

Small hive beetle, Aethina tumida, populations II: Dispersal of small hive beetles

Sebastian Spiewok, Michael Duncan, Robert Spooner-Hart, Jeff S. Pettis,

Peter Neumann

► To cite this version:

Sebastian Spiewok, Michael Duncan, Robert Spooner-Hart, Jeff S. Pettis, Peter Neumann. Small hive beetle, Aethina tumida, populations II: Dispersal of small hive beetles. Apidologie, 2008, 39 (6), pp.683-693. hal-00891988

HAL Id: hal-00891988 https://hal.science/hal-00891988

Submitted on 11 May 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Original article

Small hive beetle, *Aethina tumida*, populations II: Dispersal of small hive beetles*

Sebastian SPIEWOK¹, Michael DUNCAN², Robert SPOONER-HART², Jeff S. PETTIS³, Peter NEUMANN^{4–6}

¹ Institut für Biologie, Molekulare Ökologie, Martin-Luther-Universität Halle-Wittenberg, Hoher Weg 4, 06099 Halle (Saale), Germany

² Centre for Plant and Food Science, University of Western Sydney, Penrith South, NSW 1797, Australia ³ USDA-ARS Bee Research Laboratory, Bldg. 476 BARC-E, Beltsville, MD 20705, USA

⁴ Swiss Bee Research Centre, Agroscope Liebefeld-Posieux Research Station ALP, 3003 Bern, Switzerland

⁵ Department of Zoology and Entomology, Rhodes University, Grahamstown 6140, South Africa

⁶ Eastern Bee Research Institute of Yunnan Agricultural University, Kunming, Yunnan Province, China

Received 3 June 2008 - Revised 19 August 2008 - Accepted 25 August 2008

Abstract – Small hive beetles (= SHB), Aethina tumida, are parasites and scavengers of honeybee colonies and actively disperse for host finding. We investigated the re-infestation levels of SHB-free colonies within ten infested apiaries in South Africa, Australia and the USA. Re-infestation of 95% of the colonies indicates a high SHB exchange between colonies. Colony position and queen status had no influence on colony infestation levels. Spread into apiaries was determined at twelve SHB-free apiaries. While apiaries in Maryland remained un-infested, those in Australia showed high infestation numbers. Apiary density, SHB population levels and ongoing SHB mass reproduction seem to govern SHB infestation of newly installed apiaries. Those located in forested habitats showed higher infestation levels possibly due to the presence of wild/feral colonies. The results elucidate factors influencing SHB dispersal and the role of human-mediated spread, enabling improved control of SHB.

Aethina tumida / Apis mellifera / dispersal / honeybees / small hive beetle

1. INTRODUCTION

For pest control, knowledge of the dispersal activity of the respective species is crucial. However, the dispersal ability of novel pests, like the small hive beetle, *Aethina tumida* Murray (= SHB), is often unknown. This parasite and scavenger of honeybee, *Apis mellifera* L., colonies was introduced into different parts of the world including the United States and Australia (Neumann and Elzen, 2004), where it is now well established (Spiewok et al., 2007).

Many beetle species capable of flying show a considerable potential for disper-

Corresponding author: S. Spiewok,

S.Spiewok@web.de

sal, e.g. most individuals of *Hylobius abietis* (Coleoptera: Curculionidae) disperse >10 km and some even up to 80 km (Solbreck, 1980). SHB are also active flyers, which can move individually, in migrating swarms or join honeybee swarms (Lundie, 1940; Tribe, 2000; Ellis et al., 2003). Previous studies suggest a considerable SHB exchange between colonies of the same apiary (Elzen et al., 1999, 2000; Ellis and Delaplane, 1987). High exchange rates would render uncoordinated colony treatments within infested apiaries useless. We determined SHB dispersal expecting re-infesting rates to correlate with the average apiary infestation levels.

The high mobility of the native hosts, African honeybee subspecies (Hepburn and

^{*} Manuscript editor: David Tarpy

Radloff, 1998; Spiewok et al., 2006), makes a colony a relatively short-lived habitat for SHB. Migration tendency is usually high in species living in such habitats (cf. Hanski, 1999). Furthermore, Wenning (2001) stated that SHB are able to detect "stressed" colonies over a distance of 13-16 km. However, it is still unclear if SHB readily travel longer distances and switch between apiaries. If this is so, this could impact apiaries after successful treatment, including migratory ones. Thereby, high SHB population density, high apiary density and the occurrence of feral/wild colonies might each increase infestation levels of newly installed apiaries. Since all these parameters occur simultaneously in some Australian areas, we expect the highest infestation levels there.

Similar to other beetles (e.g. *Carabus problematicus*, Rijnsdorp, 1980), dispersing SHB individuals might prefer shaded forest habitats providing shelter. Thereby, they also increase their chances for host finding due to naturally occurring nest sites of honeybees (e.g. in hollow trees; Hepburn and Radloff, 1998). Indeed, wild/feral colonies can be infested with SHB (Benecke, 2003) and thus also act as SHB reservoirs. Therefore, newly installed apiaries in potentially more attractive habitats such as forests may suffer from higher SHB invasion pressure.

During dispersal, SHB might be attracted by colony odours and yeast-volatiles (Elzen et al., 1999; Suazo et al., 2003; Torto et al., 2005, 2007), but previous studies suggest that colony phenotype (colony size, amount of brood and stores) is unlikely to influence colony attractiveness (Ellis and Delaplane, 2006; Spiewok et al., 2007). Nevertheless, SHB might aggregate in colonies with decreased defensive behaviour such as queenless ones (Delaplane and Harbo, 1987). In this case, we expect fewer SHB in queenright colonies compared to queenless ones.

Like other beetles, SHB may also use optical cues like sharp contrasts or light conditions (Strom et al., 1999; Igeta et al., 2003; Nalepa et al., 2005), resulting in constant higher infestation and re-infestation rates of colonies at certain positions in an apiary. If this is true, the relative distribution over the colonies should be similar at two consecutive surveys with colonies at attractive positions being repeatedly highly infested.

We investigated the infestation of colonies and apiaries in South Africa, Australia, Florida and Maryland, similar to the analysis of apiary re-infestation after treatment for the mite Varroa destructor Anderson & Trueman (Greatti et al., 1992). These surveys simulated the reinfestation of treated single colonies or whole apiaries as well as newly installed migratory apiaries, by active SHB dispersal. The results of this study assist in drawing conclusions about a possible preference of dispersing SHB for certain colonies or apiaries and if those ones have to be especially considered for protection measures. Our data will elucidate factors influencing SHB dispersal and the role of human-mediated spread, enabling improved control of SHB.

2. MATERIALS AND METHODS

2.1. Visual colony inspections

The term 'SHB' refers in the following text always to adults. All visual inspections were conducted using routine protocols by investigating every single frame and hive box of a colony (Spiewok et al., 2007). We will refer to our previous survey (Spiewok et al., 2007) as the 1st inspection and to the present one as the 2nd inspection. During the 1st inspection SHB were removed from all investigated colonies. Since not all colonies of the commercial apiaries were inspected, the cleaned colonies could get re-infested by SHB from neighbouring colonies. To ensure, that the SHB found during the 2nd inspection were not merely those missed during the 1st one, the number of possible missed SHB was estimated and compared to the 2nd inspection for each apiary using Wilcoxon-matched pairs tests. According to the experience from our previous study (Spiewok et al., 2007) we estimated that 8.4% of the SHB of one colony were missed during the inspection.

2.2. Dispersal within apiaries

Re-infestation levels of 71 colonies were assessed at ten infested commercial apiaries in South Africa, Australia, Maryland and Florida two weeks after the 1st inspection. The re-infestation levels were determined considering the respective average apiary infestation levels, expecting a positive correlation between these levels. Therefore, the average infestation level was calculated for each apiary by using the infestation levels of the investigated colonies at the 1st and 2nd inspection. Then, a Spearman rank correlation was run between these average infestation levels at the 1st and the 2nd inspections.

2.3. Influence of colony position and queen status

To test for the influence of the position of a colony within an apiary on its infestation level, the relative SHB distributions over the colonies were compared between the 1st and 2nd inspection. For this purpose, the proportions of SHB found in the investigated colonies were calculated for each apiary for both inspections and then compared using χ^2 -goodness-of-fit tests (N = 8 apiaries). As a further test, a Spearman rank correlation was run between the colony infestation levels of the 1st and 2nd inspection for each apiary.

The possible influence of a colony's queen status on its infestation level was investigated in an Australian apiary. Ten randomly selected colonies were de-queened and open brood combs were replaced by honey-pollen combs to enhance laying worker development. Nine days later, emergency queen cells and SHB were removed from these colonies and ten queenright control colonies. A further 16 days later, all colonies were screened again for SHB. The infestation levels of the queenright and queenless colonies were compared for both inspections using Wilcoxon-matched-pairs tests.

2.4. Dispersal into apiaries

To investigate the immigration into apiaries, ten SHB-free experimental apiaries (5 to 6 colonies each) were installed in the vicinity of commercial apiaries (Fig. 1). The experimental colonies were obtained from low infestation areas and were screened for SHB prior to their installation. In Maryland, four naturally non-infested apiaries were used as experimental apiaries. The exact locations of all apiaries within a 10 km radius were assessed via GPS. Additionally, two apiaries ($E_{AU}5$

and $E_{AU}6$; E = experimental apiary; AU = Australia) were installed in a remote area that is usually used by migratory beekeepers. During the survey, however, no other apiary was present within a 10 km radius of the experimental ones. Comparisons were made between the infestation levels of the experimental apiaries using Kruskal-Wallistests and Mann-Whitney-U tests as post hoc tests (adjusted $\alpha = 0.0025$). To take into account possible differences in weather conditions between the regions during the survey periods, data were obtained from local weather services.

2.5. Dispersal in different habitat patches

To detect a possible influence of the apiary site on SHB infestation, the Australian experimental apiaries $E_{AU}1$ to $E_{AU}4$ were screened two more times after the 2nd inspection at two-day intervals (3rd and 4th inspection). $E_{AU}1$ was located in a clearing in a small forest, while $E_{AU}2$ was installed in a meadow. $E_{AU}3$ was situated at the edge of a forest and $E_{AU}4$ was inside a forest. The *lg*transformed numbers of collected SHB were analysed for differences between the four apiaries using one-way ANOVA and Newman-Keuls tests.

3. RESULTS

All indicated values are medians [1st; 3rd quartile] due to non parametric distributions of the data sets or non-homogenous variances (Levene's test; $\alpha = 0.05$) except the data in Section 3.4. Chosen statistics account for the non-parametric distributions and relatively low number of colonies investigated at some apiaries.

3.1. Dispersal within apiaries

After two weeks, two South African colonies at $A_{SA}3$ (11%) and one colony at $A_{MD}1$ in Maryland (8%) were not re-infested, while all colonies in Australia and Florida were re-infested with SHB. At all apiaries except $A_{SA}3$ (Wilcoxon-matched pairs tests: T = 3; P = 0.465), the SHB numbers found during the 2nd inspection were significantly



Figure 1. Positions and distances [km] of the apiaries in: (a) South Africa, (b) Australia, (c) Maryland (A = commercial apiaries, E = experimental apiaries, I = inaccessible apiaries, AU = Australia, MD = Maryland, SA = South Africa). $A_{SA}3$, $E_{AU}5$ and $E_{AU}6$ are not shown because they were located in remote areas.

higher than those that were possibly missed in the 1st inspection (T \leq 1; *P* < 0.05). The average SHB numbers collected from the apiaries are shown in Table I. There was a significant positive correlation between the average apiary infestation levels of the 1st and the 2nd inspections (r_s = 0.96; t₁₂ = 11.95; *P* < 0.001; Fig. 2).

3.2. Influence of colony position and queen status

At all commercial apiaries, the relative distribution of SHB over the colonies differed significantly between the two inspections (Tab. II). Accordingly, no correlations were found between the colony infestation levels

Table I. Average infestation and re-infestation levels of commercial and experimental apiaries after two weeks. Values are medians [1st; 3rd quartile], N = numbers of inspected colonies during the 2nd inspection at the respective apiaries. Different letters indicate significant differences between the average infestation levels (MWU tests, adjusted $\alpha = 0.0025$). Apiary A_{FL}1 is the same as H_{FL}1 in Spiewok et al. (2007).

Desien	Commercial apiaries		al apiaries	Experimental apiaries				
Region	Aniony N		SHB	SHB	. ·	NT	CUD	
	Apiary	IN	1st inspection	2nd inspection	Apiary	IN	зпв	
South Africa	A _{SA} 1	6	6 [2; 7]	7 [2; 11]	E _{SA} 1	6	6 [3; 6] ^a	
	$A_{SA}2$	6	14 [7; 17]	7 [5; 9]	$E_{SA}2$	6	7 [3; 11] ^a	
	$A_{SA}3$	6	5 [3; 7]	1 [0; 3]				
Australia	$A_{AU}1$	10	31 [17; 41]	38 [11; 47]	$E_{AU}1$	6	79 [75; 141] ^b	
	$A_{AU}2$	6	31 [20; 36]	62 [47; 83]	$E_{AU}2$	6	21 [16; 26] ^c	
	$A_{AU}3$	5	38 [25; 61]	47 [35; 60]	$E_{AU}3$	6	73 [61; 196] ^b	
	$A_{AU}4$	10	22 [11; 36]	23 [6; 42]	$E_{AU}4$	6	117 [104; 171] ^b	
					$E_{AU}5$	6	213 [120; 284] ^d	
					$E_{AU}6$	6	120 [102; 132] ^b	
Florida	$A_{FL}1$	10	148 [101; 275]	144 [127; 223]				
Maryland	$A_{MD}1$	6	6 [3; 10]	9 [8; 11]	$E_{MD}1$	5	0 [0; 0] ^e	
	$A_{MD}2$	6	2 [1; 4]	7 [4; 15]	$E_{MD}2$	6	0 [0; 0] ^e	
					$E_{MD}3$	6	0 [0; 0] ^e	
					$E_{MD}4$	5	0 [0; 0] ^e	



Figure 2. Correlation of average apiary infestation levels between 1st and 2nd inspection. (Symbols for respective apiaries: $\circ = E_{MD}$, $\bullet = A_{MD}$, $\Box = A_{SA}$, $\blacksquare = A_{AU}$, $\blacktriangle = A_{FL}$).

of the 1st and 2nd inspection (Tab. II). $A_{SA}3$ was not included in the analyses due to the low total SHB number and the resulting low variance.

Furthermore, no significant differences were found between the infestation levels in queenright colonies (22 [13; 29] SHB/colony) and those undergoing emergency queen rearing (20 [11; 35]; T = 19.5; P = 0.722), as well as 16 days later between the queenright

(17 [12; 24]) and the hopelessly queenless colonies (18 [14; 29]; T = 21; P = 0.508).

3.3. Dispersal into apiaries

After two weeks, SHB were found in all experimental apiaries in Australia and South Africa (Tab. I). SHB numbers were significantly higher than those of possibly missed SHB (T \leq 1; *P* < 0.05) with the exception of

Table II. Comparisons of SHB colony infestation levels between the 1st and 2nd inspections. Results of the χ^2 -goodness-of-fit tests as comparisons of relative SHB distribution over colonies between the two inspections and of the Spearman rank correlation of colony infestation levels between the two inspections are shown.

	Goodness-of-fit-test				Spearman rank correlation			
Region	Apiary	χ^2	df	Р	r _s	t	df	Р
South Africa	A _{SA} 1	23.6	5	< 0.001	0.51	1.20	4	0.296
	$A_{SA}2$	34.4	5	< 0.001	-0.12	-0.23	4	0.827
	$A_{AU}2$	42.9	5	< 0.001	0.71	2.04	4	0.111
Australia	$A_{AU}3$	262	4	< 0.001	-0.30	-0.54	3	0.624
	$A_{AU}4$	159.3	9	< 0.001	0.56	1.92	8	0.092
Florida	$A_{FL}1$	1440.8	9	< 0.001	0.18	0.50	8	0.627
Maryland	$A_{MD}1$	27.8	5	< 0.001	0.35	0.74	4	0.500
	$A_{MD}2$	21.5	5	< 0.001	0.79	2.62	4	0.059

 E_{SA2} (T = 8.5; P = 0.675). In sharp contrast, no SHB were found in any of the experimental apiaries in Maryland ($E_{MD}1 - E_{MD}4$), in spite of neighbouring infested commercial apiaries (≤ 3.5 km away). The Australian apiaries were significantly more highly infested than apiaries in South Africa or Maryland (Tab. I).

The average temperature, the relative humidity and the number of rainy days during the survey periods are shown in Table III.

3.4. Dispersal at different habitat patches

 $E_{AU}2$ located in a meadow was less heavily infested than the other three Australian experimental apiaries located in or next to a forest, at all three inspections (Tab. IV). In fact, no SHB were found at $E_{AU}2$ at the 3rd and 4th inspection.

4. DISCUSSION

Colonies were re-infested by SHB in every commercial apiary, but SHB did not disperse into all experimental ones. While the experimental apiaries in Maryland remained un-infested, those in South Africa and Australia became re-infested. In or next to forested areas, experimental apiaries showed higher re-infestation levels suggesting that the apiary site can influence SHB dispersal. Neither colony position nor queen status influenced SHB colony infestation levels, suggesting that they are less relevant for SHB dispersal.

The re-infestation of 95% of all commercial colonies indicates that SHB readily disperse within apiaries. Even in the low infested Maryland region (Spiewok et al., 2007), 92% were re-infested within two weeks. SHB from outside the apiaries might also have contributed to these numbers, but since no SHB influx into the experimental apiaries in Maryland could be detected (see below), the majority or all of the collected SHB most likely originated from within the respective apiary. However, in Florida, a considerable proportion of SHB may have additionally flown in from an adjacent honey house causing the high reinfestation level (Spiewok et al., 2007).

Although it is known from other beetles that populations with a higher density are more sedentary (den Boer, 1971; Davis, 1986), there was a positive correlation between the average apiary infestation levels and the re-infestation levels, suggesting that SHB also leave established aggregations. SHB might switch between colonies even by walking since SHB, which did not seem to be recently hatched from the ground, were also found in the litter underneath and around colonies. Therefore, the common practice of installing hives on palettes might facilitate SHB exchange between neighbouring colonies.

Since at every apiary the relative SHB distribution over the same colonies differed significantly between the 1st and 2nd inspection, colony position alone seems to be

high

ther.			
Factors	Maryland	South Africa	Australia
Average temperature in °C	23 ± 3	21 ± 2	21 ± 3
Relative humidity in %	24 [21; 27]	21 [20; 22]	22 [19; 23]
Number of rainy days	1	5	5
SHB population numbers	low	low	high
Wild/feral colony density	low	high	high
Apiary density	low	low	low/high
Ongoing SHB mass reproduction	no	no	yes

none

Table III. Factors possibly influencing the SHB infestation rate of newly installed apiaries in the investigated regions. The terms "high" and "low" for the different regions are not absolute, but in relation to each

Table IV. Total number of SHB collected from the colonies during three inspections from the Australian experimental apiaries. Collected SHB were removed from the colonies at each inspection. ANOVA-values are given for infestation level comparisons for each inspection. Different letters indicate significant differences within the respective inspection (Newman-Keuls test, $\alpha = 0.05$).

Infestation rate

Apiaries	2nd	3rd	4th
	inspection	inspection	inspection
E _{AU} 1	1109 ^a	488 ^a	256 ^a
$E_{AU}2$	125 ^b	0^{b}	0^{b}
$E_{AU}3$	560 ^a	109 ^c	49 ^{a,b}
$E_{AU}4$	828 ^a	376 ^a	233 ^a
ANOVA			
F ₃	12.43	15.85	5.01
MS	0.82	0.09	0.69
Р	< 0.001	< 0.001	0.009

less relevant for host attractiveness. Although queenless colonies show decreased defensiveness (Delaplane and Harbo, 1987), queenloss did not induce higher SHB infestation levels. Thus, the underlying reasons for SHB aggregations in single colonies still remain unclear, because other factors such as colony phenotype (Spiewok et al., 2007), hive entrance size (Ellis et al., 2003a) or sun exposure (Ellis and Delaplane, 2006) have no significant influence on SHB infestation level either. A simple explanation for massive aggregations might be the invasion of a migrating SHB swarm into a colony (Tribe, 2000). Furthermore, SHB might be attracted by volatiles released by associated yeast (Kodamaea ohmeri; Torto et al., 2007) that could be active only in some colonies.

Infestation of experimental apiaries was detected in Africa and Australia but not in Maryland. We want to point out that those in Maryland were already present for more than three months without any sign of infestation despite the presence of infested apiaries in close vicinity, indicating low SHB dispersal activity over long distances under these conditions.

low

Climatic and seasonal factors certainly have an impact on insect dispersal (Johnson, 1969) and may also trigger SHB dispersal (e.g. more infestations during the rainy season in Africa, Mutsaers, 1991). However, we consider them less relevant for the observed differences in the infestation of experimental apiaries between Maryland and the other regions, due to only minor differences in weather conditions (Tab. III). The more frequent rainy days in South Africa and Australia might have triggered SHB dispersal (Lundie, 1940; Mutsaers, 1991; Elzen et al., 2000), but it did not rain in Australia between the 2nd and 4th inspection and many SHB still infested the colonies. Repeated inspections during different weather conditions are required to determine the potential influence of ambient temperature and/or rain on SHB dispersal. Climatic conditions could also affect SHB dispersal by influencing population size.

Since the distances between infested commercial and non-infested experimental apiaries were similar in the respective regions $(\sim 3 \text{ km})$, we suggest that the differences in SHB dispersal is caused by other local factors such as SHB population numbers, SHB mass reproduction or host density (apiaries and wild/feral colonies, Tab. III).

As SHB are primarily associated with honeybees, SHB dispersal is most likely to be connected to host colony availability. According to the concept of metapopulation dynamics in epidemiology (Lawton et al., 1994; Grenfell and Harwood, 1997), every honeybee colony or apiary represents a habitat patch for SHB. Therefore SHB metapopulation dynamics are likely to be influenced by host population density. At lower apiary density, e.g. in Maryland and South Africa, SHB immigration might be less likely since more isolated habitat patches show a low colonization rate when individual movement ranges are limited (Hanski, 1999).

Apart from commercial apiaries, SHB also infest feral/wild colonies (Benecke, 2003), which may serve as connecting points between apiaries and as a reservoir for SHB, thereby fostering infestation of newly installed apiaries. While the density of feral/wild colonies is high in Australia and South Africa (Oldroyd et al., 1997; Hepburn and Radloff, 1998; Benecke, 2003; Moritz et al., 2007) it seems to be low in the USA (Ratnieks et al., 1991; Krause and Page, 1995). However, the density of feral colonies might change in the South-western USA with the establishment of African honeybee populations, thereby positively affecting SHB population build-up and dispersal.

Apiary infestation levels seem to be influenced by the respective habitat. Since honeybee hosts are often cavity nesting in trees (Hepburn and Radloff, 1998), dispersing SHB might prefer to head towards more suitable habitats (e.g. forests), where the chances of finding a host are higher. Indeed, in contrast to the apiaries in forested areas, only few or no immigrating SHB could be detected in M_{AU}2, which was located in a meadow lacking shade and nesting cavities. Lundie (1940) suggested that abundant alternative food sources are one reason for different apiary infestation levels but it seems that SHB do not use fruits and flowers in the presence of bees (Buchholz et al., 2008).

SHB mass reproduction in surrounding areas might result in higher infestation levels because host colonies are usually destroyed and both parental SHB and adult offspring have to search for a new host. Alternatively, in the absence of any honeybee colonies they could use alternative habitats, exploiting fruits (Eischen et al., 1999) or nests of other social bees (Mutsaers, 2006; Spiewok and Neumann, 2006) and await the arrival of new colonies. Thus, the high immigration numbers in Australia, especially in the remote areas, might be explained by SHB originating from decayed feral colonies.

In conclusion, there is no evidence that high SHB infestation levels are induced by colony characteristics as colony size, amount of stores and brood, queen state or colony position. Consequently, they cannot be prevented by manipulating these factors. SHB dispersal appears to be influenced by local factors, but the data from Maryland suggest that long distance dispersal may be more restricted than previously thought. This is in line with genetic studies, suggesting low SHB exchange between U.S. apiaries (Evans et al., 2003). Therefore, the main mode of SHB spread over longer distances seems to be human-mediated jump dispersal, e.g. via migratory beekeeping or bee packages (Hood, 2000; Caron et al., 2001), as it is the case of many invasive species (Suarez et al., 2001). As a consequence, the control of SHB dispersal should focus on humanmediated spread.

Control should take into account SHB dispersal within apiaries. We therefore suggest the simultaneous treatment of all colonies at an apiary. Otherwise, treated colonies could easily become re-infested from untreated neighbouring ones, as in case of *V. destructor* (Ritter, 1988). This is especially important for highly infested apiaries because the re-infestation level increases with the average apiary infestation level.

ACKNOWLEDGEMENTS

We like to thank all beekeepers for kindly providing access to their colonies. Appreciation is also addressed to Nelles Ruppert, Sven Buchholz, Katharina Merkel and Sandra Mustafa who contributed substantially during the inspections. Two anonymous referees made constructive comments on the manuscript. Financial support was granted to PN by the German Federal Ministry for Consumer Protection, Food and Agriculture through the Federal Agency for Agriculture and Food and a visiting fellowship at the University of Western Sydney.

Les populations du Petit coléoptère des ruches, *Aethina tumida* II : dispersion des Petits coléoptères des ruches.

Aethina tumida | parasite *| Apis mellifera |* dynamique des populations *|* dispersion *|* facteur anthropique

Zusammenfassung – Populationen des Kleinen Beutenkäfers Aethina tumida II: Ausbreitung des Kleinen Beutenkäfers. Die Kenntnis über die Ausbreitungsfähigkeit von Schadinsekten ist wichtig für deren Kontrolle. Hier berichten wir von der Befallsdynamik von zuvor unbefallenen Kolonien durch Kleine Beutenkäfer (= KBK), Aethina tumida, einem Parasiten von Honigbienenvölkern. Um die Ausbreitung des Kleinen Beutenkäfers zwischen den Völkern eines Bienenstandes zu untersuchen, wurden die Reinfektionsgrade von 71 Käfer-freien Kolonien nach zwei Wochen in zehn kommerziellen Bienenständen in Südafrika, Australien und den USA bestimmt (Abb. 1). Die Reinfektion von 95 % aller Bienenvölker weist auf einen hohen Austausch von KBK zwischen Kolonien desselben Bienenstandes hin (Tab. I). Weisellosigkeit oder Kolonieposition hatten dabei keinen Einfluss auf die Befallsstärke der Völker (Tab. II). Allerdings gab es eine signifikante positive Korrelation zwischen der durchschnittlichen Befallszahl eines Standes und dessen Reinfektionshöhe. Der Zuflug von KBK von außerhalb in die Bienenstände wurde bestimmt, indem die Reinfektionszahlen von zwölf KBK-freien, experimentellen Bienenständen mit je fünf bzw. sechs Kolonien nach zwei Wochen untersucht wurden. Die Ausbreitungsaktivität unterschied sich zwischen den verschiedenen Regionen. Während die experimentellen Bienenstände in Maryland nicht befallen wurden, wurden diese in Australien und Südafrika reinfiziert (Tab. I). Faktoren wie die Dichte von Bienenständen, die KBK-Populationsgröße sowie das Vorkommen von wilden Bienenvölkern scheinen einen Einfluss auf die Ausbreitungsaktivität des KBK zu haben (Tab. III). Der ausbleibende Zuflug von KBK in Maryland deutet daraufhin, dass die Wanderimkerei der Hauptweg für die Ausbreitung des KBK über lange Distanzen ist; insbesondere in Gegenden mit geringen KBK-Populationsgrößen. Während drei aufeinanderfolgenden Inspektionen von Australischen Bienenständen, wies ein Stand auf einer Wiese konstant geringere Befallszahlen auf als die drei übrigen Stände in einem bewaldeten Gebiet. Das Habitat eines Bienenstandes scheint somit dessen Befallszahlen beeinflussen zu können (Tab. IV). Angesichts unserer Ergebnisse, sollte die Behandlung von Völkern gegen KBK an einem Bienenstand stets zeitgleich stattfinden, um eine Reinfektion mit Käfern aus unbehandelten Völkern zu vermeiden. Wenn möglich, sollten zudem die oben genannten Faktoren bei der Einrichtung eines Bienenstandes berücksichtigt werden. Um die Ausbreitung des KBK innerhalb einer Region besser kontrollieren zu können, sollte der Fokus auf die Wanderung mit Bienenvölkern gelegt werden.

Aethina tumida / Apis mellifera / Ausbreitung / Kleiner Beutenkäfer / Honigbiene

REFERENCES

- Benecke F.S. (2003) Commercial Beekeeping in Australia. A report for the rural industries research and development corporation. RIRDC Publication No. 03/037, RIRDC, Barton, ACT, Australia.
- Buchholz S., Schäfer M.O., Spiewok S., Pettis J.S., Duncan M., Ritter W., Spooner-Hart R., Neumann P. (2008) Alternative food sources of *Aethina tumida* (Coleoptera: Nitidulidae), J. Apic. Res. 47, 202–209.
- Caron D.M., Park A., Hubner J., Mitchell R., Smith I.B. (2001) Small hive beetle in the Mid-Atlantic states, Am. Bee J. 141, 776–777.
- Davis M.A. (1986). Geographic patterns in the flight ability of a monophagous beetle, Oecologia 69, 407–412.
- Delaplane K.S., Harbo, J.R. (1987) Effect of queenlessness on worker survival, honey gain and defence behaviour in honeybees, J. Apic. Res. 26, 37–42.
- den Boer P.J. (1971) On the dispersal power of carabid beetles and its possible significance, Miscell. Paper LH Wageningen 14, 90.
- Eischen F.A., Westervelt D., Randall C. (1999) Does the small hive beetle have alternate food sources? Am. Bee J. 139, 125.
- Ellis J.D., Delaplane K.S. (2006) The effects of habitat type, ApilifeVAR, and screened bottom boards on small hive beetle (*Aethina tumida*) entry into honey bee (*Apis mellifera*) colonies, Am. Bee J. 146, 537–539.
- Ellis J.D., Delaplane K.S., Hepburn H.R., Elzen P.J. (2003a) Efficacy of modified hive entrances and a bottom screen device for controlling *Aethina tumida* (Coleoptera: Nitidulidae) infestations in *Apis mellifera* (Hymenoptera: Apidae) colonies, J. Econ. Entomol. 96, 1647–1652.
- Ellis J.D., Hepburn H.R., Delaplane K.S., Elzen P.J. (2003b) A scientific note on small hive beetle

(*Aethina tumida*) oviposition and behaviour during European (*Apis mellifera*) honey bee clustering and absconding events, J. Apic. Res. 42, 47–48.

- Elzen P.J., Baxter J.R., Westervelt D., Randall C., Delaplane K.S., Cutts L., Wilson W.T. (1999) Field control and biology studies of a new pest species, *Aethina tumida* Murray (Coleoptera, Nitidulidae) attacking European honey bees in the Western hemisphere, Apidologie 30, 361–366.
- Elzen P.J., Baxter J.R., Westervelt D., Randall C., Wilson W.T. (2000) A scientific note on observations of the small hive beetle, *Aethina tumida* Murray (Coleoptera, Nitidulidae) in Florida, USA, Apidologie 31, 593–594.
- Evans J.D., Pettis J., Hood W.M., Shimanuki H. (2003) Tracking an invasive honey bee pest: mitochondrial DNA variation in North American small hive beetles, Apidologie 34, 103–109.
- Greatti M., Milani N., Nazzi F. (1992) Reinfestation of an acaricide-treated apiary by *Varroa jacobsoni* Oud., Exp. Appl. Acarol. 16, 279–286.
- Grenfell B., Harwood J. (1997) (Meta)population dynamics of infectious diseases, Trends Res. Ecol. Evol. 12, 395–399.
- Hanski I. (1999) Metapopulation ecology, Oxford University Press, New York.
- Hepburn H.R., Radloff S.E. (1998) Honeybees of Africa, Springer Verlag, Berlin.
- Hood W.M. (2000) Overview of the small hive beetle *Aethina tumida* in North America, Bee World 81, 129–137.
- Igeta Y., Esaki K., Kato K., Kamata N. (2003) Influence of light condition on the stand-level distribution and movement of the ambrosia beetle *Platypus quercivorus* (Coleoptera: Platypodidae), Appl. Entomol. Zool. 38, 167–175.
- Johnson C.G. (1969) Migration and dispersal of insects by flight, Methuen, London.
- Krause B., Page R.E. Jr (1995) Effect of Varroa jacobsoni (Mesostigmata: Varroidae) on feral Apis mellifera (Hymenoptera: Apidae) in California, Environ. Entomol. 24, 1473–1480.
- Lawton J.H., Nee S., Letcher A.J., Harvey P.H. (1994) Animal distributions: patterns and processes, in: Edwards P.J., May R.M., Webb N.R. (Eds.), Large-scale Ecology and Conservation Biology, Blackwell, Oxford, pp. 41–58.
- Lundie A.E. (1940) The small hive beetle *Aethina tumida*, Science Bulletin 220, Dept. Agr. Forestry, Government Printer, Pretoria.

- Moritz R.F.A., Kraus F.B., Kryger P., Crewe R.M. (2007) The size of wild honeybee populations (*Apis mellifera*) and its implications for the conservation of honeybees, J. Insect Conserv. 11, 391–397.
- Mutsaers M. (1991) Bees in their natural environment in South-western Nigeria, Nigerian Field 56, 3–18.
- Mutsaers M. (2006) Beekeepers' observations on the small hive beetle (*Aethina tumida*) and other pests in bee colonies in West and East Africa, in: Veselý V., Titira D. (Eds.), Proc. 2nd Eur. Conf. Apidology EurBee, Prague Czech Republic, p. 44 [online] http://www.eurbee.org/Files/Sbornik% 20EurBee%20pro%20web250107.pdf (accessed on 16 September 2008).
- Nalepa C.A., Kennedy G.G., Brownie C. (2005) Role of visual contrast in the alighting behavior of *Harmonia axyridis* (Coleoptera: Coccinellidae) at overwintering sites, Environ. Entomol. 34, 425– 431.
- Neumann P., Elzen P.J. (2004) The biology of the small hive beetle (*Aethina tumida* Murray, Coleoptera: Nitidulidae): Gaps in our knowledge of an invasive species, Apidologie 35, 229–247.
- Oldroyd B.P., Thexton E.G., Lawler S.H., Crozier R.H. (1997) Population demography of Australian feral bees (*Apis mellifera*), Oecologia 111, 381–387.
- Ratnieks F.L.W., Piery M.A., Cuadriello I. (1991) The natural nest and nest density of the Africanized honey bee (Hymenoptera, Apidae) near Tapachula, Chipas, Mexico, Can. Entomol. 123, 353–359.
- Ritter W. (1988) Varroa jacobsoni in Europe, the tropics, and subtropics, in: Needham G.R., Page R.E. Jr, Delfinado-Baker M., Bowman C.E. (Eds.), Africanized honey bees and bee mites, Ellis Horwood Ltd., Chichester, pp. 349–359.
- Rijnsdorp A.D. (1980) Pattern of movement in and dispersal from a dutch forest of *Carabus problematicus* Hbst. (Coleoptera, Carabidae), Oecologia 45, 274–281.
- Solbreck C. (1980) Dispersal distances of migrating pine weevils, *Hylobius abietis*, Coleoptera: Curculionidae, Entomol. Exp. Appl. 28, 123–131.
- Spiewok S., Neumann P. (2006) Infestation of commercial bumblebee (*Bombus impatiens*) field colonies by small hive beetles (*Aethina tumida*), Ecol. Entomol. 31, 623–628.
- Spiewok S., Neumann P., Hepburn H.R. (2006) Preparation of disturbance-induced absconding of Cape honeybee colonies (*Apis mellifera capensis* Esch.), Insectes Soc. 53, 27–31.

- Spiewok S., Pettis J., Duncan M., Spooner-Hart R., Westervelt D., Neumann P. (2007) Small hive beetle, *Aethina tumida*, populations I: Infestation levels of honeybee colonies, apiaries and regions, Apidologie 38, 595–605.
- Strom B.L., Rotton L.M., Goyer R.A., Meeker J.R. (1999) Visual and semiochemical disruption of host finding in the southern pine beetle, Ecol. Appl. 9, 1028–1038.
- Suarez A.V., Holway D.A., Case T.J. (2001) Patterns of spread in biological invasions dominated by longdistance jump dispersal: Insights from Argentine ant, Proc. Natl. Acad. Sci. USA 98, 1095–1100.
- Suazo A., Torto B., Teal P.E.A., Tumlinson J.H. (2003) Response of the small hive beetle (*Aethina tumida*) to honey bee (*Apis mellifera*) and beehiveproduced volatiles, Apidologie 34, 525–533.

- Torto B., Suazo A., Alborn H., Tumlinson J.H., Teal P.E.A. (2005) Response of the small hive beetle (*Aethina tumida*) to a blend of chemicals identified from honeybee (*Apis mellifera*) volatiles, Apidologie 36, 523–532.
- Torto B., Boucias D.G., Arbogast R.T., Tumlinson J.H., Teal P.E.A. (2007) Multitrophic interaction facilitates parasite– host relationship between an invasive beetle and the honey bee, Proc. Natl. Acad. Sci. USA 104, 8374–8378.
- Tribe G.D. (2000) A migrating swarm of small hive beetles (*Aethina tumida* Murray), S. Afr. Bee J. 72, 121–122.
- Wenning C.J. (2001) Spread and threat of the small hive beetle, Am. Bee J. 141, 640–643.