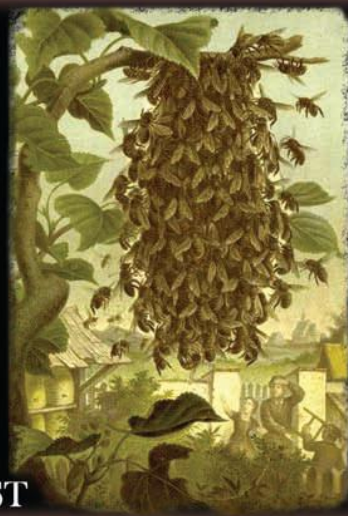
THE PERFECT SWARM



PART ONE

by PETER LORING BORST

Many of us were fortunate to be able to listen to Tom Seeley on NPR's Science Friday which aired Christmas Eve, 2010. He passed on a lot of valuable information about honey bees and their decision-making processes. At the end, he was asked what question is yet strong in his mind. He said that he "would love to learn how the bees decide when they're going to swarm. It's still an utter mystery." This is an old question, as yet unresolved. So, what is swarming and why does it happen? And how, in this most studied insect, can it continue to be a mystery?

In 1958, J. Simpson of the Bee Research Department at the Rothamsted Experimental Station, Harpenden summarized what was known by mid-century in "The Factors which Cause Colonies of *Apis mellifera* to Swarm." He states:

> Reproduction of colonies of the honey bee is achieved by swarming. Normally only one queen is present in each colony, but, before swarming, the colony begins to rear additional queens. The first swarm usually leaves the parental nest to found a new colony.
>
> Attempts to elucidate the factors which encourage swarming and to devise methods of eliminating it have received a great deal of attention in beekeeping literature and a wide variety of opinions have been expressed as to the conditions under which swarming or swarm preparations most frequently occur.
>
> Unfortunately, a large proportion of these opinions appear to have no sound basis in observation, experiment or beekeeping experience.

The history of beekeeping has two basic phases. Modern beekeeping began in the mid 1800s, with the invention on the moveable frame, which brought with it the ability to observe the internal workings of the honey bee colony. Prior to this, a hive was a "black box" from which honey was stolen and swarms came forth. The emergence of a swarm was a fortuitous event, because this was the chief way that beekeepers obtained new colonies. If lucky, the keeper would capture and hive the swarm; often it headed for the woods.

Swarm Prevention

Soon it was realized that a hive that *did not* swarm would produce much more honey. Bee colonies could be divided by the operator, as needed, so the issuance of a swarm became something to be prevented rather than encouraged. Thus, the questioning began. Most beekeeping books written since 1850 give instructions on how to prevent swarming. Some extremely complicated manipulations have been devised, but generally the plan is to enlarge the hive so that progressively more room is available to the colony as it increases its population in the spring.

These instructions are all based upon an intimate knowledge of the conditions that exist when colonies begin to prepare to swarm, so we are pretty clear on what those conditions are. Swarms most often occur in late spring, when the colony is growing rapidly. If the hive is filled at this point, the bees may decide to divide the colony and cast a swarm. Most radical swarm preventative measures involve dividing the colony which

Rob Szczepanski with his prize

creates such a setback that they forego swarming for that season. However, this probably won't work if swarm preparations are already underway.

So, beekeepers through learning and experience have found ways to minimize the swarming out of their hives. Then why is it still considered such a mystery? The truth is, that given all the "right conditions," some colonies swarm and some don't. Beyond that, some honey bee colonies swarm under circumstances that to their owners seem downright foolish! What it boils down to is this: the most you can say is that there are times when bees are more liable to swarm than others. For this reason, the time is often referring to as the swarming season. But swarming is in no way inevitable for a particular colony, the way it is certain that migratory birds will leave for their winter homes.

Going Inside

The study of swarming behavior in honey bees has proceeded from external to internal conditions. We have already touched on the external: it most often occurs during beautiful spring weather when fruit trees are blooming and their perfume is filling the air. Edward Bevan writing in 1853 gives the "symptoms of swarming" as:

> The inactivity of the working bees, which neither gather honey nor farina, though the morning be sunny, and the weather altogether inviting. Reaumur regarded this as the most indubitable sign of preparation for swarming.
>
> Unusual silence in the hive, during which the separatists are supposed to be taking in a cargo of honey before their flight, as well for a security against bad weather, as to be in a state of forwardness for the secretion of wax.

By opening the hives, the effect of the external conditions can be plainly seen. The edges of the honey comb cells are extended with fresh white wax, there is newly packed pollen in many of the cells, and others are glistening with fresh wet nectar. The queen is reaching her maximum egg-laying capacity, and there may be a phenomenal quantity of brood in the combs. That is, if the beekeeper has provided adequate room for all of this.

But the signs that the hive owner is looking for are even more distinctive. Along the bottoms of the frames, visible only if the frames are removed from the hive, may be seen the queen cups. These look like acorn caps, or thimbles. The appearance of many cups is an indication that the colony is "thinking about swarming." The sure sign, however, is the presence inside these cups of larvae, fairly taking a bath in a puddle of royal jelly, the substance that turns an ordinary bee egg into a queen. For the keeper knows that before the old queen and her bees will set forth on a quest for a new

Swarm

home, their old home must be provisioned with honey, pollen, and a new queen to take her mother's place.

Basic Instinct

So, we have covered the visible appearance of a colony of bees prior to swarming. For most beekeepers it is sufficient to know what to look for and what to do. The reasons *why* the bees swarm may be of passing interest. Something to speculate upon at the bee club's summer picnic, or a topic for a long article in a bee journal. E. F. Phillips summed it up beautifully in his 1915 treatise on "Beekeeping; a discussion of the life of the honeybee and of the production of honey":

> The simplest way to account for this phenomenon is to attribute it to "instinct" but naturally in doing this we are no nearer an explanation than we were before. Instinct is blamed for many things in bee literature, it being overlooked that instincts are called into action only by definite conditions in the environment. This kind of error is mentioned again here because it appears so frequently in the discussion of swarming. It is worthy of more serious investigation than it has so far received.

I remember when I first thought about swarming, back in my youth, trying to ponder why bees would *do such a thing.* I realized pretty quickly that they are just like teenagers, at the height of their strength and vigor, ready to embark on the great arc of their lives. Then they do something really dumb, like get pregnant. So, maybe it is instinct after all, the urge to reproduce, that causes the honey bee colony to drop what it's doing and just *throw caution to the wind.*

But yet, we are driven to look more deeply. After all, Dr. Seeley has described for us the movement of the swarm from its hive, to a branch where the deliberations are made for choosing a new home, to actually occupying that home. All of this requires a highly complex system of evaluation, deliberation, communication, and decision making. So it is reasonable to assume that much of this sort of thing goes on inside the hive, too; days or even weeks prior to the issuance of the swarm.

Catch the Scent

It was wonderful that Karl von Frisch was able to interpret the "meaning" of the honey bee dance, but the detection of chemical communication in the hive pointed to a whole new world of understanding. Most communication in the living world is not done with words or symbols but by means of scents. Using odors, plants with their flowers and fruits advertise their gifts to animals. And animals use scents to suggest their availability to potential mates. Odor cues are responsible for communicating specific information about the reproductive state of organisms. Modern humans tend to be acutely visual or auditory, getting so much information from seeing and hearing. So, we may forget momentarily the great importance of scent in our lives. The attractiveness of food, flowers, the opposite sex – even clothing and new cars – all are enhanced by specific aromas that proclaim their availability and attractiveness.

It was known early on that if a colony loses its queen that they become aware of this fact rather quickly. At first it was believed it was because she gives off a particular odor. In fact, honey bees do emit a variety of odors that can be easily identified by us, and they indicate particular functions. Anyone can learn to recognize the honey bee alarm odor and the swarm orientation scent. The discovery of the "queen substance" really changed the way we look at a colony of bees. Colin Butler conducted important studies in the 1950s and concluded that the queen produces a substance, which may indeed have an odor, but it is passed physically from bee to bee. In 1955, Butler states:

> It seems probable that either a deficiency in the amount of queen substance available, or, perhaps, a breakdown in its collection and subsequent distribution plays an important part in the phenomenon of swarming. It is not yet clear whether queen substance merely serves as a trigger mechanism. If queen substance is indeed only a trigger mechanism it seems quite probable that other releasing mechanisms, possibly psychological ones, may exist.

With this discovery, the beekeeping community really thought they had discovered the secret to controlling swarming. Butler went so far as to get a patent on synthetic "queen substance" with the idea of marketing it for swarm suppression and to facilitate the introduction of replacement queens into unwilling honey bee colonies. Somewhat remarkably, it was an idea that caught hold and dies hard. Perhaps it is human nature to want to find an easy answer.

Even after Butler's failed attempts to bottle queen spirit and sell it as a solution to the beekeeper's hard problem, the idea reappeared in the 1990s. Products like "Bee Boost" could be purchased by the gallon. Despite high hopes for such an application of the product, Mark Winston proclaimed in a 1998 article in the *American Bee Journal* that "Honey Bee Pheromones Do Not Improve Requeening Success."

More To It

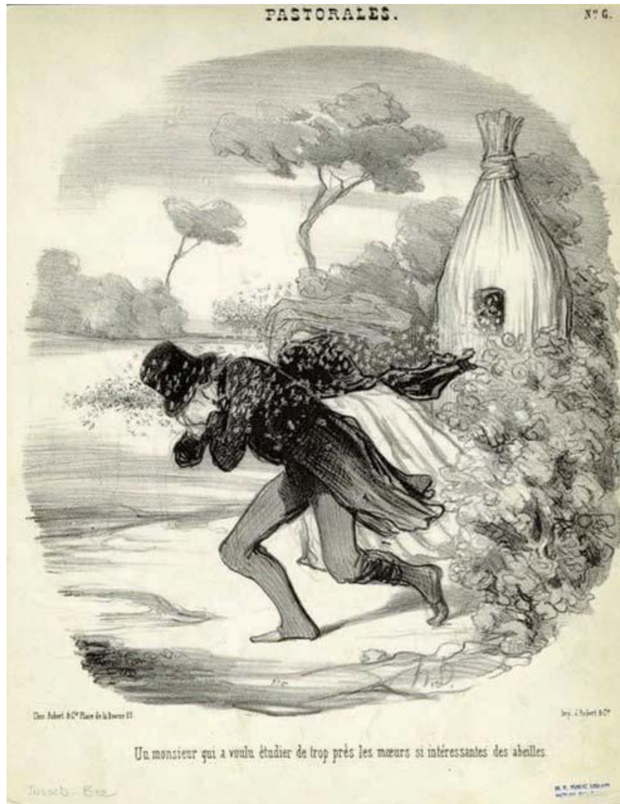
J. Simpson of the Rothamsted Experimental Station at Harpenden had already pointed out that the mere presence or absence of queen substance was not likely to be the whole story, in 1958. He stated, "The rearing of queens which accompanies swarm preparations presumably involves insufficiency or ineffectiveness of queen substance, but it is not yet certainly known whether this is a cause or a consequence of the swarm preparations."

And yet, the notion that the quantity of queen substance is an important regulator of honey bee colony dynamics is still repeated without questioning. Certainly a queen that is no longer producing an adequate amount of this substance is more liable to be replaced with a younger, more capable one. Butler assures us that failing queens "have one quarter the queen substance of a normal, mated, laying queen." But even this can hardly be said to be an infallible correlation, as beekeepers know that some colonies fail to replace their queen long after she has lost the capacity to lay sufficient eggs to keep the colony from plunging into permanent decline. Furthermore, it is not an absolute fact that having a young prolific queen will prevent a colony from swarming out, nor ensure that she won't be prematurely replaced. Determining what are the actual factors that control swarming in honey bee colonies has proved to very elusive indeed. Clearly, there is more to it.

Old Idea Dies Hard

The idea was still going strong well up till the end of the Twentieth Century, despite a preponderance of evidence to the contrary. Ken Naumann of Simon Fraser University wrote in 1991: "The production of virgin queens prior to swarming may be mediated by a decrease in colony-wide levels of queen pheromones." It certainly seems plausible that as the colony population expands in the spring, queen substance would become in short supply and perhaps not get distributed to all the members of the colony. However, it is right in the middle of the nest, where the queen spends most of her time, that the queen cells are built.

Researchers began to refer to the "suite of behaviors" in honey bee colonies, and to recognize that the queens, workers, and even the brood have characteristic chemical substances that indicate particular states. More to the point, in 2006 Nina Fefferman



A swarm disrupts a wedding party.

of Tufts University states: "An alternative explanation for the inability to support a single mechanism is that instead of being causal triggers, the hypothesized mechanisms are simultaneous artifacts (i.e. correlates) of the actual mechanistic cause of swarming."

In other words, there is no one thing that starts the colony down the path to cast their fate to the wind. Furthermore, all of the so-called causes we have been studying and dutifully trying to correlate may just be symptoms after all. We witness observable signs, but the honey bees have long since made the decision and are just now obviously engaged in the final push to get ready to go.

Perhaps we have to look even deeper. Henry Thoreau tells the story of a traveler preparing to cross a swamp. He asks a local boy if the swamp has a hard bottom, to which the boy replies: yes it does. Out in the swamp, the traveler is quickly sinking up to the saddle. "I thought you said that this bog had a hard bottom." "So it has, but you have not got half way to it yet."

To be continued in the May issue!

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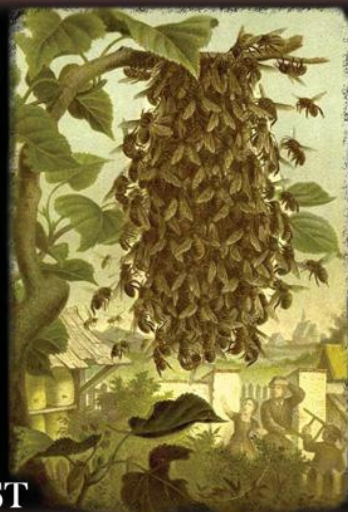

PART TWO

by PETER LORING BORST

Swarm Prevention

The prevention of swarming in honey bees has been the subject of intense interest for more than one hundred years, so we can be sure that beekeepers have developed both theories and techniques in abundance. Everett Phillips, who was in charge of Bee Culture Investigations at the Bureau of Entomology of United States Department of Agriculture at the time, wrote in 1915:

> The principle involved in swarm control and the differences in the amount and persistence of swarming observed in different regions and under different systems of manipulations indicate that swarming colonies have at least one condition in common. While this condition may not be the cause of swarming, it is at least interesting to study its application. Gerstung advances the theory that swarming is caused by the presence of too many young bees in the hive.

This presents the keystone of most swarm control measures. The removal of excess young bees during the swarming season effectively prevents the colony from swarming, but tells us very little about the reasons behind the colony's decision making process. Beekeepers have studied keenly the visible appearance of honey bees in the weeks leading up to the swarming event, for subtle signs that might give clues about the colony's "intentions."

Faraway Dancing

It has long been known that the honey bees "dance" to communicate a variety of information to their nestmates. They can identify the location and quality of such diverse things as patches of flowers and potential nest sites. Furthermore, it has been shown that in tropical species which engage in annual migrations, honey bees perform intriguing migration dances. These dances indicate distances far from the nest; so far, in fact, that the bees themselves could not have visited these sites. In other words, they are projecting the idea of where they "could go," which is much more abstract than simply reporting on where they had already been.

But it is quite surprising to discover such dances in our European bees, which do not migrate. And then, to find them only in the weeks immediately prior to swarming, is more remarkable still. In 2008, Lee Anne Lewis reported this new finding in the journal *Apidologie*. According to her, these migration dances were quite distinct from the usual waggle dances that bees use to advertise food sources. They didn't have the usual figure eight pattern, and they were seen throughout the nest, rather than at the dancing area where foragers usually dance. Also, the dances went on for a very long time and did not correlate to external changes the way nectar dances do. Finally, and this is what they have in common with migratory

dances: they referred to very large and varying distances.

Queen Substance(s)

Still, this dancing activity would have to fall under the category of a symptom of the swarming behavior, rather than the initiating cue. Therefore, we must return to the chemistry of the honey bee colony. By 2006, we were getting new information that not only refutes the idea that the quantity of QMP regulates the hive, but also raises the possibility that there may be a mixture of substances which regulate the various activities of the colony. New Zealand researcher Kyle Beggs refers to a "sophisticated array of chemical signals (pheromones) that influence both the behavior and physiology of their nest mates." In particular, he states that queen mandibular pheromone (QMP) serves to control the behavior of the hive bees. QMP has profound effects on dopamine levels in worker bees, which in turn appear to particularly influence the behavior of the nurse bees. It may help to create the tiered labor system and keep the younger nurses from prematurely maturing into foragers. Conversely, changes in queen control could alter the organization and cause a profound shift in colony behavior, like swarm preparation. The concept of modulated pheromones has emerged over the past several years, to the point where we realize that queens release not one but many substances and the mixture of these is what hive bees are using to get a sense of the queen and her reproductive state.

Who's in charge?

It is very difficult to know whether the queen uses these chemicals to control behavior; or all the bees are willing participants in the system; or if in fact the worker bees are functioning as a command and control system, directing the queen to meet the colony's needs. To determine intentionality in any organism is hard. Even people have

difficulty understanding their own and other people's motives. All the same, Katrin Strauss writes in the journal of *Behavioral Ecology and Sociobiology* (2008):

> We suggest that the mandibular gland pheromones are unlikely to function as reliable indicators of queen reproductive value and rather operate as an agent to suppress worker reproduction. This does not exclude the possibility that other "honest" pheromone signals exist in the honeybee colony, but these would have to arise from other semiochemicals, which could be produced by both the queen and the brood.

Actually, two schools of thought have emerged on this topic, each declaring the case closed. Sarah Kocher nicely expresses the opposing viewpoint in her 2009 PhD Thesis: "These results support a model in which queen pheromone composition is linked to her reproductive status and fecundity, such that queen pheromone serves as an honest signal to the workers." The chief argument against queen control of the workers centers on the evolutionary consequences of cooperation and non cooperation.

Keep It Together

Most researchers refer to the supposition that if it was not in their interest to cooperate, honey bee workers would evolve that ignore queen pheromones. Just how workers could develop and pass on these traits is never really shown. The queen is the only individual that passes on traits and natural selection could clearly favor a queen that could amass and control workers over a queen that could not.

That is, a more harmonious and efficient colony could outcompete an anarchistic one, perpetrating the traits of queens that have complete control over their colonies. Of course, this does not preclude the presence of multiple cooperating queens as is often seen in honey bee colonies, and regularly seen in many other species of social insects. In fact, in many wasps, the differentiation between queen and worker is much more flexible.

The question of how sterile, cooperating insects could be produced by natural selection was a source of vexation to Charles Darwin. For a clear explanation of the dilemma and its resolution, I turned to Francis Ratnieks, one of the most knowledgeable researchers on honey bee matters and evolution. It is our good fortune that in November of 2010, he published an article titled "Darwin's special difficulty: the evolution of 'neuter insects.'" He relates that Darwin had an especially difficult time reconciling his nascent theory of evolution by natural selection with the presence of insects which developed characteristics that their parents did not appear to have. Further, as these offspring were sterile, there seemed to be no means for them to inherit or pass on their unusual features. Darwin himself confesses:

> [There is] one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory. I allude to the neuters or sterile females in insect communities: for these neuters often differ widely in instinct and in structure from both the males and fertile females, and yet, from being sterile, they cannot propagate their kind.

Dr. Ratnieks says that Darwin answered the question himself. He saw that if a species could produce sterile offspring that enhance the survival of their parents, then this would provide the impetus to do so. And being sterile, they would be compliant and not compete with the queen for domination.

With the advent of genomics, we can see the underlying mechanism that allows insects to pass the same genomes to their various daughters but enable the development of different forms. This includes queens, workers, and in the case of ants soldiers. One particular army ant, *Eciton burchellii*, has four worker castes.

Francis Ratnieks is Professor of Apiculture and head of the Laboratory of Apiculture & Social Insects at Sussex University. He obtained his PhD at Dyce Laboratory for Honey Bee Studies, Cornell University, and worked for the New York State Apiary Inspection Service and as a commercial beekeeper in California. He has studied honey bees on all continents, taught honey bee biology at 5 universities and published 250 articles on honey bees and social insects.

A Rich Bouquet

The honey bee colony is certainly one of the most successful of the social insects and its level of sophistication is incredible. It certainly does not seem to me that the question of queen control is anyway near to being settled. These disagreements notwithstanding, there is general consensus on the importance that chemicals have in the internal mechanisms of the honey bee colony function. As we have already pointed out, chemical communication is the most common method that plants and animals use to pass on information. Looking at the ways in which other organisms communicate by using scents and odors helps us to understand the range of information that can be transmitted by these means. Sandra Steiger studies the evolution of chemical communication at the Illinois State University. In her article published online in December of 2010, she states:

> Chemicals may merely indicate the presence or location of an individual, but because they are frequently very plastic and respond to many extrinsic (e.g. temperature and nutrition) and intrinsic (e.g. hormones and age) factors, they may inform about sex, health, reproductive state or dominance status.

It is hardly surprising that honey bees, which spend so much time among plants and their natural chemicals, would employ similar substances that pass through a network that quite nearly resembles an endocrine system. Through trophallaxis, these substances migrate throughout the colony so that the entire super organism can be kept up to date on a variety of important conditions, including that of the queen.

The Chemical Crown

Luke Holman, of the Department of Biology at the University of Copenhagen, aptly titles his recent article "Queen pheromones: The chemical crown governing insect social life." He states that insect queens organize the whole of colony life, including the hierarchical system of task allocation. And, they do this using chemicals. Especially important for this discussion is his proposal that queen pheromones are associated with the queen's reproductive output.

Work continues on the intriguing composition and function of the complex substances that the honey bee queen exudes. In addition to QMP, the queen mandibular pheromone, researchers have identified a mixture of nine chemicals which they have named QRP or queen retinue pheromone. This particular recipe seems to be associated with that familiar circle of bees that is often seen courting the queen. Alban Maisonnasse and colleagues have further expanded our knowledge with their 2010 report "New Insights Into Honey Bee Pheromone Communication." Interestingly, they do not take sides on the debate over whether the queen controls the worker population with pheromones or the workers simply respond as needed to support the colony and maintain their own fitness.

Quite clearly, the more we study the chemical structure of the signals, we see that it is hardly a simple matter of the queen signaling her presence or absence to which her offspring respond to either by suppressing the urge to reproduce, or nurturing her replacement. Following Maisonasse, et al, we read:

> In summary, each chemical may not be effective by itself, but altogether, they enable the queen to develop a complex and precise chemical "syntax" during the colony life cycle. In addition, worker behavior and physiology is regulated by multiple hormone signaling pathways (e.g. juvenile hormone, vitellogenin, insulin), so it is possible that the different but redundant queen chemicals each act on different targets of the worker hormonal system.

These chemicals control the amount of brood, the stages of development, and the raising of new queens, as well as males in the appropriate season. Also, her nestmates have a wide range of responses to these signals or cues, including their maturation, brain development and learning. Clearly, if

the urge to swarm originates with the queen, she has the system firmly in place to stimulate, initiate or even control the timing of swarm preparations, leading up to the final departure.

Passing the Inheritance

The queen's reproductive life mirrors that of solitary bees. Just like them   but using an army of helpers   she creates a nest, provisions it, raises her young, and ultimately abandons them to found families of their own. The queen, of course, is not a separate thing from her colony. The workers are raised by her to carry out the tasks that she is unable to perform, has no need to perform.

They are the ones that choose a suitable site for her new nest, direct the necessary work force to the new location, coordinate the building and provisioning of the nest, and defend it to the death, so that she doesn't have to do any of these things. Her strength is preserved and focused on two main tasks. She produces hundreds of thousands of eggs from which the workers are raised, as well as the next generation of queens and drones.

Mary Jane West-Eberhard's Reproductive Ground Plan

This hypothesis implies that these trait-correlations are signatures of a fundamental principle in social evolution: the segregation of queen and worker forms and subsequent division of labor between workers rely on evolutionary co-option of phases from the ancestral ovarian cycle.

And, she synthesizes the steady stream of substances that communicate her needs to the entire colony simultaneously.

I will describe colony life in this new light. As we know, a queen bee can live for several years. Upon birth she finds herself in a fully provisioned nest, surrounded by adoring workers who have already begun to forget their mother in order to lavish the same care and attention on her daughter. The young queen soon faces her most dangerous task. She must sail forth into the sky, looking for drones who will supply her with a lifetime supply of semen.

It is evidently in her best interest (and the best interests of her colony) to mate with a variety of drones, mostly completely unrelated to her. In this way, she may bring in a range of traits and talents, gathered from the colonies living in her immediate geographic vicinity. This will have the added benefit of allowing the bees of her area to adapt over time to its specific features. That is, they will coevolve with the native flora, tune their activities to the seasons and climate.

The New Year

In her second year, having repopulated the nest with her own offspring, she is in fine form to duplicate the process that created her in the first place. Probably the urge to swarm is one of those ancestral urges we all feel at times, the urge to create a life for our children and get out of their way. But, the conditions must be optimal.

The queen is faced with two equal perils: the risks of finding a new site suitable for herself and her colony, and the dangers of leaving her daughters unprotected against the vagaries of fate. Often the whole thing comes to ruin. The young queen may be lost on her mating flight, leaving the nest queenless and unable to raise another queen from the remaining brood. The swarm may be unable to find a suitable home, or may not have enough time to get it ready for winter, and so perish.

This conditional uncertainty more than adequately accounts for the fact that each colony seems to evaluate the appropriateness of swarming, choose the particular day to depart, or forgo this altogether until an other year. They, like us, are not privy to the future; quite often they misread the signs and plunge into disaster.

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