly has evolved in the Cape Bee (*Apis mellifera capensis*). Laying workers produce worker offspring (thelytokous parthenogenesis) conferring a survival trait rarely available in other European or African races of *Apis mellifera*[6] though Butler records very occasional self requeening of hopelessly queenless European honey bee colonies[7]. Cape bees can also produce queens from laying workers in normally classified hopelessly queenless colonies, while laying workers drifting to normal honey bee colonies produce offspring that generally results in the demise of the parent hive. An informative discussion of the risks that this and other honey bees present to apicultural practice is presented by Barry *et al*[8].

Non reproductive swarming behaviour

Supersedure – Non reproductive queen replacement

Butler[9] defines queen supersedure as 'the process by which a colony of honeybees replaces its queen without swarming'.' He also notes that it is of 'frequent occurrence'. Although opinions vary widely, and there may be significant differences between different bee races, supersedure often goes undetected and may occur in up to 40% of colonies in any one given year.

In a very elegant series of experiments this research worker showed that the reigning queen produces too little ‘queen substance’ and that replacement queens are raised while she remains in the hive. He demonstrated that – contrary to popular belief – factors attendant to colony dwindling, such as reduced fecundity or the queen becoming a drone layer, do not initiate supersedure. He further observed that the queen and her daughter could coexist and continue to lay in a single colony for an extended period. Autumn and spring supersedure are most common.

I observe many colonies in 'queen replacement transition' building supersedure cells. For example the cells (illustrated) appeared shortly after a new marked queen was introduced. They disappeared sometime after the queen was released from her cage by the bees demonstrating that they did not need to be removed.

Supersedure cells developing after direct requeening into a top-bar colony
Photo: Alan Wade

Of course, in both normal and supersedure induced swarming, the parent colony also replaces its reigning queen. In many instances the old queen in the prime swarm – once established and settled – will herself be superseded. However small supersedure swarms have a reputation of rarely surviving.

Usurping swarms

There also appears to be some evidence that 'late swarms' are not primarily destined to be reproductive swarms and may, instead, be issued for the express purpose of taking over existing colonies[10], an idea first proposed by Magnum[11]. Hence bee colonies, unlikely to build up and survive another season, may simply supplant less genetically fit colonies exploiting their stores and bee population. Such an adaptive strategy is not dissimilar to that of the already-described parasitising Cape Bee.

Absconding – Non reproductive swarming in response to predation and limited resource availability

Absconding, where a whole colony abandons its nest, is an entirely different type of swarming. It is also non-reproductive. While it is rare for European honey bee races to abscond – they usually starve if conditions are poor – they will leave a cavity if conditions are unsuitable at the outset, especially if the cavity is too small or contaminated by the likes of solvents or oils. Even amongst cavity dwelling species, there is considerable variation in their propensity to abscond: tropical ecotypes of *Apis cerana* more readily abscond than do temperate *Apis mellifera*[12].

Amongst the broad group of tropical *Apis* species and subspecies, their propensity to leave a hive has arisen from the selective pressures of more intermittent resource availability. The trait of absconding has evolved in response to entirely different environmental conditions to those that exist in Europe where reliable annual honey flows and long winters favour a strategy of storage.

Hepburn and Radloff[13] describe the behavioural disparity between European and African races of the Western Honey Bee very succinctly:

> 'Perhaps the most striking differences among the lineages of *Apis mellifera* involve the extent of resource investment in the reproduction and mobility of the colonies.'

African races of the Western Honey Bee and tropical Asian honey bee species, including a number of races of *Apis cerana* and its close allies, *Apis koschevnikovi, Apis nuluensis* and *Apis nigrocincta,* regularly abscond. Indeed all swarm both reproductively and non-reproductively more regularly than the European honey bee.

With absconding there is, of course, no increase in the number of colonies. Open nesting *Apis* species (*Apis dorsata, Apis laboriosa, Apis florea* and *Apis andreniformis*) not only also swarm reproductively in a fast and furious manner, an extreme strategy based on taking full advantage of excellent conditions, they also abscond when and as conditions dictate. They also leave nesting sites in response to heavy or repeated predation, important factors for species that nest on a single comb in the open. There is less investment in storage and comb building and more investment in nest defense and in moving the nest to food sources than in cavity dwelling species.

Migration – Non-reproductive swarming in response to climatic and regionally predictable resource availability

Further examination of the swarming behaviour across the *Apis* genus suggests that the phenomenon of 'failed local condition-induced' absconding may extend to seasonally programmed colony migration. Hepburn and Radloff[14] describe the major swarming differences between the sub-genera, dwarf Micrapis, cavity dwelling Apis and giant Megapis honey bees in evolutionary terms.

Oldroyd and Wongsiri[15] provide a wide ranging review of the biology and evolution of Asian honey bees including an overview their reproduction, swarming and migration. For example *Apis dorsata* will never use wax from old comb even if returning swarms nest within centimeters of deserted comb whereas *Apis florea,* while not reestablishing nests on old comb, may nevertheless scavenge old wax. Such strategies involving a tradeoff between employing wax, a valuable resource, and not using wax from old comb to minimise the risk of disease and mite transmission. This behaviour is in strong contrast to that of cavity dwelling species that readily occupy comb in old nest cavities. There the reward of much larger amounts of wax enhances their chance of survival and reproduction. There are also nuanced differences between cavity-dwelling honey bees (*Apis mellifera* and *Apis cerana*) and the open-nesting giant and dwarf honey bees in normal reproductive swarming behaviour. There appears to be evidence that at least some open-nesting species fly directly to a new nesting site and that this may be orchestrated by bees performing orientation dances inside the parent colony prior to swarming. However, in most open-nesting species dancing associated with location of a new nesting site has not been observed reflecting the fact that they do not need to locate a scarce nesting hollow.

A parallel perspective of the pan tropical Western Honey Bee subspecies by Hepburn and Radloff[16] suggests separate evolution of swarming and migration in *Apis mellifera* bees of African origin. The patterns of swarming are highly nuanced, vary between races and vary regionally even within the one race of bees. For example they state pointedly that:

> 'The phenology [natural cycling or timing] of reproductive swarming in African honeybees closely corresponds with local climate and weather and the availability of forage.'

The behaviour of all of these bees is instructive and the findings of these authors and others is outlined in the following.

(a) *The Giant honey bees* (*Apis dorsata* and *Apis laboriosa*)

Giant honey bee colonies occupy a single comb, where colonies may nevertheless cluster communally. Robinson[17] as well as Underwood[18] and Woyke and Wilde[19] have described the cyclical annual swarming and migratory behaviours of these species. Like migratory birds, colonies often return to the same nesting locations but not their original nest. Their movement patterns vary widely so that, while lower altitude populations of *Apis dorsata* may migrate over large distances, up to hundreds of kilometers, Himalayan Honey Bee (*Apis laboriosa*) migrations are elevational and colony relocation distances are relatively short. The overall annual pattern is one of colonies expanding rapidly and swarming to establish new colonies, then abandoning their nests and migrating. Robinson also describes a bivouacking (staged migration) behaviour of *Apis dorsata* and the importance of preservation of these sites to protect the integrity of populations of this bee. These bees are famously raided for their honey stores and are important wild pollinators[20].

***Apis dorsata dorsata* colony in high canopy at Preah Khan Temple Siem Reap in Cambodia mid November 2014**
Photo: Alan Wade

(b) *The Cavity dwelling honey bees* (*Apis cerana , Apis koschevnikovi, Apis mellifera, Apis nigrocinta* and *Apis nuluensis*)

Koeniger, Koeniger, and Smith[21] provide a broad interpretation of the swarming behaviour of this group of honey bees in evolutionary terms:

> ... 'cavity-dwelling honeybees like *A. cerana* and *A. mellifera* could extend their distribution to subtropical and temperate conditions, where colony reproduction would require large swarms that are forced to locate a nest cavity within a short time. Under tropical conditions, however, small swarms resulting from high colony reproduction may survive for a longer period outside and such honeybees could exploit seasonal differences in nectar availability. At the end of this development, the transition to open-nesting forms might have taken place to avoid the limitations of which result from the scarcity of nest cavities'.

Hepburn[22] is more specific about the nature of honey bee migration:

> '… Seasonal migration is characteristic of *Apis cerana, Apis florea, Apis andreniformis, Apis dorsata, Apis laboriosa* and African (not Eurasian) *Apis mellifera* ...[a] behaviour [that] is dampened at colder latitudes."

Little is known of the migration patterns of the other species closely allied to *Apis cerana* namely *Apis koschevnikovi, Apis nigrocincta* and *Apis nuluensis* other than the fact some some are sympatric [occupying the same area] and either maintain breeding barriers or show variable habitat preference, partly in response to competition from each other.

Swarming and absconding of African races of honey bees including *Apis mellifera andansonii*, *Apis mellifera scutellata*, *Apis mellifera monticola*, *Apis mellifera litorea* and *Apis mellifera nubica* and the influences of resource availability, pests and diseases on these behaviours is outlined by Mutsaers[23]. Schneider and McNally[24] provide detailed accounts of colony growth and impacts of a wide range of factors on migratory behaviour of African honey bees demonstrating the fine-tuned responses of honey bees to resource availability and climatic condition.

Koetz[25] provides an in-depth overview of the swarming behaviour of *Apis cerana*, particularly of the Javanese strain that has spread across the Indonesian Archipelago and into Irian Jaya, Papua New Guinea and northern Australia.

(c) *The Dwarf honey bees* (*Apis florea* and *Apis andreniformis*)

Robinson[26] has made a detailed observation on a serially absconding *Apis andreniformis* swarm indicating some difference in this species behaviour to that of the much better studied *Apis florea* but the account is purely anecdotal. A substantial review of the biology of the two dwarf honey bees by Wongsiri and coworkers[27] signal some striking differences in their biology and absconding behaviour.

Apis andreniformis is more prone to absconding and over greater distances and is less adaptable than *Apis florea* in that its distribution is restricted to undisturbed habitat. *Apis florea* decamps over relatively short distances sometimes returning to the parent nest location to harvest wax for comb building. Over much of its range reproductive swarming occurs at the end of the dry season and in many areas there is a secondary absconding swarming before the onset of the dry season[28].

Overall significance of swarming in honey bees

Swarming, the propensity of colonies to abandon nesting sites, either for colony increase under favourable conditions or to survive in response to dearth and predation, enhances honey bee survival at a whole of population scale rather than at an individual colony level. Hence swarming signals a complex array of honey bee survival strategies.

As we have seen, swarming, critical to establishment of new colonies, may also result in queenright swarms taking over established colonies. Over time both strategies impact on honey bee gene flow and both confer long term survival of different bee lines.

In contrast, swarming involving colony absconding is a separate, but well recognised, response to adverse in-hive or environmental conditions. New colonies encountering poor nesting conditions may immediately seek more suitable nesting sites, that is abscond. For cavity dwelling species, this may be a response to inadequate space or hive contamination; amongst dwarf and giant honey bees temporary nesting or bivouacking may simply facilitate colony movement to exploit resources elsewhere. More generally, absconding behaviour would appear to be a response to disease, to predation, to resource competition or to local resource depletion, where relocation of the bee colony and some of its resources confers an improved chance of survival.

On the other hand, colony migration, where bees return to their original nesting locations on a cyclical basis, sometimes over large distances, would appear to be an adaptive response to regional and seasonal availability of floral resources.

Parts I and II of this four part series have reviewed what is known about the biology of swarming in honey bees. They outlined our understanding of the underlying environmental and in-hive conditions that give rise to swarming both amongst temperate European honey bees and all other species and races of honey bees.

In Parts III and IV we will examine case studies of swarm control measures, the legacy of nearly two and a half centuries of beekeeping observation and practice[29]. They will cover widely-adopted swarm control practices and explain how and why they work and how they can be adapted to harness full bee potential.

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