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Original article

Honey bees of the Arnot Forest: a population of feral colonies persisting with *Varroa destructor* in the northeastern United States*

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Abstract – Feral colonies of European honey bees living in the Arnot Forest, a 1651-ha research preserve in New York State, were studied over a three-year period, 2002 to 2005. This population of colonies was previously censused in 1978. A census in 2002 revealed as many colonies as before, even though *Varroa destructor* was introduced to North America in the intervening years. Most colonies located in fall 2002 were still alive in fall 2005. The Arnot Forest colonies proved to be infested with *V. destructor*, but their mite populations did not surge to high levels in late summer. To see if Arnot Forest bees can suppress the reproduction rate of mites, colonies of Arnot Forest bees and New World Carniolan bees were inoculated with mites from an apiary and the growth patterns of their mite populations were compared. No difference was found between the two colony types. Evidently, the stable bee-mite relationship in the Arnot Forest reflects adaptations for parasite (mite) avirulence, not host (bee) resistance.

***Apis mellifera* / *Varroa destructor* / host-parasite relationship / tolerance / avirulence**

1. INTRODUCTION

The mite *Varroa destructor* is a new parasite of European honey bees living in North America, having been introduced to these bees only in the mid 1980s (Wenner and Bushing, 1996; Sanford, 2001). It is also a virulent parasite. As a rule, if a colony of European honey bees does not receive mite control treatments, the mite population will grow from just a few mites to several thousand mites in three to four years, ultimately killing the colony (Ritter, 1988; Korpela, et al., 1992; Wenner and Thorp, 2002). It seems that there is little opportunity for the evolution of a stable host-parasite relationship in areas where the population of colonies consists primarily of colonies managed by beekeepers. This is partly because beekeepers control mite populations to avoid loss of colonies, thereby preventing selection for *V. destructor*-tolerant bees, and partly because beekeepers manage their bees in ways (e.g. crowding colonies into apiaries, transferring combs of bees and brood between colonies, and preventing swarming) that promote the horizontal transmission of the mites between colonies. Virulence theory suggests that horizontal transmission, defined as infectious transfer among unrelated hosts, promotes the evolution of virulent parasites by favoring those that strongly (and thus harmfully) reproduce in current hosts before moving on to new hosts (Ewald, 1983; Bull, 1994).

One might expect, however, the evolution of a balanced host-parasite relationship in areas with little or no beekeeping, hence where the population of colonies is mostly feral (Mobus and de Bruyn, 1993). Here there will be little or no control of the mites, allowing selection for *V. destructor*-tolerant bees, and

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there will mainly vertical transmission of the mites between colonies. Virulence theory suggests that vertical transmission, in which parasites are passed from host parent to offspring, promotes the evolution of avirulent parasites because the reproduction of the parasites is linked to that of their hosts. There are strong indications that a balanced host-parasite relationship, in which both bees and mites survive, has evolved in isolated populations living under feral or feral-like conditions in several locations (Tunisia: Ritter et al., 1990; Austria: Ruttner, 1991; Büchler, 1994; Brazil: de Jong and Soares, 1997, United States: Wenner and Thorp, 2002; Sweden: Fries et al., 2006). There is also evidence that in these populations the bees have evolved resistance mechanisms (Boecking and Ritter, 1993) and/or the mites have evolved reduced reproduction (Milani et al., 1999). However, the extent to which these stable host-parasite relationships reflect adaptations for host resistance or parasite avirulence, or both, remains uncertain.

This paper reports a three-year study (fall 2002 to fall 2005) of a feral population of honey bee colonies living in the Arnot Forest, a research preserve near Ithaca, New York State. This population was previously censused in 1978, prior to the introduction of *V. destructor* to North America (Visscher and Seeley, 1982). The current study had four goals: (1) to determine whether feral colonies remain abundant in the Arnot Forest; (2) to determine if the colonies in this population are infested with *V. destructor*; (3) to determine if the colonies in this population are long-lived despite being infested with *V. destructor*; and (4) if they are long-lived with *V. destructor*, then to determine how they have achieved a stable host-parasite relationship.

2. MATERIALS AND METHODS

2.1. Study site

The feral bee population of interest lives in the Arnot Forest (42°17’N, 76°39’W, altitude 585 m), a 1651-ha research preserve owned by Cornell University, outside the town of Cayuta, Schuyler County, New York State, USA. Most of this preserve is forested, with forest types ranging from young old-field successional forest to mature hardwood forest, with the latter predominant (see Fig. 1 in Odell et al., 1980). Most of the surrounding land is also mature hardwood forest, as it consists largely of protected forests owned by New York State (see Fig. 1 in Visscher and Seeley, 1982). When the study began in the fall of 2002, there were no known hives of bees within 3 km of the boundary of the Arnot Forest, but in the summer of 2004 one beekeeper established a small apiary with eight hives along Cayuta Creek, 1 km from the forest’s southern boundary.

2.2. Locating feral colonies in trees

During the fall of 2002, I located all the feral bee colonies within the western two-thirds of the Arnot Forest. Using a modification of beelining techniques (Edgell, 1949; Visscher and Seeley, 1989), I captured foraging bees, fed them scented 2.5-mol/L sucrose syrup from a piece of old comb, and then released them to fly home. Usually some bees would eventually return to the feeding station, recruiting nestmates as well. Once bees were well oriented to the feeding station, they would leave in a beeline homeward, and I would record the vanishing bearings for these bees; these bearings indicated the approximate direction of the bee’s nest in a tree (“bee tree”). The distance to the nest could be estimated from the minimum round-trip times of individually marked bees.

To census the colonies, I systematically initiated beelines from feeding stations (Fig. 2, 1–12) located in open areas spaced throughout the western half of the forest, generally < 1 km apart. At a single feeding station, I often initiated beelines from multiple colonies. Once the beelines were established, foragers at the feeder were again trapped, and carried along one of the beelines to another clearing. Here the bees were released, and their vanishing bearings again noted. By repeating such moves, the tree that the colony inhabited could be located. The census appears to have been exhaustive for the western two-thirds of the Arnot Forest (time limitations prevented censusing the entire forest). Bees from all eight colonies (Fig. 2, A–H) were captured at 3.0 ± 0.4 locations in the forest, and this redundancy reassured me that there were not colonies in the western half of the forest whose members I did not capture.

All colonies were inspected for life each year with inspections made around May 1, June 15, and October 1. Bees flying around a nest entrance do

Figure 1. One of five bait hives installed in trees in the Arnot Forest to attract swarms and so provide feral colonies living in movable-frame hives. Installation shown is typical: hive mounted some 4 m off the ground and with entrance opening reduced to 16 cm^2 and oriented to south.

not by themselves indicate a living colony within – they could be robber bees or scout bees, plundering or inspecting the nest of a dead colony – so I used the criterion of the presence of pollen foragers as my indicator of a live colony. The nests of colonies that had died were kept in the inspection program to provide data on the occurrence of nest reoccupation. The May 1 inspection preceded the swarming season for the Ithaca area (Fell et al., 1977), so all colonies alive at that time were assumed to have survived the winter. The mid-June inspection served to check for late spring mortality among colonies that survived winter. The October 1 inspection provided data on nest reoccupation and colony survivorship for the preceding summer. A prior study of the demography of feral colonies in central New York State (Seeley, 1978) found that 98% of colony mortality occurred during winter, so it is highly likely that each bee tree colony that was found alive in May and June and again in October was alive all summer (i.e., did not die out and then get reoccupied).

2.3. Establishing feral colonies in hives and monitoring mite levels

To accurately measure the mite levels in feral colonies in the Arnot Forest, I needed to have feral colonies living in movable-frame hives. To acquire such colonies, during the summer of 2003 I mounted a hive in a tree in each of five locations (near sites 1, 2, 5, 7, and 10 in Fig. 2) and waited for swarms to occupy them. Each hive consisted

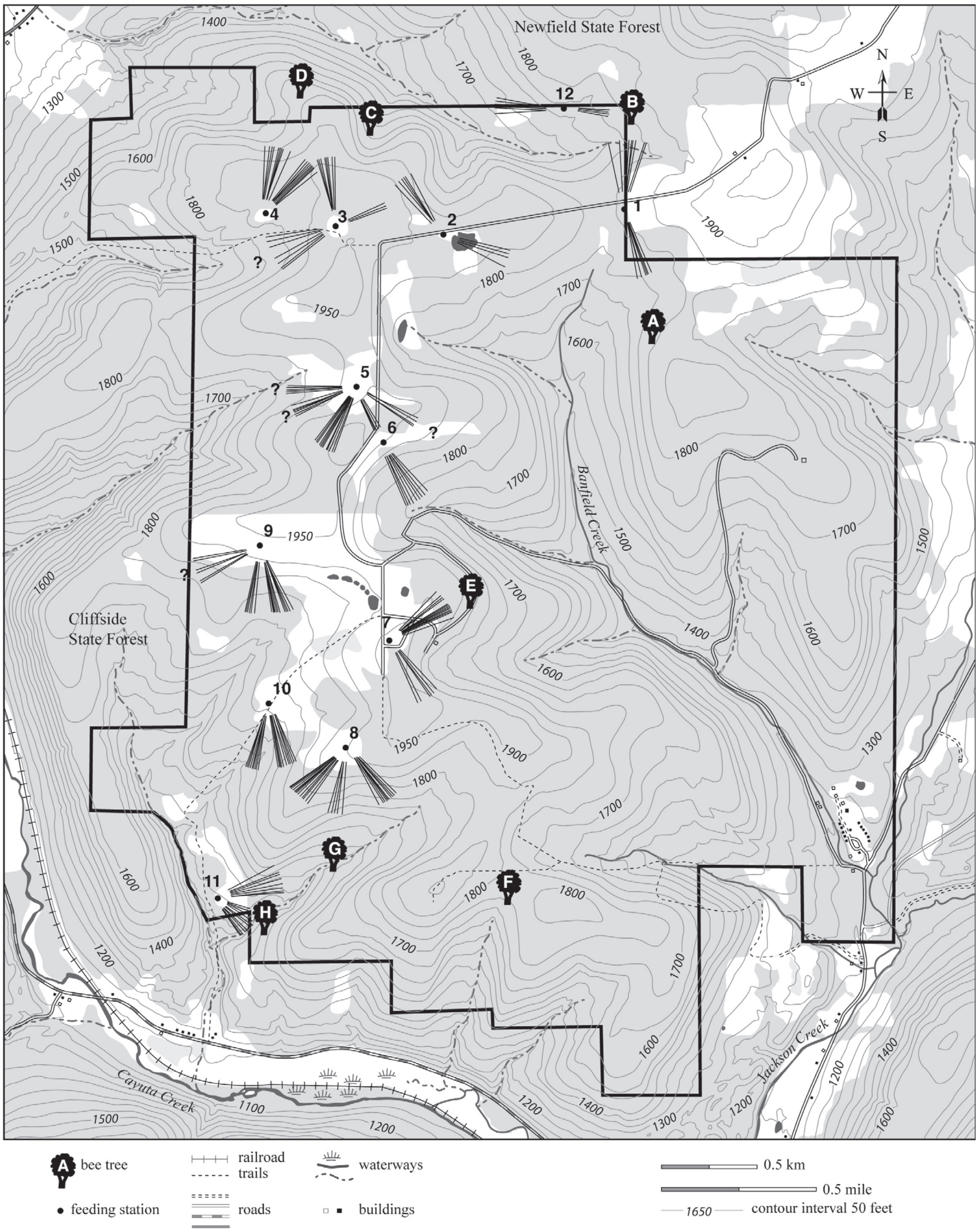

Figure 2. Map of the Arnot Forest. Shown are the locations of the bee trees (8) and of the feeding stations (12) used to establish beelines that led to the bee trees. Feeding stations are numbered in order of use. The lines radiating from each feeding station depict vanishing bearings of bees leaving the station. Note that most of these lines occur in clusters which point toward identified bee trees; the clusters that do not are marked with question marks. Grey areas denote forested land and white areas denote cleared land.

of a single, deep Langstroth hive body filled with eight frames of old worker comb and two frames of old drone comb (placed in the #2 and #9 positions in the hive). Thus each hive contained a typical amount of worker comb and drone comb and had the drone comb positioned in its typical location, toward the edge of the nest (Seeley and Morse, 1976). I placed a Dadant Varroa Screen (Dadant and Sons, Inc., Hamilton, Illinois, USA) between the bottom board and hive body of each hive, so that I could later place a sticky board for catching mites inside each hive without disturbing the colony. As shown in Figure 1, the entrance of each hive consisted of an opening that was 2 cm high × 8 cm wide, faced south, and was located 3.9–4.6 m off the ground. Hives configured in this manner match the nest-site preferences of European honey bees (Seeley and Morse, 1978) and are highly attractive to swarms (Morse and Seeley, 1979). These bait hives were set up in early May, 2003, hence before the start of the swarm season.

Each hive was inspected at the start of each month to see if it had been occupied by a swarm. Once a hive was occupied, I began making monthly readings of the mite population in the resident colony by counting the mites caught on a sticky board placed on the hive's bottom board (Webster, 2001). At the start of each month, I inserted a sticky board (Varroa Mite Trap, Phero Tech, Inc., Delta, British Columbia, Canada) into each hive, left it there for 48 hours, and then removed it and counted the number of mites that had fallen onto and become trapped on the sticky board. No acaricide was applied.

2.4. Comparing Arnot Forest and New World Carniolan bees for *V. destructor* resistance

I wished to see if colonies of Arnot Forest bees were resistant to *V. destructor* mites, i.e., were able to inhibit the growth of their mite populations. To do so, in the summer of 2005, I set up in the vicinity of the Liddell Field Station of Cornell University in Ithaca, NY, six pairs of matched colonies in which one colony was headed by an Arnot Forest (AF) queen and one was headed by a New World Carniolan (NWC) queen. I inoculated each colony with the same number of mites from the same source, and then made a monthly reading of the mite population in each colony. I reasoned that if bees in AF colonies can inhibit the growth of mite populations, then the colony mite counts of the AF bees should be lower than those of the NWC bees.

The six AF queens were produced from one of the Arnot Forest colonies that had moved into a bait hive in 2003 (colony 2 in Tab. I). This colony was removed from the forest in mid-October 2004, in preparation for rearing queens from it in the summer of 2005. The colony swarmed in mid June 2005, just before larvae were to be grafted from it for queen rearing. Fortunately, it contained numerous queen cells, so I was able to divide it to create six small colonies, each containing at least two capped queen cells. These "mating nucs" were moved back to the Arnot Forest, so that each colony's virgin queen would be apt to mate with drones from feral colonies there. By the end of June, all six colonies contained a mated and laying AF queen. Meanwhile, I had obtained six naturally-mated NWC queens that were sisters (Strachan Apiaries, Yuba City, California, USA) and had installed each one in a small colony, the same size as the mating nucs housing the AF queens, so that the NWC queens would be laying at the start of the experiment. All the queens were given paint marks to ensure that any supersedure queens could be identified.

On 1 July 2005, I established the six pairs of experimental colonies. Within each pair, both colonies were created by taking one frame of bees and brood, one frame of bees and food (pollen and honey), and one frame of honey from one of the strong "stock" colonies in the apiary at the Liddell Field Station and placing these three frames in a hive with seven more frames of empty, drawn comb. None of the ten frames contained drone comb. Thus, both colonies in each pair started out with approximately the same number of bees from the same source and with approximately the same number of mites from the same source. (Note: the bees and mites for each pair of colonies came from a different stock colony; these six different stock colonies were unrelated.) The exact number of mites that each colony received is unknown. Both colonies in each pair were then moved together to one of six locations in the vicinity of the Liddell Field Station; these locations were some 50 km from the Arnot Forest and were at least 5 km from each other. At each location, the colonies were placed at least 10 m apart to minimize drifting of bees and were given a caged queen, either one of the AF queens or one of the NWC queens. An inspection of the colonies on 5 July revealed that the queen in each had been released from her cage and had begun laying eggs.

Two weeks later, on 15 July, I started a series of monthly assays of the mite populations in each hive, using the 48-hour mite drop method described above. Each of the hives used in this experiment was equipped with a Dadant Varroa Screen between hive body and bottom board so that I could insert and remove a sticky board without disturbing the colony. These colonies received no treatments with acaricides. Mite assays were made on 15–17 July, 12–14 August, 16–18 September, and 16–18 October. After each of these mite assays, each colony was inspected for queen turnover; the final round of inspections in mid-October 2005 revealed that each colony still had its original AF or NWC queen. Also, near the end of August, by which time virtually all the adult bees and certainly all the immature bees in each hive were the offspring of the AF or NWC queen, each colony was examined to determine the number of frames covered by adult bees and the number of frames filled with brood.

3. RESULTS

3.1. Feral colonies still exist in the Arnot Forest

Between 20 August and 30 September 2002, I bee hunted in the Arnot Forest for 117 hours spread over 27 days, during which time I started beelines from 12 feeding stations in clearings spread over about two-thirds of the forest (Fig. 2). This work revealed eight colonies living in trees. It should be noted that only four of the 29 beelines pointed out of the Arnot Forest: just those pointing west into the adjacent Cliffside State Forest, from feeding stations 3, 5, and 9. This indicates that few, if any, managed colonies in hives were living just outside the boundary of the Arnot Forest.

3.2. The Arnot Forest colonies are infested with *V. destructor*

Three of the five bait hives set up in the Arnot Forest were occupied in the summer of 2003, sometime between 30 June and 31 July. It is likely that the swarms occupying these bait hives came from feral colonies living in trees because each of the three occupied bait hives (located near sites 2, 5, and 7 in Fig. 2) was surrounded by forest for more than 2 km, and prior work has shown that most (86%) swarms travel less than 2 km to reach a new home site (see Fig. 1 in Seeley and Morse, 1977).

Table I. Monthly assays of mite populations in feral colonies living in hives in the Arnot Forest. Each assay is the number of mites that dropped onto a sticky board over a 48-h period at the start of the month indicated.

Date	Colony 1	Colony 2	Colony 3
August 2003	30	14	21
September 2003	16	21	39
October 2003	36	3	22
May 2004	2	2	1
June 2004	3	11	2
July 2004	2	10	4
August 2004	3	5	7
September 2004	16	15	13
October 2004	42	40	22

Following the bait hive occupations in the summer of 2003, and throughout the summer of 2004, I took monthly readings of the mite population in each colony by counting the mites that fell onto a sticky board over 48 h. All three colonies were infested with *V. destructor* mites, evidently from the times they moved into the hives (Tab. I). We also see that the population of mites in each colony was rather stable during the summer of 2003, dropped markedly over the winter of 2003–2004, and increased only slowly and gradually over the summer of 2004.

There are no data for 2005 because one of the colonies (colony 2) was removed from the forest in mid-October 2004 to provide larvae for future queen rearing, and the other two colonies were destroyed by black bears (*Ursus americanus*) sometime between the last check of the colonies in 2004 (in mid-October) and the first check in 2005 (in mid-April).

All three feral colonies in hives were inspected internally toward the end of the summer in 2003 (on 4 September) and again in 2004 (on 29 August). Both years, the inspections revealed that all three colonies were strong and healthy with adult bees covering all ten frames, brood in three to six

Table II. Fates of the feral colonies living in trees in the Arnot Forest. Each bee tree was inspected at least three times a year, around 1 May, 15 June, and 1 October.

Date	Colonies alive	Notes
Oct 2002	8	8 colonies found by bee lining
May 2003	6	2 colonies died over winter
June 2003	6	0 colonies died in late spring
Oct 2003	6	2 empty bee trees were not reoccupied
May 2004	5	1 colony died over winter (tree toppled)
June 2004	5	0 colonies died in late spring
Oct 2004	6	1 empty bee tree reoccupied
May 2005	6	0 colonies died over winter
June 2005	6	0 colonies died in late spring
Oct 2005	7	1 empty bee tree reoccupied

frames (including frames with drone comb), and honey filling several frames.

3.3. The Arnot Forest colonies are persisting with *V. destructor*

Table II summarizes the information about the fates of the feral colonies living in trees over the three-year period of fall 2002 to fall 2005. We see that five of the eight colonies found in the fall of 2002 were still alive in the fall of 2005. Regarding the three colonies that died during the three-year period, two perished in the winter of 2002–2003 (cause of deaths is unknown) and one perished in the winter of 2003–2004 (a gale in early October 2003 toppled the tree housing the colony). The two intact but empty bee trees were eventually reoccupied by swarms, one in 2004 and one in 2005. Thus this population of feral colonies remained essentially stable over three years, with a net loss of just one colony due to the natural destruction of a nesting site.

3.4. The Arnot Forest bees are not inhibiting *V. destructor* population growth

There are no signs that colonies of Arnot Forest bees, relative to those of New World Carniolan bees, are better at limiting the population growth of *V. destructor* mites. As is shown in Figure 3, the monthly mite-drop counts indicate that both colonies in each pair were initially infested with similar levels of mites and that their mite populations increased markedly over the summer (except in the NWC colony in pair B). Furthermore, we

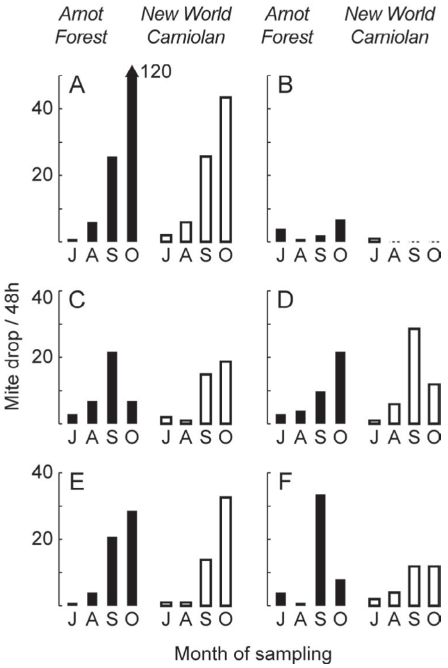

Figure 3. Results of the monthly assays of the mite populations in six pairs (A–F) of colonies, with each pair containing one Arnot Forest colony and one New World Carniolan colony. Changes in the mite population of each colony were monitored by counting the mites that dropped onto a sticky board over 48 h. Sampling dates: mid-month in July (J), August (A), September (S), and October (O).

Table III. Strength comparisons of the colonies headed by Arnot Forest (AF) or New World Carniolan (NWC) queens. Measurements were made on 26 August 2005. *P*-values are based on paired-comparison *t* tests of significance of the differences between treatment means.

	Frames of adult bees		Frames of brood	
Colony pair	AF	NWC	AF	NWC
A	7	7	5	3.5
B	5	4	4	3.5
C	7	6	5	4.5
D	5.5	3.5	4.5	3
E	5	7	4	5
F	6	6	4	4
Mean	5.92	5.58	4.42	3.92
SD	0.92	1.50	0.49	0.74
P		> 0.58		> 0.26

see that each month the mite-drop counts were similar for the two types of colonies. Paired-comparison *t* tests of significance of the difference between the mean mite-drop counts for AF and NWC colonies confirmed a lack of difference in each month: July: $t_5 = 1.37$, $P > 0.23$; August: $t_5 = 0.62$, $P > 0.57$; September: $t_5 = 0.58$, $P > 0.59$; October: $t_5 = 0.92$, $P > 0.41$). As is shown in Table III, measurements taken at the end of August, by which time virtually all the bees in each experimental colony were the offspring of its AF or NWC queen, indicate that both colonies in all six pairs were queenright. These measurements also reveal that all the colonies, though still quite small, having been established with just two frames of bees on 1 July, were well stocked with bees and brood. The two types of colonies were similar in strength (frames of bees, Student's *t* test: $t_5 = 0.60$, $P > 0.58$; frames of brood, Student's *t* test: $t_5 = 1.29$, $P > 0.26$).

4. DISCUSSION

It is generally believed, probably correctly, that the introduction of *Varroa destructor* in the mid-1980s has all but wiped out the feral populations of European honey bees in North America (Sanford, 2001; Wenner and Bushing, 1996). Nevertheless, it is now clear that a feral population of these bees, infested with *V. destructor*, persists in the Arnot Forest in New York State. Indeed, there as many, if not more, feral colonies living in this forest now as when they were censused 24 years earlier in 1978, hence long before the arrival of *V. destructor* (Visscher and Seeley, 1982). In the previous survey covering the entire Arnot Forest, nine feral colonies were found, whereas in the present survey covering only the western two-thirds of the forest, eight feral colonies were found. It should be noted that both the 1978 and the 2002 census were made by the same person (the author) in the same season (mid-August to late September) and in the same way (by bee lining), so it is meaningful to compare their results.

The population of European honey bees surviving in the Arnot Forest is probably not unique. Anecdotal reports suggest that feral populations of European honey bees also exist in other areas of North America where there are few colonies kept by beekeepers (Wenner and Thorp, 2002). Certainly the cases of European honey bees surviving mite infestations without acaricide treatments on isolated islands in Brazil (De Jong and Soares, 1997) and Sweden (Fries et al. in press) shows that European honey bees have the potential to develop a stable host-parasite relationship with *V. destructor*.

What is particularly intriguing about the colonies living in the Arnot Forest is that many of them (five out of the original eight colonies living in trees) have survived for more than three years even though *V. destructor* probably infests every colony living in this forest (all three swarms that occupied the bait hives came infested with the mites). The long-term survival of these colonies begs the question: how are they surviving with *V. destructor*?

There are several possible answers. One is that these bees have evolved mechanisms of resistance to the mites, such as grooming of phoretic mites off adult bees, hygienic behavior that removes worker brood infested with mites, or inhibition of mite reproduction on worker brood (reviewed by Boecking and Spivak, 1999; Rosenkranz, 1999). The hypothesis that bees have evolved resistance mechanisms was tested by setting up pairs of colonies headed by Arnot Forest (AF) and

New World Carniolan (NWC) queens, seeding both colonies in each pair with mites from the same source colony, and comparing the growth patterns of the mite populations in the paired colonies. If the AF bees have evolved resistance, then the AF colonies in this experiment should have had slower mite population growth than the NWC colonies. This prediction was not supported. The mite populations grew as briskly in the AF colonies as in the NWC colonies. (Note: the mite drop counts shown in Fig. 3 are low not because the mites were reproducing slowly in the AF and NWC colonies, but because these colonies were small, each with only about 6 frames of bees; see Tab. III.) It looks, therefore, rather doubtful that the Arnot Forest bees have evolved mechanisms of resistance to *V. destructor* mites.

A second possible explanation for the long-term survival of the *V. destructor* infested but untreated Arnot Forest colonies is that the mites have evolved avirulence, that is, reduced reproduction. Avirulence is predicted to evolve in parasites which undergo vertical (parent to offspring) rather than horizontal (infectious spread) transmission (Ewald, 1983; Bull, 1994). This is because the vertical transmission of parasites favors ones that leave the host healthy enough to produce offspring. Vertical transmission of *V. destructor* mites will occur when an infested honey bee colony swarms and so creates an offspring colony also infested with the mites. Horizontal transmission, however, will occur when infested workers drift into uninfested colonies or when uninfested workers rob a weak colony containing mites and then bring them home. In the Arnot Forest, where the colonies are living in forest trees separated by hundreds, if not thousands, of meters (see Fig. 2), drifting of bees between colonies is most unlikely and robbing may also be exceedingly rare. If so, then we can expect avirulence to have evolved in the *V. destructor* mites in the Arnot Forest, especially if the bees/mites living there are largely isolated from bees/mites in colonies being managed by beekeepers, which is probably the case. At present, however, there is no direct evidence of reduced reproduction by the *V. destructor* mites in the Arnot Forest, though this hypothesis is indirectly supported by the curious absence of explosive growth in the mite populations in the Arnot Forest colonies in late summer (see Tab. I).

Still a third possible cause of the longevity of the Arnot Forest colonies could be related to frequent swarming, which is typical of feral colonies in this locality (Seeley, 1978). When a colony swarms, approximately half the adult bees leave and along with them go a substantial portion of the adult mites, probably 15–20%, given the distribution of adult mites between adult worker bees and sealed brood cells (Fuchs, 1985; Martin et al., 1998). Moreover, after a colony swarms, there will be no brood produced in the colony for two to three weeks, during which time there will be no mite reproduction. Nevertheless, when Fries et al. (2003) compared the mite populations of swarming and non-swarming colonies in Sweden, they found that swarming did not prevent mite populations from growing to detrimental levels. All 150 of the colonies in the Swedish study were given a small number (36–89) of mites in July 1999, and within three years 129 of the colonies were dead, mostly due to the mites, regardless of whether they did or did not swarm in the summers of 2000 and 2001. It seems unlikely, therefore, that swarming alone could explain why many of the Arnot Forest colonies have survived for 3+ years without treatments to control *V. destructor*.

The logical next step in the study of the honey bees of the Arnot Forest is to test rigorously the hypothesis that the basis for this stable host-parasite relationship is the evolution of avirulence in the mites. There is evidence that mite avirulence evolved in an isolated, experimental population of European honey bees in Austria (Büchler, 1994; Milani et al., 1999), and it will be interesting to see if the same has happened in the northeastern United States. If so, then this will reinforce the idea that European honey bees and *V. destructor* mites can evolve a host-parasite relationship that is stable.

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Les abeilles de la forêt d'Arnot : une population de colonies sauvages dans le nord-est des États-Unis qui se maintiennent avec *Varroa destructor*.

***Apis mellifera* / *Varroa destructor* / relation hôte-parasite / tolérance / avirulence**

Zusammenfassung – Honigbienen im Arnot Forest: eine Population von mit *Varroa destructor* fortdauernden wilden Bienenvölkern in den nordöstlichen USA. Über den Zeitraum von drei Jahren (Herbst 2002 – Frühjahr 2005) wurde eine wildlebende Population von europäischen Honigbienen im Arnot Forest, einem 1.651 ha großen Forschungsreservat im Staat New York, untersucht. Die Untersuchung verfolgte 4 Ziele: (1) festzustellen, ob wildlebende Honigbienenvölker im Arnot Forest häufig vorkommen, (2) festzustellen, ob die Bienenvölker dieser Population mit *V. destructor* befallen sind, (3) festzustellen, ob die Völker dieser Population trotz eines Befalls mit *V. destructor* langfristig überleben und (4) festzustellen, wie diese Bienenvölker ein stabiles Parasit-Wirt-Verhältnis erreicht haben.

Die Anzahl der wildlebenden Bienenvölker war im Jahr 2002 ähnlich hoch wie bei einer Zählung im Jahr 1978, lange bevor *V. destructor* eingeschleppt wurde (Visscher and Seeley, 1982). Die Untersuchung wurde im westlichen Teil des Gebietes von derselben Person, während derselben Jahreszeit und mit denselben Methoden wie 1972 durchgeführt. Acht Bienenvölker wurden in Bienenbäumen entdeckt (Abb. 2). Diese acht Völker wurden von Oktober 2002 bis Oktober 2005 regelmäßig inspiziert. Die meisten Völker (fünf von acht) waren nach diesen drei Jahren noch am Leben (Tab. II).

Die wildlebenden Völker im Arnot Forest waren mit *V. destructor* befallen. Fünf Schwarmkisten (Abb. 1) wurden im Sommer 2003 aufgestellt, um den Milbenbefall in wildlebenden Völkern zu ermitteln. In drei dieser Kästen nisteten sich Schwärme ein. Bei diesen Völkern wurden über zwei Sommer die Milbenpopulationen monatlich anhand der Anzahl abgefallener Milben in den Bodeneinlagen („sticky boards") überprüft. Alle drei Völker waren mit Milben befallen, blieben aber bei schwachem bis mittlerem Milbenbefall vital.

Um zu überprüfen, ob die Bienenvölker des Arnot Forest den Anstieg ihrer Milbenpopulation kontrollieren können, wurden zwei vergleichbare Gruppen von Bienenvölkern paarweise aufgestellt. Jedes Paar bestand aus einem Volk mit einer Königin aus der Arnot Forest-Population und einem Volk mit einer Carnica-Königin. Beide Völker wurden jeweils mit einer ähnlichen Anzahl an Varroamilben infiziert, die aus demselben Bienenvolk stammten. Die Milbenpopulation wurde in der Folge monatlich durch Auszählen des Milbenfalls in die Bodeneinlagen bestimmt. In allen Monaten waren die durchschnittlichen Milbenzahlen in den beiden Gruppen von Bienenvölkern gleich (Abb. 3). Das heißt, die Milbenpopulation wuchs in den Arnot Forest-Völkern genauso rasch an wie in den Carnica-Völkern.

Für das Überleben der Bienenvölker im Arnot Forest scheint demnach eher die Evolution einer geringeren Virulenz bei den *V. destructor*-Milben (geringere Reproduktion) als die Entwicklung einer Resistenz bei den Bienen (Mechanismen der Milbenabwehr) verantwortlich zu sein. Allgemein sollte bei Parasiten eine Evolution in Richtung geringerer Virulenz dann von Vorteil sein, wenn sie sich eher vertikal (Eltern zu Nachkommen) als horizontal (infektiöse Verbreitung innerhalb der Population) ausbreiten. Im Arnot Forest, in dem die Bienenvölker in Bäumen leben, die mehrere hundert Meter voneinander entfernt stehen, dürfte die Verbreitung von *V. destructor* eher vertikal (durch Schwärme) als horizontal (Verflug und Räuberei) erfolgen. Eine weitere Untersuchung der Bienenvölker im Arnot Forest wird die Hypothese testen, dass die offensichtlich stabile Beziehung dieser Bienen mit *V. destructor* die Folge der Evolution einer geringeren Virulenz der Milben ist.

***Apis mellifera* / *Varroa destructor* / Parasit-Wirt Verhältnis / Toleranz / Avirulenz**

REFERENCES

Boecking O., Ritter W. (1993) Grooming and removal behavior of *Apis mellifera intermissa* in Tunisia against *Varroa jacobsoni*, J. Apic. Res. 32, 127–134.

Boecking O., Spivak M. (1999) Behavioral defenses of honey bees against *Varroa jacobsoni* Oud., Apidologie 30, 141–158.

Büchler R. (1994) *Varroa* tolerance in honey bees – occurrence, characters, and breeding, in: Matheson A. (Ed.), New perspectives on *Varroa*, IBRA, Cardiff, pp. 12–23.

Bull J.J. (1994) Perspective: virulence, Evolution 48, 1423–1437.

De Jong D., Soares A.E.E. (1997) An isolated population of Italian bees that has survived *Varroa jacobsoni* infestation without treatment for over 12 years, Am. Bee J. 137, 742–745.

Edgell G.H. (1949) The bee hunter, Harvard University Press, Cambridge, Mass.

Ewald P. (1983) Host parasite relations, vectors, and the evolution of disease severity, Annu. Rev. Ecol. Syst. 14, 465–485.

Fell R.D., Ambrose J.T., Burgett D.M., De Jong D., Morse R.A., Seeley T.D. (1977) Seasonal cycle of swarming in honey bees (*Apis mellifera* L.), J. Apic. Res. 16, 170–173.

Fries I., Hansen H., Imdorf A., Rosenkranz P. (2003) Swarming in honey bees (*Apis mellifera*) and *Varroa destructor* population development in Sweden, Apidologie 34, 389–397.

Fries I., Imdorf A., Rosenkranz P. (2006) Survival of mite infested (*Varroa destructor*) honey bee (*Apis mellifera*) colonies in a Nordic climate, Apidologie 37, 564–570.

Fuchs S. (1985) Untersuchungen zur quantitativen Abschätzung des Befalls von Bienenvölkern mit *Varroa jacobsoni* Oudemans und zur Verteilung des Parasiten im Bienenvolk, Apidologie 16, 343–368.

Korpela S., Aarhus A., Fries I., Hansen H. (1992) *Varroa jacobsoni* Oud. in cold climates: population growth, winter mortality and influence on survival of honey bee colonies, J. Apic. Res. 31, 157–164.

Martin S.A., Hogarth A., van Breda J., Perrett J. (1998) A scientific note on *Varroa jacobsoni* Oudemans and the collapse of *Apis mellifera* L. colonies in the United Kingdom, Apidologie 29, 369–370.

Milani N., Pechhacker H., Della Vedova G. (1999) Reduced fertility in a European population of *Varroa jacobsoni* Oudemans, Apidologie 30, 435–436.

Mobus B., de Bruyn C. (1993) The new *Varroa* handbook, Northern Bee Books, Mytholmroyd, p. 146.

Morse R.A, Seeley T.D. (1979) New observations on bait hives, Gleanings Bee Culture 107, 310–311, 327.

Odell A.L., Lassoie J.P., Morrow R.W. (1980) A history of Cornell University's Arnot Forest, Dept of Natural Resources Research and Extension Series 14, 1–53, Cornell University, Ithaca, New York, [online] http://www.dnr.cornell.edu/arnot/about/history.htm (accessed on 15 January 2006).

Ritter W. (1988) *Varroa jacobsoni* in Europe, the tropics and subtropics, in: Needham G.R., Page R.E., Delfinado-Baker M., Bowman C.E. (Eds.), Africanized honey bees and bee mites, Ellis Horwood, Chichester, pp. 349–359.

Ritter W., Michel P., Bartholdi A., Schwendemann A. (1990) Development of tolerance to *Varroa jacobsoni* in bee colonies in Tunisia, in: Ritter W. (Ed.), Proc. Int. Symp. on recent research on bee pathology, Sept. 5–7, 1990, Gent, Belgium, pp. 54–59.

Rosenkranz P. (1999) Honey bee (*Apis mellifera* L.) tolerance to *Varroa jacobsoni* Oud. in South America, Apidologie 30, 159–172.

Ruttner F. (1991) Auf dem Wege zu einer varroatoleranten Carnica, Allgemeine Dtsch. Imkerztg. 25, 10–15.

Sanford M.T. (2001) Introduction, spread, and economic impact of *Varroa* mites in North America, in: Webster T.C., Delaplane K.S. (Eds.), Mites of the honey bee, Dadant and Sons, Hamilton, Illinois, pp. 149–162.

Seeley T.D. (1978) Life history strategy of the honey bee, *Apis mellifera*, Oecologia 32, 109–118.

Seeley T.D., Morse R.A. (1976) The nest of the honey bee (*Apis mellifera*), Insectes Soc. 23, 495–512.

Seeley T.D., Morse R.A. (1977) Dispersal behavior of honey bee swarms, Psyche 84, 199–209.

Seeley T.D., Morse R.A. (1978) Nest site selection by the honey bee, Insectes Soc. 25, 323–337.

Visscher P.K., Seeley T.D. (1982) Foraging strategy of honeybee colonies in a temperate deciduous forest, Ecology 63, 297–301.

Visscher P.K., Seeley T.D. (1989) Bee-lining as a research technique in ecological studies of honey bees, Am. Bee J. 129, 536–539.

Webster T.C. (2001) Detection and measurement of *Varroa* mite populations, in: Webster T.C., Delaplane K.S. (Eds.), Mites of the honey bee, Dadant and Sons, Hamilton, Illinois, pp. 163–178.

Wenner A.M., Bushing W.W. (1996) *Varroa* mite spread in the United States, Bee Culture 124, 342–343.

Wenner A.M., Thorp A.M. (2002) Collapse and resurgence of feral colonies after *Varroa* arrival, in: Erickson E.H., Page, R.E., Hanna A.A. (Eds.), Proc. 2nd Int. Conf. on Africanized honey bees and bee mites, A.I. Root Co., Medina, Ohio, pp. 150–166.