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ORIGINAL ARTICLE

Distribution of *Varroa destructor* between swarms and colonies

JERZY WILDE,[1]* STEFAN FUCHS,[2] JANUSZ BRATKOWSKI[1] AND MACIEJ SIUDA[1]

[1]Apiculture Division, Warmia and Mazury University, ul. Sloneczna 48, 10-710 Olsztyn, Poland

[2]Institut für Bienenkunde (Polytechnische Gesellschaft), Fachbereich Biologie und Informatik, JW Goethe-Universität Frankfurt am Main, Germany, Karl-von-Frisch-Weg 2, 61440 Oberursel, Germany

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SUMMARY

Bee colonies reproduce by colony division during swarming. In colonies infested by the parasitic mite, *Varroa destructor*, colony division will at the same time split the mite population between the swarms and the remaining parent colonies. The present investigation compares infestation of swarms with that of parent colonies. We found that an average of 25 ± 9% of mites left the colonies with natural swarms, while 75 ± 9% remained in parent colonies of which 39 ± 11% were on bees and 36 ± 10% were within sealed brood cells. The relative swarm infestation did not differ from that of the remaining parent colony in this study, but very low proportions of mites within sealed worker brood and a clear negative correlation to the proportion of mites in sealed brood strongly suggest that swarm infestation is asymmetric and lower than that of the remaining colonies.

Keywords: swarms, *Apis mellifera*, *Varroa destructor*, brood, worker honey bees

INTRODUCTION

One of the main challenges faced by parasites and pathogens during their life history is how to infest new hosts within or after the lifetime of their current host. Two main pathways exist. One is horizontal transmission through spread to adjacent hosts, the other is vertical transmission through infesting offspring and thus being passed down the successive host generations. Commonly, the way of transmission is considered to be a main factor shaping virulence of a parasite, as longevity and fitness of the host is more important in vertical transmission (Lipsitch *et al*., 1996). Virulence of different honey bee pathogens has been shown to correlate with their mode of spread, with bee diseases more virulent whenever horizontal spread prevails (Fries & Camazine, 2001). To complicate matters, transmission takes place on two levels, between individual bees or between colonies.

Many gaps in the knowledge of spread patterns remain to be clarified in the parasitic mite *Varroa destructor*. While the frequent host change between individual bees or bees and bee brood within colonies is comparatively well investigated, much less is known about the spread between colonies. Horizontal transmission between colonies is known to occur through drifting of forager bees or drones between colonies (Hüttinger *et al*., 1981; Sakofski & Fuchs, 1990), but knowledge is scarce about the distances covered and number of mites transmitted (Renz & Rosenkranz, 2001). However, considerable numbers of mites appear to be transported during robbing events, where the honey resources of weakened colonies are taken over by adjacent colonies within the foraging flight range (Sakofski, 1987).

Vertical transmission differs from that in many other parasite-host systems as colonies reproduce by colony division. During this process, about 60% to 70% of the worker bees, together with the queen, leave the parent colony and establish a new colony (Seeley, 1985; Winston, 1987). The parent colony lives on with a new queen for a potentially indefinite period, without constraining the parasite by a limited lifetime. A predominance of vertical spread of *V. destructor* during colony division fits well with the benign nature of the parasite in its original host (Oldroyd, 1999; Fries & Camazine, 2001), underlining the maladaptation to its newly acquired host *A. mellifera*. Beekeeper practices with high colony density and transport of colonies enhance vertical spread (Fries & Camazine, 2001) and select for high virulence.

Colony division together with perpetual life of both its parts raises the question of the distribution of the mites between parent colonies and swarms, which is likely to affect the future life prospects of the respective components. If one of these components receives a major share of the mites, colony division can act as a mechanism that, at the same time, serves to reduce the mite population in the other component. While part of the varroa mites reside on worker bees (phoretic mites), considerable parts of the mite population are enclosed within the sealed brood cells (Fuchs, 1985; Rosenkranz & Renz, 2003). As only phoretic mites can leave the colony with the swarms, this could result in a lower infestation of swarms than of the parent colonies. An asymmetric distribution of mites could potentially lead to a reduction of the mite infestation in the population, where highly infested colonies perish and thus remove the parasites from the population, while new colonies with reduced populations prevail. It was shown in model calculations that such a process might eventually lead to stable equilibriums between parasite and host (Fuchs *et al*., 1998; Eggelbusch *et al*., 2000).

While it is obvious that swarms may carry considerable numbers of mites (Rademacher & Böttcher, 1984), with exception of a small study of Schmidt-Bailey (1999) little is known about how varroa populations would distribute between parent colonies and swarms, and whether this would lead to asymmetric infestation of the parent colonies and the swarms. The current experiment sets out to study infestation in natural swarms and in parent colonies. Supplemental experiments were carried out with artificial swarms to gain additional information about the factors influencing the mite distribution.

*Corresponding author: jerzy.wilde@uwm.edu.pl

MATERIALS AND METHODS

The experiment was conducted in the summer of 2001 and 2002 in the Apiculture Division of Warmia and Mazury University in Olsztyn, Poland. We chose 16 colonies of *Apis mellifera*, apparently ready to swarm (i.e. that had queen cups with larvae). The space within the hives was limited to increase swarming tendency. Colonies were observed daily from 3 June to 25 June between 08:00 h and 16:00 h to detect the incidence of swarms. Swarming colonies were recorded and swarms were followed until they settled down. Then, they were caught in swarm boxes equipped with a bottom mesh.

Bee numbers were determined by weighing empty and filled boxes, and by weighing and counting a subsample of at least 100 worker bees. Varroa numbers were determined from a sticky sheet placed under the boxes. Fumigation by burning one tablet of Apivarol® containing 12.5 mg Amitraz®. Fumigation lasted over a period of 20 min after placing the box with bees into a larger box and closed hermetically. Mites which fell down after transportation and within 24 h after fumigation were counted. Bee infestation was calculated as number of mites per bee.

In the evening of the swarming day, after cessation of bee flight, bees in parent colonies were brushed off the combs into swarm boxes, and bees as well as mites were counted as above. Combs were evaluated for open and sealed brood area, which was determined by measuring the axes of the elliptic brood areas (empty brood cells in ellipses were not excluded). The area covered by bee bread and honey was also determined, and the numbers of open or sealed queen cells were counted. Open and sealed worker cells, cells filled with honey or pollen, and sealed drone cells were calculated from the measured comb areas, assuming four worker cells/cm^2 and three drone cells/cm^2.

Brood combs from different hives were placed in separate boxes in a room kept at 35 °C and 75% RH to incubate the sealed brood. Combs remained there over a period of 14 days. Mites were counted on sticky papers placed under the boxes over the period of incubation and after fumigation at the end of this period. After this period cells were inspected for presence of adult varroa mites. Letting the mites hatch naturally is considered to be a more appropriate measure of parent colony infestation before the start of the brood production from the new queen than opening of the sealed cells shortly after swarming.

Colonies which had not swarmed by 25 June were divided artificially, simulating natural swarming. Between 8 July and 13 July, during conditions of good bee flight weather, all bees were shaken off the combs on a platform that was placed 5 cm away from the hive entrance to ensure a separation of bees. The old queen was confined in a cage under the platform. By evening, some of the bees had clustered around the queen under the platform, while others flew back to the hive. Numbers of bees and mites as well as other colony parameters were determined in an identical manner as in the naturally swarming colonies. Data were analysed by non-parametric statistics (Mann-Whitney U test, Wilcoxon matched pair rank test, Spearman's rank correlation). Calculations of proportions were calculated as means of the respective proportions for individual colonies.

RESULTS

Of the 16 colonies, eight issued natural swarms. One of these swarms contained only 1600 bees and no sealed queen cells were found in the parent colony. It was considered atypical and was removed from the analysis. At the time of swarming, the undivided parent colonies contained an average and standard deviation of 33149 ± 7765 bees. The average numbers of cells containing open brood cells, sealed worker or drone brood cells, cells containing pollen and honey, and sealed queen cells are given in table 1. All seven colonies contained sealed queen cells. Before swarming, parent colonies contained 361 ± 504 mites (sum of all mites). An average proportion of 36 ± 10% of the

TABLE 1. Characteristics of seven honey bee colonies that issued natural swarms. Measurements are taken from the remaining parent colonies and from the swarms. Values give means and standard deviations. Mean percentages were calculated by averaging the colony values.

	Remaining parent colonies	Swarms
Colony composition		
Bees	19440 ± 7307	13709 ± 5899
Open brood cells	2073 ± 2171	
Sealed worker cells	7397 ± 5244	
Sealed drone cells	1322 ± 1008	
Total sealed cells	9875 ± 5950	
Cells with pollen	4714 ± 1865	
Cells with honey	8549 ± 2857	
Queen cells	15.1 ± 4.5	
Mite numbers		
On bees	171 ± 249	72 ± 81
In sealed brood cells	118 ± 185	
Infestation		
Mites per bee	0.0075 ± 0.0098	0.0093 ± 0.0149
Mites per sealed brood cell	0.0143 ± 0.0169	
Mite distribution		
% on bees	39 ± 11	25 ± 9
% in sealed brood cells	36 ± 10	

TABLE 2. Characteristics of eight, artificially swarmed honey bee colonies. Measurements are taken from the remaining parent colonies and from the swarms. Values give means and standard deviations. Mean percentages were calculated by averaging the colony values.

	Remaining parent colonies	Swarms
Colony composition		
Bees	15903 ± 6867	18439 ± 4681
Open brood cells	7973 ± 1331	
Sealed worker cells	9410 ± 2915	
Sealed drone cells	745 ± 597	
Total sealed cells	10154 ± 3176	
Cells with pollen	3982 ± 2991	
Cells with honey	12629 ± 5651	
Queen cells	1.1 ± 0.9	
Mite numbers		
On bees	60 ± 30	255 ± 267
In sealed brood cells	355 ± 518	
Infestation		
Mites per bee	0.0044 ± 0.0030	0.0107 ± 0.0092
Mites per sealed brood cell	0.0314 ± 0.0344	
Mite distribution		
% on bees	15 ± 6	36 ± 11
% in sealed brood cells	49 ± 12	

mites was in the sealed brood cells. This proportion showed a high correlation with the number of sealed worker cells (r = 0.85, P = 0.015) while the correlation with the number of sealed drone cells, though also high (r = 0.50, P = 0.25), was not significant.

The swarms comprised an average of 42 ± 17% of the bees, calculated as the means of the individual colonies proportions (fig. 1a). This percentage did not correlate with either the total number of bees in the parent colonies before swarming, or with the amount of open or sealed brood cells, or the sum of these. Relative swarm size, calculated as the percentage of bees in swarms of the sum of all bees and sealed brood cells, was 31.6 ± 12.3%. An average of 25 ± 9% of mites left the colonies with the swarms (fig. 1b; table I). This percentage did not correlate with the amount of brood cells, neither with the numbers of open nor sealed brood cells, nor the sum of these. Also it did not correlate with the ratio between sealed brood cells and bees before swarming. The percentage of mites leaving with swarms also did not correlate with the relative swarm sizes. However, a negative correlation between the percentage of mites in swarms and the percentage of mites in the brood was almost significant (r = – 0.71, P = 0.07), while no significant correlation was found with the percentage of mites on worker bees remaining in parent colonies. Infestation of bees in the swarms was on average about 1.28-fold higher than that of the bees in parent colonies after swarming, though this difference was not significant (Wilcoxon matched pair rank test).

The eight colonies that were artificially divided contained 34341 ± 6292 bees before division. Five colonies had one or two unsealed queen cells. The average numbers of cells containing open brood cells, sealed worker or drone brood cells, cells containing pollen and honey, and sealed queen cells are given in table 2. Colony characteristics did not differ significantly between naturally swarming and artificially divided colonies, except that the amount of open brood cells was higher and the number of sealed queen cells was lower in the non-swarming colonies(P < 0.001, Mann-Whitney U Test). Before artificial swarming, colonies contained 640 ± 793 mites, 51 ± 12% of which were on the bees and 49 ± 12% were in the sealed brood cells. The percentage of mites in brood cells did not correlate with the number of sealed brood cells.

Artificial swarms contained 55 ± 14% of the bees (fig. 1c), and this percentage again did not correlate with the number of bees in the parent colony before swarming or the amount of sealed and open brood. Swarms contained 36 ± 11% of the mites (fig. 1d; table 2), this proportion showed no significant relationship to most colony traits as tested above for naturally swarming colonies. In particular, it did not correlate with the percentage of mites on worker bees remaining in the parent colonies. However, a significant negative correlation was found between the percentage of mites in swarms and the percentage of mites in the sealed brood (r = – 0.91, P = 0.002), and an almost significant positive correlation to the relative swarm size (r = 0.66, P = 0.07). Infestation of the bees in the swarms was on average 2.28-fold higher than that of the bees in parent colonies, which was a significant difference (P = 0.012, Wilcoxon matched pair rank test).

DISCUSSION

Although colonies contained over 30 000 workers and a normal amount of pollen and brood stores, only seven of them issued natural swarms. While numbers of bees or sealed brood cells did not differ between swarming and non-swarming colonies, the amount of open brood was considerably higher in the non-swarming colonies. This is likely to be due to cessation of egg-laying in the queen in the swarming colonies. In particular, all of the swarming colonies, except the one excluded by untypical small size, contained sealed queen cells, which was not the case in the non-swarming ones. Although the artificial swarming procedure is not a perfect simulation of natural

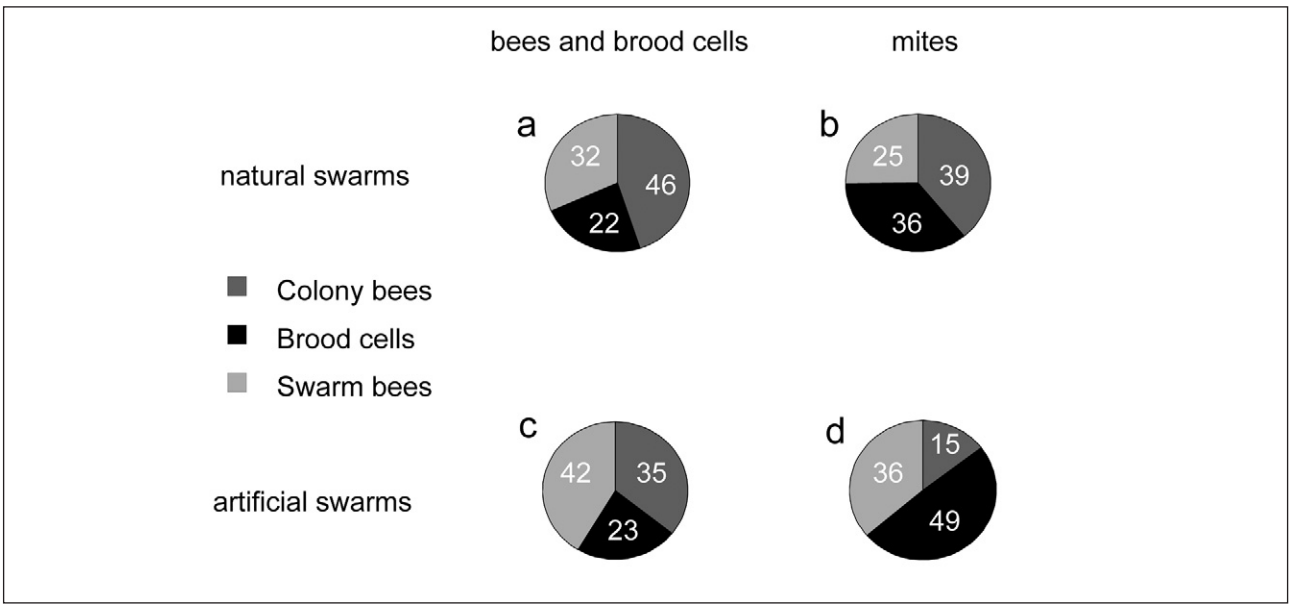

FIG. 1. Proportions of worker bees in remaining colonies, sealed brood cells and worker bees in swarms (a and c), and of *Varroa destructor* in these parts (b and d) for naturally swarming or artificially swarmed colonies, respectively. Numbers in the charts indicate proportions in percentage.

swarming, data are useful for additional insight into the splitting of the mite population between colony components.

Less than half (42%) of the bees left the colonies with the natural swarms, which is below the range of 60% to 70% given by Winston (1987) and Seeley (1987) for the size of prime swarms. Within the small sample size, no striking relations of swarm sizes to colony parameters were apparent. Only a minor proportion of one-fourth of the mite population left the colonies together with the swarms. Again, data were too few to prove the relationship of this proportion to colony parameters. However, a trend in the data indicates an inverse relationship between the percentage of mites which left with the swarms and the percentage of mites present in sealed brood. This underlines that sealed brood is a reservoir for mites closing them away from the population splitting during swarming process, and is additionally supported by the highly significant negative relation ($r = -0.91$) in the experiment with artificial swarming.

The most interesting point is whether infestation would differentiate between swarms and the parent colonies. Though the mean swarm infestation rate did not differ statistically from that of bees left in the parent colonies, it is important to also consider the mites left in the brood of the parent colony. After emergence of bees from the sealed brood, thus freeing the mites enclosed in the brood, bee infestation would increase. By calculating the resulting bee infestation (number of mites on bees and within brood divided by bees and sealed brood cells, average 0.0094), infestation of all colony bees would be by on average 5% higher than that of swarm bees, which is again not significant. In the artificial swarms, mean infestation rate was about twice that of the workers remaining in parent colonies. The apparent reason for this is that in these experiments artificial swarms are likely to contain mostly young hive bees, while forager bees would return to the old colony. *V. destructor* are known to have a marked preference for hive bees (Kraus *et al*., 1986). This also might explain the somewhat higher infestation in natural swarm bees compared to the parent hive bees, as swarms are known to contain also proportionally more young bees (Winston, 1987).

Although the data of our experiments did not show a marked difference between the infestation of the parent colonies and the natural swarms, results nevertheless are consistent with the suggestion that swarm infestation is likely to be rather lower than the infestation of parent colonies. In the current experiment, out of the total mite population only a comparatively small fraction, about one-third, of the mites was found in sealed brood cells. This is partly an effect of the small proportion of sealed brood to bees (0.29:1) in this study, which is markedly lower than the ratio given by Rosenkranz & Renz (2003) during the main season (0.6:1 to 1.5:1), or by Winston (1979, 0.55:1) in colonies of Africanized bees at the time of primary swarms. The difference is even more marked, as in our experiment brood was allowed to hatch, increasing the amount of offspring. In addition, in the current experiment cell infestation relative to that of the bees was particularly low (2.2:1) in comparison to other studies (3.7:1 Fuchs, 1985; 2.9:1 Woyke, 1987b; 5.1:1 Woyke, 1987c; 3.55:1 Berg, unpublished data), but higher than 0.78 :1 in subtropical conditions in south Vietnam (Woyke, 1987a). As a result, on average only 36% of the mites were in sealed brood cells, which contrasts to proportions reported in the literature (51% Fuchs, 1985; 69% Hoffmann, 1996; 60% Calis *et al*., 1999; 58%-91% Rosenkranz & Renz, 2003). A marked sensitivity of swarm infestation to the percentage of mites in sealed brood cells was apparent from this study, and particularly clear in the experiment with artificial swarms, where infestation of parent colonies was significantly lower than that of the artificial swarms in spite of an exaggerated swarm bee infestation due to prevalence of young workers in the artificial swarms. Without the very low proportion of mites in sealed brood in the naturally swarming colonies, swarm infestation would have been distinctly lower than that of the remaining parent colonies after emergence of the sealed brood. This conclusion is also supported by results on five swarms obtained by Schmidt-Bailey (1999), where swarm infestation was half that of the remaining colony after emerging of the brood.

The distribution of *V. destructor* between colonies and swarms thus appears to be influenced mainly by the proportion of the mite population enclosed in sealed cells, which depends on the amount of cells present at the time of swarming, as well as the rate of brood infestation relative to that of the workers. Other factors such as a prevalence of the mites for young hive bees, which might increase the numbers of mites leaving with the swarm, or size of the swarms were of minor impact and not significant in his study.

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