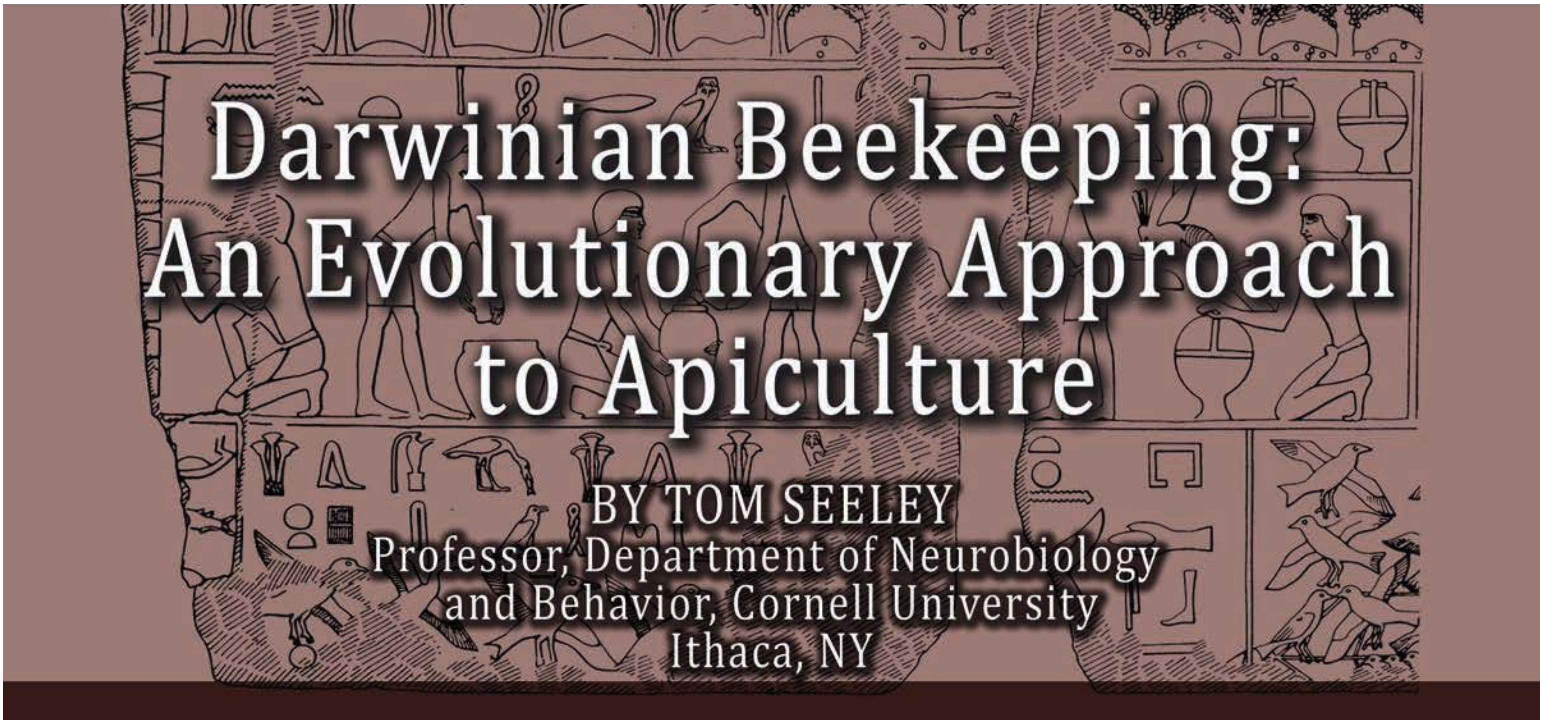

Darwinian Beekeeping: An Evolutionary Approach to Apiculture

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Evolution by natural selection is a foundational concept for understanding the biology of honey bees, but it has rarely been used to provide insights into the craft of beekeeping. This is unfortunate because solutions to the problems of beekeeping and bee health may come most rapidly if we are as attuned to the biologist Charles R. Darwin as we are to the Reverend Lorenzo L. Langstroth.

Adopting an evolutionary perspective on beekeeping may lead to better understanding about the maladies of our bees, and ultimately improve our beekeeping and the pleasure we get from our bees. An important first step toward developing a Darwinian perspective on beekeeping is to recognize that honey bees have a stunningly long evolutionary history, evident from the fossil record. One of the most beautiful of all insect fossils is that of a worker honey bee, in the species *Apis henshawi*, discovered in 30-million-year-old shales from Germany (Fig. 1). There also exist superb fossils of our modern honey bee species, *Apis mellifera*, in amber-like materials collected in East Africa that are about 1.6 million years old (Engel 1998).

We know, therefore, that honey bee colonies have experienced millions of years being shaped by the relentless operation of natural selection. Natural selection maximizes the abilities of living systems (such honey bee colonies) to pass on their genes to future generations. Colonies differ in their genes, therefore colonies differ in all the traits that have a genetic basis, including colony defensiveness, vigor in foraging, and resistance to diseases. The colonies best endowed with genes favoring colony survival and reproduction in their locale have the highest success in passing their genes on to subsequent generations, so over time the colonies in a region become well adapted to their environment.

This process of adaptation by natural selection produced the differences in worker bee color, morphology, and behavior that distinguish the 27 subspecies of *Apis mellifera* (e.g., *A.m. mellifera*, *A. m. ligustica*, and *A. m. scutellata*) that live within the species' original range of Europe, western Asia, and Africa (Ruttner 1988). The colonies in each subspecies are precisely adapted to the climate, seasons, flora, predators, and diseases in their region of the world.

Moreover, within the geographical range of each subspecies natural selection produced ecotypes, which are fine-tuned, locally adapted populations. For example, one ecotype of the subspecies *Apis mellifera mellifera* evolved in the Landes region of southwest France, with its biology tightly linked to the massive bloom of heather (*Calluna vulgaris* L.) in August and September. Colonies native to this region have a second strong peak of brood rearing in August that helps them exploit this heather bloom. Experiments have shown that the curious annual brood cycle of colonies in the Landes region is an adaptive, genetically based trait (Louveaux 1973, Strange et al. 2007).

Modern humans (*Homo sapiens*) are a recent evolutionary innovation compared to honey bees. We arose some 150,000 years ago in the African savannahs, where honey bees had already been living for aeons. The earliest humans were hunter gatherers who hunted honey bees for their honey, the most delicious of all natural foods. We certainly see an appetite for honey in one hunter-gatherer people still in existence, the Hadza of northern Tanzania. Hadza men spend 4-5 hours per day in bee hunting, and honey is their favorite food (Marlowe et al. 2014).

Bee hunting began to be superseded by beekeeping some 10,000 years ago, when people in several cultures started farming and began domesticating plants and animals. Two regions where this transformation in human history occurred are the alluvial plains of Mesopotamia and the Nile Delta. In both places, ancient hive beekeeping has been documented by archaeologists. Both are within the original distribution of *Apis mellifera*, and both have open habitats where swarms seeking a nest site probably had difficulty finding natural cavities and occupied the clay pots and grass baskets of the early farmers (Crane 1999).

In Egypt's sun temple of King Ne-user-re at Abu Ghorab, there is a stone bas-relief ca. 4400 years old that shows a beekeeper kneeling by a stack of nine cylindrical clay hives (Fig. 2). This is the earliest indication of hive beekeeping and it marks the start of our search for an optimal system of beekeeping. It also marks the start of managed colonies living in circumstances that differ markedly from the environment in which they evolved and to which they were adapted. Notice, for example, how the colonies in the hives depicted in the Egyptian bas-relief lived crowded together rather than spaced widely across the land.

WILD COLONIES VS. MANAGED COLONIES

Today there are considerable differences between the environment of evolutionary adaptation that shaped the biology of wild honey bee colonies and the current circumstances of managed honey bee colonies. Wild and managed live under different conditions because we beekeepers, like all farmers, modify the environments in which our livestock live to boost their productivity. Unfortunately, these changes in the living conditions of agricultural animals often make them more prone to pests and pathogens. In Table 1, I list 20 ways in which the living conditions of honey bees differ between wild and managed colonies, and I am sure you can think of still more.

Difference 1: Colonies are vs. are not genetically adapted to their locations. Each of the subspecies of *Apis mellifera* was adapted to the climate and flora of its geographic range and each ecotype within a subspecies was adapted to a particular environment. Shipping mated queens and moving colonies long distances for migratory beekeeping forces colonies to live where they may be poorly suited. A recent, large-scale experiment conducted in Europe found that colonies with queens of local origin lived longer than colonies with queens of non-local origin (Büchler et al. 2014).

Difference 2: Colonies live widely spaced across the landscape vs. crowded in apiaries. This difference makes beekeeping practical, but it also creates a fundamental change in the ecology of honey bees. Crowded colonies experience greater competition for forage, greater risk of being robbed, and greater problems reproducing (e.g., swarms combining and queens entering wrong hives after mating). Probably the most harmful consequence of crowding colonies, though, is boosting pathogen and parasite transmission between colonies (Seeley & Smith 2015). This facilitation of disease transmission boosts the incidence of disease and it keeps alive the virulent strains of the bees' disease agents.

Difference 3: Colonies live in relatively small nest cavities vs. in large hives. This difference also profoundly changes the ecology of honey bees. Colonies in large hives have the space to store huge honey crops but they also swarm less because they are not as space limited, which weakens natural selection for strong, healthy colonies since fewer colonies reproduce. Colonies kept in large hives also suffer greater problems with brood parasites such as *Varroa* (Loftus et al. 2015).

Difference 4: Colonies live with vs. without a nest envelope of antimicrobial plant resin. Living without a propolis envelope increases the cost of colony defense against pathogens. For example, workers in colonies without a propolis envelope invest more in costly immune system activity (i.e., synthesis of antimicrobial peptides) relative to workers in colonies with a propolis envelope (Borba et al. 2015).

Difference 5: Colonies have thick vs. thin nest cavity walls. This creates a difference in the energetic cost of colony thermoregulation, esp. in cold climates. The rate of heat loss for a wild colony living in a typical tree cavity is 4-7 times lower than for a managed colony living in a standard wooden hive (Mitchell 2016).

Difference 6: Colonies live with high and small vs. low and large entrances. This difference renders managed colonies more vulnerable to robbing and predation (large entrances are harder to guard), and it may lower their winter survival (low entrances get blocked by snow, preventing cleansing flights).

Difference 7: Colonies live with vs. without plentiful drone comb. Inhibiting colonies from rearing drones boosts their honey production (Seeley 2002) and slows reproduction by *Varroa* (Martin 1998), but it also hampers natural selection for colony health by preventing the healthiest colonies from passing on their genes (via drones) the most successfully.

Difference 8: Colonies live with vs. without a stable nest organization. Disruptions of nest organization for beekeeping may hinder colony functioning. In nature, honey bee colonies organize their nests with a pre-

Fig. 1. Photograph of a 30-million-year-old fossil of a worker honey bee in the species *Apis henshawi*. This worker is 0.55 inches long, so its size is close to that of workers in *Apis mellifera*. *Photo courtesy of Laurie Burnham.*

cise 3-D structure: compact broodnest surrounded by pollen stores and honey stored above (Montovan et al. 2013). Beekeeping practices that modify the nest organization, such as inserting empty combs to reduce congestion in the broodnest, hamper thermoregulation and may disrupt other aspects of colony functioning such as egg laying by the queen and pollen storage by foragers.

Difference 9: Colonies experience infrequent vs. sometimes frequent relocations. Whenever a colony is moved to a new location, as in migratory beekeeping, the foragers must relearn the landmarks around their hive and must discover new sources of nectar, pollen, and water. One study found that colonies moved overnight to a new location had smaller weight gains in the week following the move relative to control colonies already living in the location (Moeller 1975).

Difference 10: Colonies are rarely vs. frequently disturbed. We do not know how frequently wild colonies experience disturbances (e.g., bear attacks), but it is probably rarer than for managed colonies whose nests are easily cracked open, smoked, and manipulated. In one experiment, Taber (1963) compared the weight gains of colonies that were and were not inspected during a honey flow, and found that colonies that were inspected gained 20-30% less weight (depending on extent of disturbance) than control colonies on the day of the inspections.

Difference 11: Colonies do not vs. do deal with novel diseases. Historically, honey bee colonies dealt only with the parasites and pathogens with whom they had long been in an arms race. Therefore, they had evolved means of surviving with their agents of disease. We humans changed all this when we triggered the global spread of the ectoparasitic mite *Varroa destructor* from eastern Asia, small hive beetle (*Aethina tumida*) from sub-Saharan Africa, and chalkbrood fungus (*Ascosphaera apis*) and acarine mite (*Acarapis woodi*) from Europe. The spread of *Varroa* alone has resulted in the deaths of millions of honey bee colonies (Martin 2012).

Difference 12: Colonies have diverse vs. homogeneous food sources. Some managed colonies are placed in agricultural ecosystems (e.g., huge almond orchards or vast fields of oilseed rape) where they experience low diversity pollen diets and poorer nutrition. The effects of pollen diversity were studied by comparing nurse bees given diets with monofloral pollens or polyfloral pollens. Bees fed the polyfloral pollen lived longer than those fed the monofloral pollens (Di Pasquale et al. 2013).

Difference 13: Colonies have natural diets vs. sometimes being fed artificial diets. Some beekeepers feed their colonies protein supplements ("pollen substitutes") to stimulate colony growth before pollen is available, to fulfill pollination contracts and produce larger honey crops. The best pollen supplements/substitutes do stimulate brood rearing, though not as well as real pollen (http://scientificbeekeeping.com/a-comparative-test-of-the-pollen-sub/) and may result in workers of poorer quality (Scofield and Mattila 2015).

Difference 14: Colonies are not vs. are exposed to novel toxins. The most important new toxins of honey bees are insecticides and fungicides, substances for which the bees have not had time to evolve detoxification mechanisms. Honey bees are now exposed to an ever increasing list of pesticides and fungicides that can synergise to cause harm to bees (Mullin et al. 2010).

Difference 15: Colonies are not vs. are treated for diseases. When we treat our colonies for diseases, we interfere with the host-parasite arms race between *Apis mellifera* and its pathogens and parasites. Specifically, we weaken natural selection for disease resistance. It is no surprise that most managed colonies in North America and Europe possess little resistance to *Varroa* mites, or that there are populations of wild colonies on both continents that have evolved strong resistance to these mites (Locke 2016). Treating colonies with acaracides and antibiotics may also interfere with the microbiomes of a colony's bees (Engel et al. 2016).

Difference 16: Colonies are not vs. are managed as sources of pollen and honey. Colonies managed for honey production are housed in large hives, so they are more productive. However, they are also less apt to reproduce (swarm) so there is less scope for natural selection for healthy colonies. Also, the vast quantity of brood in large-hive colonies renders them vulnerable to population explosions of *Varroa* mites and other disease agents that reproduce in brood (Loftus et al. 2015).

Difference 17: Colonies do not vs. do suffer losses of beeswax. Removing beeswax from a colony imposes a serious energetic burden. The weight-to-weight efficiency of beeswax synthesis from sugar is at best

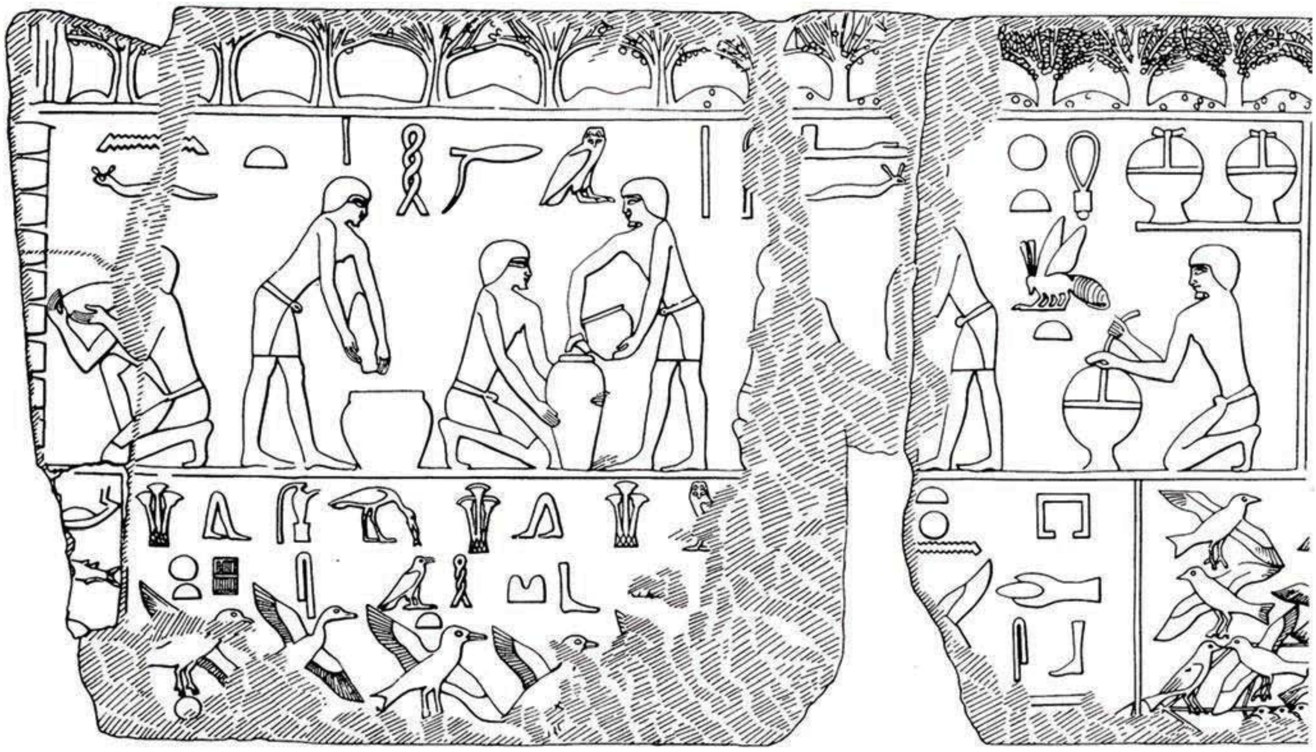

Fig. 2. Earliest known depiction of beekeeping and honey preparation, from the sun temple of King Ne-user-re, at Abu Ghorab, Egypt, built around 2400 BCE. Harvesting honey from a tall stack of cylindrical hives on the left, handling honey in the middle, and packing honey on the right. Drawing based on Fig. 20.3a in Crane (1999).

	Environment of evolutionary adaptedness	Current circumstances
1.	Colonies genetically adapted to location	Colonies not genetically adapted to location
2.	Colonies live widely spaced in landscape	Colonies live crowded in apiaries
3.	Colonies occupy small (ca 1.5 cu ft) cavities	Colonies occupy large (ca. 3+ cu ft) hives
4.	Nest cavity walls have a propolis coating	Hive walls have no propolis coating
5.	Nest cavity walls are thick (ca. 4+ in)	Hive walls are thin (ca. 3/4 in)
6.	Nest entrance is high & small (ca. 4 sq in)	Nest entrance is low & large (ca. 12 sq in)
7.	Nest has 10-25% drone comb	Nest has little (< 5%) drone comb
8.	Nest organization is stable	Nest organization is often altered
9.	Nest-site relocations are rare	Hive relocations can be frequent
10.	Colonies are rarely disturbed	Colonies are frequently disturbed
11.	Colonies deal with familiar diseases	Colonies deal with novel diseases
12.	Colonies have diverse pollen sources	Colonies have homogeneous pollen sources
13.	Colonies have natural diets	Colonies sometimes have artificial diets
14.	Colonies are not exposed to novel toxins	Colonies exposed to insecticides & fungicides
15.	Colonies are not treated for diseases	Colonies are treated for diseases
16.	Pollen not trapped, honey not taken	Pollen sometimes trapped, honey often taken
17.	Beeswax is not removed	Beeswax is removed during honey harvests
18.	Bees choose larvae for queen rearing	Beekeepers choose larvae for queen rearing
19.	Drones compete fiercely for mating	Queen breeder may select drones for mating
20.	Drone brood not removed for mite control	Drone brood sometimes removed and frozen

Table 1. Comparison of the environments in which honey bee colonies lived (and sometimes still do) as wild colonies and those in which they live currently as managed colonies.

about 0.10 (data of Weiss 1965, analyzed in Hepburn 1986), so every pound of wax taken from a colony costs it some 10 pounds of honey that is not available for other purposes, such as winter survival. The most energetically burdensome way of harvesting honey is removal of entire combs filled with honey (e.g., cut comb honey and crushed comb honey). It is less burdensome to produce extracted honey since this removes just the cappings wax.

Difference 18: Colonies are vs. are not choosing the larvae used for rearing queens. When we graft day-old larvae into artificial queen cups during queen rearing, we prevent the bees from choosing which larvae will develop into queens. One study found that in emergency queen rearing the bees do not choose larvae at random and instead favor those of certain patrilines (Moritz et al. 2005).

Difference 19: Drones are vs. are not allowed to compete fiercely for mating. In bee breeding programs that use artificial insemination, the drones that provide sperm do not have to prove their vigor by competing amongst other drones for mating. This weakens the sexual selection for drones that possess genes for health and strength.

Difference 20: Drone brood is not vs. is removed from colonies for mite control. The practice of removing drone brood from colonies to control *Varroa destructor* partially castrates colonies and so interferes with natural selection for colonies that are healthy enough to invest heavily in drone production.

SUGGESTIONS FOR DARWINIAN BEEKEEPING

Beekeeping looks different from an evolutionary perspective. We see that colonies of honey bees lived independently from humans for millions of years, and during this time they were shaped by natural selection to be skilled at surviving and reproducing wherever they lived, in Europe, western Asia, or Africa. We also see that ever since humans started keeping bees in hives, we have been disrupting the exquisite fit that once existed between honey bee colonies and their environments. We've done this in two ways: 1) by moving colonies to geographical locations to which they are not well adapted, and 2) by managing colonies in ways that interfere with their lives but that provide us with honey, beeswax, propolis, pollen, royal jelly, and pollination services.

What can we do, as beekeepers, to help honey bee colonies live with a better fit to their environment, and thereby live with less stress and better health? The answer to this question depends greatly on how many colonies you manage, and what you want from your bees. A beekeeper who has a few colonies and low expectations for honey crops, for example, is in a vastly different situation than a beekeeper who has thousands of colonies and is earning a living through beekeeping.

For those interested, I offer 10 suggestions for bee-friendly beekeeping. Some have general application while others are feasible only for the backyard beekeeper.

1. *Work with bees that are adapted to your location*. For example, if you live in New England, buy queens and nucs produced up north rather than queens and packages shipped up from the south. Or, if you live in a location where there are few beekeepers, use bait hives to capture swarms from the wild colonies living in your area. (Incidentally, these swarms will build you beautiful new combs, and this will enable you to retire old combs that could have heavy loads of pesticide residues and pathogen spores/cells.) The key thing is to acquire queens of a stock that is adapted to your climate.
2. *Space your hives as widely as possible*. Where I live, in central New York State, there are vast forests filled with wild honey bee colonies spaced roughly a half mile apart. This is perhaps ideal for wild colonies but problematic for the beekeeper. Still, spacing colonies just 30-50 yards apart in an apiary greatly reduces drifting and thus the spread of disease.
3. *House your bees in small hives*. Consider using just one deep hive body for a broodnest and one medium-depth super over a queen excluder for honey. You won't harvest as much honey, but you will likely have reduced disease and pest problems, particularly *Varroa*. And yes, your colonies will swarm, but swarming is natural and research shows that it promotes colony health by helping keep *Varroa* mite populations at safe levels (see Loftus et al 2015).
4. *Roughen the inner walls of your hives, or build them of rough-sawn lumber*. This will stimulate your colonies to coat the interior surfaces of their hives with propolis, thereby creating antimicrobial envelopes around their nests.
5. *Use hives whose walls provide good insulation*. These might be hives built of thick lumber, or they might be hives made of plastic foam. We urgently need research on how much insulation is best for colonies in different climates, and how it is best provided.
6. *Position hives high off the ground*. This is not always doable, but if you have a porch or deck where you can position some hives, then perhaps it is feasible. We urgently need research on how much entrance height is best in different climates.
7. *Let 10-20% of the comb in your hives be drone comb*. Giving your colonies the opportunity to rear drones can help improve the genetics in your

area. Drones are costly, so it is only the strongest and healthiest colonies that can afford to produce legions of drones. Unfortunately, drone brood also fosters rapid growth of a colony's population of *Varroa* mites, so providing plentiful drone comb requires careful monitoring of the *Varroa* levels in your hives (see suggestion 10, below).

8. *Minimize disturbances of nest structure*. When working a colony, replace each frame in its original position and orientation. Also, avoid inserting empty frames in the broodnest to inhibit swarming.

9. *Minimize relocations of hives*. Move colonies as rarely as possible. If you must do so, then do so when there is little forage available.

10. *Refrain from treating colonies for Varroa*. WARNING: This last suggestion should only be adopted if you can do so carefully, as part of a program of extremely diligent beekeeping. If you pursue treatment-free beekeeping without close attention to your colonies, then you will create a situation in your apiary in which natural selection is favoring virulent *Varroa* mites, not *Varroa*-resistant bees. To help natural selection favor *Varroa*-resistant bees, you will need to monitor closely the mite levels in all your colonies and kill those whose mite populations are skyrocketing long before these colonies can collapse. By preemptively killing your *Varroa*-susceptible colonies, you will accomplish two important things: 1) you will eliminate your colonies that lack *Varroa* resistance and 2) you will prevent the "mite bomb" phenomenon of mites spreading en masse to your other colonies. If you don't perform these preemptive killings, then even your most resistant colonies could become overrun with mites and die, which means that there will be no natural selection for mite resistance in your apiary. Failure to perform preemptive killings can also spread virulent mites to your neighbors' colonies and even to the wild colonies in your area that are slowly evolving resistance on their own. If you are not willing to kill your mite-susceptible colonies, then you will need to treat them and requeen them with a queen of mite-resistant stock.

TWO HOPES

I hope you have found it useful to think about beekeeping from an evolutionary perspective. If you are interested in pursuing beekeeping in a way that is centered less on treating a bee colony as a honey factory, and more on nurturing the lives of honey bees, then I encourage you to consider what I call Darwinian Beekeeping. Others call it Natural Beekeeping, Apicentric Beekeeping, and Bee-friendly Beekeeping (Phipps 2016). Whatever the name, its practitioners view a honey bee colony as a complex bundle of adaptations shaped by natural selection to maximize a colony's survival and reproduction in competition with other colonies and other organisms (predators, parasites, and pathogens). It seeks to foster colony health by letting the bees live as naturally as possible, so they can make full use of the toolkit of adaptations that they have acquired over the last 30 million years. Much remains to be learned about this toolkit—How exactly do colonies benefit from better nest insulation? Do colonies tightly seal their nests with propolis in autumn to have an in-hive water supply (condensate) over winter? How exactly do colonies benefit from having a high nest entrance? The methods of Darwinian Beekeeping are still being developed, but fortunately, apicultural research is starting to embrace a Darwinian perspective (Neumann and Blacquiere 2016).

I hope too that you will consider giving Darwinian Beekeeping a try, for you might find it more enjoyable than conventional beekeeping, especially if you are a small-scale beekeeper. Everything is done with bee-friendly intentions and in ways that harmonize with the natural history of *Apis mellifera*. As someone who has devoted his scientific career to investigating the marvelous inner workings of honey bee colonies, it saddens me to see how profoundly—and ever increasingly—conventional beekeeping disrupts and endangers the lives of colonies. Darwinian Beekeeping, which integrates respecting the bees and using them for practical purposes, seems to me like a good way to be responsible keepers of these small creatures, our greatest friends among the insects.

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