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Original article

Confinement of small hive beetles (*Aethina tumida*) by Cape honeybees (*Apis mellifera capensis*)

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Abstract – In this study we quantify small hive beetle (*Aethina tumida* Murray) and Cape honeybee (*A.m. capensis* Esch., an African subspecies) behaviours that are associated with beetle confinement in an effort to understand why Cape bees can withstand large beetle infestations. Four observation hives were each inoculated with 25 beetles and were observed for 11–17 days. Data collected included guard bee (worker bees who guard beetle confinement sites) and confined beetle behaviour. There was considerable colony variation for many bee and beetle behaviours. Overall, there were more beetle guards during evening, which was likely an effort to keep increasingly active beetles contained. About one-fifth of the beetles were found at the comb periphery although the colonies suffered no ill effects. Although beetles reached the combs, the bees were able to prevent beetle reproduction. Our data suggest that confinement is more likely an initial defence against invading beetles and not the sole reason African subspecies of honeybees are usually immune to beetle infestations while European bees are not.

***Aethina tumida* / *Apis mellifera* / confinement / Cape honeybee / defense behavior**

1. INTRODUCTION

The confinement of small hive beetles, *Aethina tumida* Murray (Coleoptera: Nitidulidae), in cracks and crevices throughout hives and their continual guarding by worker bees of African subspecies of *Apis mellifera* L. was noted by Hepburn and Radloff (1998) and explored in further detail by Neumann et al. (2001) and Solbrig (2001). Although beetle-naïve, subspecies of European honeybees were also discovered to confine and guard these beetles (Ellis et al., 2003b, c); however, they remain susceptible to depredation caused by beetles while their African counterparts rarely do (Ellis et al., 2003a).

One explanation for differing susceptibilities of European and African bees to beetle depredation could be that the relative efficacy of beetle confinement and guarding might differ between subspecies (Solbrig, 2001; Ellis et al., 2003b). However, studies on confinement behaviour of African bees have not been conducted in precisely the same way as studies on the behaviour by European bees; therefore, it has not been possible to make a direct comparison between confinement schemes of African and European honeybees.

In this study, we quantify the behaviour of an African honeybee subspecies, the Cape honeybee (*A.m. capensis* Escholtz), to determine if there are any significant differences in the behavioural repertoires of African and European subspecies of honeybees that could explain their different susceptibilities to beetle infestations. Further, we describe morning and evening differences in these behaviors as honeybees are less active at evening (Kaiser, 1988; Moritz and Southwick, 1992) and the nocturnal activity peaks of small hive beetles recorded in the United

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States (Ellis et al., 2003b) may be present in Africa as well. By comparison to data on beetle confinement by European bees (Ellis et al., 2003b, c), our data aid in determining if confinement is (1) essential to the relative immunity of African bees to beetles, (2) an initial defence of European and African bees against invading beetles, or (3) a more general defence by honeybees against small colony intruders.

2. MATERIALS AND METHODS

Experiments were conducted in Grahamstown, South Africa (January–March 2003) using four observation colonies (each containing two frames of brood, one of honey, about 8 000 bees, and a laying queen). All bees, combs, and queens were from established colonies of Cape honeybees and in a geographic region where beetles commonly occur. A transparent grid, which divided each side of the colony into 160 squares (each 5 cm^2) was used to define intra-colonial locations that consisted of the top wall (above the uppermost frame), bottom board, front wall, back wall, and rest of the colony (among the combs).

Twenty-five, unsexed beetles were randomly introduced into each hive 2–3 days after the hives were established. Random assignments of beetles minimized the chance of sex-specific behaviours biasing the results. Hives were monitored twice daily (at about hours 0800 and 2000) once beetles were confined and guarding behaviour by workers was apparent (after 24 hours). During the 2000 hour, hives were observed under red-light conditions in order to minimize disturbances.

At each monitoring interval, the observer moved across the top row of the grid, from left to right, and then down one block (or one 5 cm^2 area) in the grid, followed by another left to right motion. This pattern was followed from top to bottom on both sides of the hive. Neither beetles nor workers were counted twice in any observation, because guard bees and beetles do not readily move between locations in the nest. The entire procedure lasted about 30 minutes per hive. Data were collected for 17 subsequent days for 2 colonies, 16 for a third, and 11 for a fourth.

Intra-colonial distribution, behaviour, and number of confined beetles, and number and behaviour of worker honeybee guards were recorded. Observed beetle behaviours included resting, antennal contact with guard bees, trophallactic contact with guard bees, and mating. Guard bee behaviour included biting at, antennal contact with, and trophallactically feeding beetles, and biting the area around beetle prisons. Neumann et al. (2001), Solbrig (2001), and Ellis et al. (2003b, c) collectively described these same beetle and guard bee behaviours in both African and European honeybees. All behaviours are reported as the proportion of observed individuals performing a given behaviour. This is important when reporting beetle behaviour, as the total number of introduced beetles (n = 25) was not always observed. Three main reasons exist for our inability to locate all of the beetles: (1) beetles are often difficult to observe, especially if well-hidden, (2) it is possible that there was drift between colonies by beetles, and/or (3) the beetles may have left the colonies completely.

Data analysis

Guard bee and beetle behavioural data were analysed with a repeated measure ANOVA design recognizing time (morning and evening) and colony (1, 2, 3, or 4) as main effects. Where analysed data were proportions (as with bee and beetle behaviours), the data were transformed before analyses using arcsin-proportion to stabilize the variance. Where applicable, means were separated using Tukey's test. There was an interaction between time and colony for the number of guard bees per beetle, so this variable was analysed by colony using dependent variable *t*-tests. Beetle intra-colonial distribution was tested for differences between times using Pearson's χ^2 tests. All differences were accepted at the $\alpha \le 0.05$ level and all analyses were conducted using the software package Statistica (2001).

3. RESULTS

3.1. Confinement dynamics

The number of guard bees per beetle was analysed by colony because of the significant interaction between time and colony (Tab. I). Although the interaction term was significant, the difference in the number of guard bees per beetle during morning and evening between each colony was a matter of differing magnitudes between each colony (colony 1 morning: 0.74 ± 0.10, evening: 1.11 ± 0.09; colony 2 morning: 0.54 ± 0.06, evening: 0.75 ± 0.05; colony 3 morning: 0.81 ± 0.07, evening: 1.38 ± 0.12; colony 4 morning: 0.69 ± 0.04, evening: 1.07 ± 0.07, mean standard error, n = 11, 17, 17, and 16 for colonies 1, 2, 3, and 4 respectively). Indeed there were significantly more guard bees per confined beetle during evening than morning in all colonies [$4.8 \le t \le 5.6$; df = 10, 16, 16, 15 (colonies 1, 2, 3, and 4 respectively); $0.00004 \le P \le 0.0002$]. Colony effects (Tab. I) indicated that colonies 1 and 3 had more guard bees per beetle than colony 2, with the number

Table I. Analysis of variance testing effects of colony (c), time (t), and time × colony (t × c) on confinement dynamics, confined beetle behaviour, and guard bee behaviour.

variable	source	df	F	P
confinement dynamics				
number of guard bees per beetle	c	3	8.2	0.0001
	t	1	93.9	<0.0001
	t × c	3	4.0	0.0119
number of prisons per colony	c	3	17.4	<0.0001
	t	1	1.8	0.1831
	t × c	3	1.8	0.1538
number of beetles per prison	c	3	44.6	<0.0001
	t	1	1.4	0.2358
	t × c	3	1.0	0.4197
number of guard bees per prison	c	3	6.3	0.0009
	t	1	26.4	<0.0001
	t × c	3	0.9	0.4247
beetle behaviour				
resting	c	3	6.5	0.0008
	t	1	11.4	0.0013
	t × c	3	1.5	0.2169
making antennal contact with guard bees	c	3	2.9	0.0413
	t	1	37.0	<0.0001
	t × c	3	0.5	0.7110
getting fed by guard bees	c	3	2.7	0.0543
	t	1	9.8	0.0028
	t × c	3	0.4	0.7816
mating	c	3	4.4	0.0079
	t	1	1.7	0.1915
	t × c	3	1.0	0.4137
guard bee behaviour				
biting at beetles	c	3	6.3	0.0009
	t	1	3.7	0.0611
	t × c	3	0.5	0.6908
making antennal contact with beetles	c	3	1.0	0.3795
	t	1	1.4	0.2346
	t × c	3	1.0	0.4018
feeding beetles	c	3	2.8	0.0464
	t	1	1.5	0.2193
	t × c	3	1.1	0.3574
prison wall-working	c	3	2.7	0.0523
	t	1	2.0	0.1663
	t × c	3	1.2	0.3137

of guard bees per beetle in colony 4 not being different from those in any other colony (Tab. II).

There were no time effects or time × colony interactions for the number of confinement sites (prisons) per colony or the number of beetles per prison although there were colony effects for both (Tab. I). The number of prisons per colony was significantly higher in colony 4 than in all other colonies (Tab. II). Colonies 1, 2, and 3 had similar numbers of prisons (Tab. II). Further, colony 2 had the most beetles per prison, followed by colonies 3, 1, and 4 in decreasing order (Tab. II).

The number of guard bees per prison varied significantly by time and colony (Tab. I). There were more guard bees per prison during evening than during morning (Tab. III). Further, colonies 3 and 2 had the highest number of guard bees per prison followed by colonies 1 and 4 in decreasing order (Tab. II). There were no time × colony interactions for this variable (Tab. I).

3.2. Beetle behaviour

There were colony and time effects for the proportion of beetles resting and making antennal contact with guard bees (Tab. I). Beetles rested more in colonies 4 and 2, followed in colonies 1 and 3 in decreasing order (Tab. II). There were also more beetles resting during the morning than evening (Tab. III). Beetles made antennal contact with guard bees more in colony 3 than in 4 (Tab. II). The proportion of beetles making antennal contact with guard bees in colonies 1 and 2 was not different from those in any other colony. Further, more beetles made antennal contact with guard bees during evening than morning (Tab. III). There were no time × colony interactions for either variable (Tab. I).

There were no colony effects or time × colony interactions for the proportion of beetles being fed by guard bees (Tab. I); however, there was a time effect (Tab. I). Beetles were fed more during evening than morning (Tab. III). Also, there were no time effects or time × colony interactions for the proportion of beetles mating although there were colony effects (Tab. I). Beetles mated more in colony 3 than in colonies 2 and 4 (Tab. II). The proportion of

Table II. Colony effects for confinement dynamics, and guard bee and confined beetle behaviour.

	colony 1	colony 2	colony 3	colony 4
confinement dynamics				
number of guard bees per beetle	0.92 ± 0.08a	0.65 ± 0.04b	1.09 ± 0.09a	0.88 ± 0.05a, b
number of beetle prisons per colony	7.05 ± 0.51a	6.50 ± 0.24a	6.00 ± 0.30a	10.19 ± 0.52b
number of beetles per prison	2.25 ± 0.16a	3.87 ± 0.16b	2.60 ± 0.15a	1.61 ± 0.09c
number of guard bees per beetle prison	1.97 ± 0.19a, b	2.52 ± 0.22a	2.62 ± 0.24a	1.45 ± 0.14b
beetle behaviour				
resting	0.67 ± 0.04a	0.75 ± 0.02a, b	0.64 ± 0.03a	0.83 ± 0.02b
making antennal contact with guard bees	0.19 ± 0.03a, b	0.16 ± 0.02a, b	0.23 ± 0.03a	0.11 ± 0.02b
getting fed by guard bees	0.06 ± 0.01a	0.03 ± 0.01a	0.06 ± 0.01a	0.02 ± 0.01a
mating	0.05 ± 0.02a, b	0.01 ± 0.01a	0.05 ± 0.01b	0.01 ± 0.01a
guard bee behaviour				
biting at beetles	0.53 ± 0.04a, b	0.66 ± 0.03b	0.50 ± 0.04a	0.46 ± 0.03a
antennal contact with beetles	0.16 ± 0.02a	0.17 ± 0.02a	0.15 ± 0.02a	0.11 ± 0.02a
feeding beetles	0.07 ± 0.02a	0.03 ± 0.01a	0.05 ± 0.01a	0.02 ± 0.01a
biting the area around beetle prisons	0.11 ± 0.03a	0.16 ± 0.02a	0.12 ± 0.02a	0.07 ± 0.02a

For beetle and guard bee behaviour, data are the proportion of individuals observed doing the particular behaviour. Values are mean standard error. For all colony 1, 2, 3, and 4 data, n = 11, 17, 17, and 16 respectively. Row totals followed by the same letter are not different at the $\alpha \leq 0.05$ level. Means were compared using Tukey's test.

Table III. Time effects on confinement dynamics, confined beetle behaviour, and guard bee behaviour.

	morning	evening
confinement dynamics		
number of guard bees per beetle*	0.69 ± 0.03	1.07 ± 0.05
number of beetle prisons per colony	7.26 ± 0.37a	7.60 ± 0.33a
number of beetles per prison	2.70 ± 0.15a	2.56 ± 0.15a
number of guard bees per beetle prison	1.73 ± 0.11a	2.61 ± 0.18b
beetle behaviour		
resting	0.76 ± 0.02a	0.69 ± 0.02b
making antennal contact with guard bees	0.12 ± 0.01a	0.22 ± 0.02b
getting fed by guard bees	0.03 ± 0.01a	0.05 ± 0.01b
mating	0.03 ± 0.01a	0.02 ± 0.01a
guard bee behaviour		
biting at beetles	0.58 ± 0.03a	0.50 ± 0.03a
antennal contact with beetles	0.15 ± 0.02a	0.15 ± 0.01a
feeding beetles	0.04 ± 0.01a	0.04 ± 0.01a
biting the area around beetle prisons	0.13 ± 0.02a	0.10 ± 0.01a

For beetle and guard bee behaviours, data are the proportion of individuals observed doing the particular behaviour. Values are mean standard error; n = 61 for all data. Where applicable, row totals followed by the same letter are not different at the $\alpha \leq 0.05$ level. Means were compared using ANOVAs. *This variable was analysed by colony because of a significant time × colony interaction; therefore, Tukey's test is not applicable.

beetles mating was not different between colony 1 and any other colony (Tab. II).

3.3. Guard bee behaviour

There was a colony effect but no time effect or time × colony interaction for the proportion of guard bees biting at confined beetles (Tab. I). Higher proportions of guard bees in colony 2 were biting at beetles than in 3 and 4 (Tab. II). The proportion of guard bees biting at beetles was not different between colony 1 and any other colony (Tab. II).

There were no colony or time effects or time × colony interactions for the proportion of guard bees making antennal contact with beetles or biting the area around beetle prisons (Tab. I). Further, there were no time effects or time × colony interactions for the proportion of guard bees feeding beetles. There was an overall colony effect for the proportion of guard bees feeding beetles (Tab. I) although Tukey mean comparison tests indicated that means for no two colonies were different at the 0.05 level (Tukey colony separation values: $0.0714 \leq P \leq 0.9864$).

3.4. Intra-colonial beetle distribution

Intra-colonial beetle distributions remained consistent between morning and evening ($\chi^2 = 4.6$, df = 4, $P = 0.3256$) (Tab. IV). The highest proportions of beetles were found on the bottom board (~ 33%) and front wall (~23%) of the colonies, followed by the combs (~22%), back wall (~18%), and top wall (~4%; percentages are average percentages of beetles found in each location during morning and evening based on the data in Tab. IV). Although 22% of the beetles were found among the combs, most (>90% based on visual estimations) of the beetles reaching the combs were kept out of the brood, honey, and pollen areas by bee aggression and were being guarded by workers in empty cells around the comb periphery.

4. DISCUSSION

We propose using 'confinement' as opposed to 'social encapsulation' (previously used by Neumann et al., 2001 and Ellis et al., 2003b, c) because encapsulation implies that trapped beetles are actively encased in prison-like structures (of wax or propolis) especially made for beetles. Actually, we found that beetles are restricted (or confined) to these locations by guard bees but are not completely encapsulated and sealed off; such locations can be voids, crevices, or cracks created by propolis deposits of the kind that beetles seek out, giving the impression that propolis was used especially for beetle confinement. Newly introduced or free-roaming beetles run from bee aggression into cracks and crevices throughout the colony (Schmolke, 1974) and we observe that it is at these places workers guard. Such sites can even include individual cells within the combs. We conclude that workers do not actively encapsulate beetles; they only station guards where invading beetles hide.

Table IV. Proportion of beetles confined to various intra-colonial locations during morning and evening.

Location	Morning	Evening
top wall of hive	0.03 ± 0.01	0.05 ± 0.01
bottom board of hive	0.34 ± 0.03	0.32 ± 0.03
front wall of hive	0.23 ± 0.03	0.23 ± 0.03
back wall of hive	0.17 ± 0.02	0.19 ± 0.02
combs	0.23 ± 0.03	0.21 ± 0.03

Values are mean standard error; $n = 61$ for all data.

Our data highlight a number of quantitative differences in confinement efforts between the four colonies tested. However, due to the almost complete absence of time × colony interactions, behavioural trends were similar for every colony during morning and evening suggesting that all colonies handled beetles similarly, unlike that observed for European colonies (Ellis et al., 2003b). Despite these minor differences, our results show that confinement schemes of Cape and European subspecies of honeybees are not apparently different within the limits of this study.

The number of guard bees per beetle for each colony was within the same range reported for guard bees per beetle in European-derived colonies (Ellis et al., 2003b). Further, trends were similar between both European and Cape bees for the number of beetle prisons and guard bees per beetle, both increasing during evening in European (Ellis et al., 2003b) and Cape colonies (Tabs. II and III). Increased guard bee presence during evening may be a response to increased beetle activity during evening in an effort to keep increasingly active beetles confined (Ellis et al., 2003b). If so, that more beetle guards are present in the colony during evening may suggest that some foragers engage in prison guarding, although most foragers remain inactive during evening (Kaiser, 1988; Moritz and Southwick, 1992) and evidence suggests that foraging and guarding subpopulations are distinct groups of workers (Moore et al., 1987; Breed et al., 1990).

Another possibility is that workers guarding beetle confinement sites are a distinct subpopulation of 'guard' bees not previously considered. Breed et al. (1990) has shown that guarding behaviour, in general, can be further compartmentalized based on indications that genetically and behaviourally different workers perform different subsets of guarding duties (including those workers entrance guarding, 'soldiering', and perhaps even beetle guarding).

The number of beetle prisons per Cape colony was only moderately higher than the range reported for European bees (Ellis et al., 2003b). It is unlikely that the number of prisons per colony affects the success workers have at containing beetle outbreaks. Instead beetle density may be more crucial (Ellis et al., 2003c) and the number of beetles per prison (or density per prison) for Cape bees in our study was similar to that reported for European bees (Ellis et al., 2003b).

Beetle activity in Cape (Solbrig, 2001 and present study) and European colonies (Ellis et al., 2003b) increased during evening (indicated by there being fewer beetles resting in the evening than during day). This increase in beetle activity corresponded to an increase in their soliciting for food and getting fed in the evening by Cape bees. Similar results have been found for European bees (Ellis et al., 2003b). These findings make the trophallactic relationship between workers and beetles quite unclear. Beetles are obviously afforded a benefit by the behaviour, as they are able to feed while being confined away from foodstuffs in the nest (Ellis et al., 2002). However, in both European and Cape colonies, workers feed beetles more when beetle activity increases (Solbrig, 2001; Ellis et al., 2003b) and this may indirectly benefit the bees as fed beetles may be less likely to escape confinement.

Ellis et al. (2003b) found that the proportion of guard bees biting at beetles in three European colonies was similar to those found in this study on Cape bee colonies. This suggests that this particular behaviour by guard bees of both Cape and European origin is very similar quantitatively. However, aggressive similarities between both bee subspecies may only hold true in instances of beetle confinement as worker bees from African colonies are generally more aggressive toward free-roaming beetles than are European bees (Elzen et al., 2001). Concerning prison wall working, Cape bees never reached the level of this behaviour reported for European bees (Ellis et al., 2003b).

There was considerable variation between colonies for a number of the measured parameters. This variability may suggest that there are environmental and/or genotypic effects on confinement behaviours. However, we cannot speculate on the possibility of genotypic effects because the true lineages of the colonies were not known. It is important that more studies be done where the genetic origin of the bees are known.

In earlier work on beetle confinement by Cape bees (Solbrig, 2001) it was found that most beetles were restricted to areas on the bottom board. Lundie (1940) noted this for beetles in African colonies as well. Our data and that of Schmolke (1974) do not support this although more beetles were found on the bottom board in this study than in the European bee studies (Ellis et al., 2003b) (however, intra-colonial beetle location in observation hives may not accurately reflect beetle location in full, Langstroth-style hives). The proportion of beetles restricted to various intra-colonial locations did not vary with time although it did in European colonies (Ellis et al., 2003b). This may indicate that at low intra-colonial populations, beetles move around more freely in European, but not Cape, colonies. If this is true, then the free-roaming beetles may play a crucial role in successful reproduction. Regardless, about one-fifth of the beetles were found at the comb periphery (as opposed to only ~7% in the European study, Ellis et al., 2003b) although the colonies suffered no ill effects. Therefore, although beetles reached the combs, the workers were able to keep the beetles from reproducing.

Our results suggest that beetle confinement by Cape bees is not apparently different from that in European bees except that confinement behaviour seems to be more consistent over time within Cape colonies than within European ones. This further suggests that confinement may be a general defence against small nest intruders or the first line of defence against beetle invaders (hypotheses 2 and 3) and not the sole reason Cape bees are virtually immune to beetle infestations while European bees are not (hypothesis 1) (Ellis et al., 2003b). However, to more confidently assert this it is important that direct comparisons between Cape and European bees under the same environmental conditions be made in the future. Regardless, our data suggest that additional factors external to confinement efforts (such as soil moisture, colony strength, and especially bee hygienic behaviour towards beetle eggs) are probably responsible for Cape bee immunity to beetles.

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Résumé – Confinement du Petit Coléoptère des ruches (*Aethina tumida*) par les abeilles du Cap (*Apis mellifera capensis*). Dans cette étude nous quantifions les comportements du Petit Coléoptère des ruches (PCR), *Aethina tumida* Murray, et de l'Abeille du Cap (*Apis mellifera capensis* Escholtz) qui sont associés au confinement du coléoptère, afin de déterminer s'il existe des différences dans le répertoire comportemental des sous-espèces européennes et africaines d'abeilles domestiques qui pourraient expliquer leur différence de sensibilité vis-à-vis de l'infestation par ce coléoptère parasite. Nos données doivent aider à déterminer si le confinement est (i) indispensable à l'immunité relative des abeilles africaines vis-à-vis des PCR, (ii) une première défense des abeilles européennes et africaines contre l'invasion par le coléoptère ou (iii) une défense plus générale contre les petits intrus du nid. Vingt cinq PCR ont été introduits au hasard dans chacune des quatre colonies d'observation, deux à trois jours après l'installation des ruches. Les ruches ont été observées deux fois par jour (à 8 h et 20 h), une fois les PCR confinés et le comportement de garde mis en place (24 h plus tard). A chaque période d'observation, l'observateur balayait du regard une grille transparente divisée en carrés de 5 cm^2 en commençant par la rangée supérieure de gauche à droite, puis de nouveau de gauche à droite sur la rangée d'au-dessous. Ce schéma était répété du haut vers le bas sur les deux côtés de la colonie. Le comportement des PCR confinés et des abeilles gardiennes était enregistré. Les données ont été récoltées durant 17 j consécutifs pour deux colonies, 16 j pour la troisième et 11 j pour la quatrième. Un certain nombre de paramètres ont présenté des différences significatives (Tab. I et II). Pourtant, en raison de l'absence presque totale d'interaction temps × colonie (Tab. I), les tendances comportementales des gardiennes et des PCR étaient semblables pour toutes les colonies le matin et le soir (Tab. III). Il y a eu plus de gardiennes de PCR (abeilles gardant les lieux de confinement) le soir (Tab. III), ce qui correspondait vraisemblablement à un effort pour maintenir confinés les PCR de plus en plus actifs. Un cinquième environ d'entre eux a été observé à la périphérie du rayon (Tab. IV), bien que les colonies n'aient montré aucun effet dommageable. Nos résultas suggèrent que le confinement des PCR par les abeilles du Cap ne diffère pas de celui imposé par les abeilles européennes, sauf que le comportement de confinement semble plus stable dans le temps chez les premières. Finalement le confinement semble être un moyen de défense général contre l'intrusion de petits organismes ou la première réaction de défense contre les PCR (hypothèses 2 et 3) et non la seule raison expliquant l'immunité apparente des abeilles du Cap vis-à-vis des PCR contrairement aux abeilles européennes (hypothèse 1). Nos résultats impliquent donc que d'autres facteurs, indépendants de la réaction de confinement, sont probablement responsables de l'immunité des abeilles du Cap vis-à-vis du Petit Coléoptère des ruches.

***Aethina tumida* / *Apis mellifera capensis* / confinement / comportement défensif**

Zusammenfassung – Einsperrung des kleinen Beutenkäfers (*Aethina tumida*) durch Kap Honigbienen (*Apis mellifera capensis*). Wir quantifizierten das Verhalten des kleinen Beutenkäfers (*Aethina tumida* Murray) und der Kap Honigbienen (*A.m. capensis* Escholtz, eine afrikanische Unterart), um Unterschiede im Verhaltensrepertoire zwischen afrikanischen und europäischen Unterarten von Honigbienen zu bestimmen, die mit dem Einsperren des Käfers zusammenhängen. Mögliche Unterschiede könnten die unterschiedliche Empfindlichkeit der Unterarten gegenüber dem Befall durch den Käfer erklären. Unsere Daten sollen bei der Bestimmung helfen, ob das Einsperren (1) essentiell für die relative Immunität der afrikanischen Bienen gegen die Käfer ist, (2) eine anfängliche Abwehr von europäischen und afrikanischen Bienen gegen eindringende Käfer oder (3) eine allgemeine Abwehrreaktion von Honigbienen gegen alle kleinen Nesteindringlinge ist. Zwei bis drei Tage nachdem vier Beobachtungsvölker eingerichtet waren, wurden 25 Käfer zufällig in die Völker verteilt. Die Völker wurden zweimal täglich beobachtet (um 08:00 and 20:00 Uhr). Waren

die Käfer erst einmal eingesperrt, wurden sie von den Arbeiterinnen bewacht (24 Stunden später). Bei jedem Überwachungsintervall verfolgte der Beobachter die oberste Reihe eines Gitters von links nach rechts, dann eine Reihe tiefer im Gitter (oder eine Fläche von 5 cm^2), um anschließend von links nach rechts zu beobachten. Dieses Muster wurde von oben bis unten auf beiden Seiten des Volkes eingehalten. Das Verhalten von eingesperrten Käfern und Wächterbienen wurde bestimmt. Die Daten wurden bei zwei Völkern an 17 aufeinander folgenden Tagen erhoben, beim dritten waren es 16 und beim vierten 11 Tage. Es ergaben sich signifikante Unterschiede bei mehreren „Einsperrparametern" (Tab. I und II). Wechselwirkungen von Zeit × Volk waren fast nicht vorhanden (Tab. I). Deshalb waren die Trends im Verhalten von Wächterbienen und Käfern am Morgen und am Abend in allen Völkern ähnlich (Tab. III). Am Abend gab es mehr Wächter für Käfer (Arbeiterinnen, die die Gefängnisse der Käfer bewachen) (Tab. III), das wahrscheinlich auf der Bemühung beruhte die zunehmend aktiven Käfer in Schach zu halten. Etwa 1/5 der Käfer wurden in der Waben-Peripherie beobachtet (Tab. IV) obwohl die Völker keine Anzeichen von Befall zeigten. Auf Grund unserer Ergebnisse nehmen wir an, dass die „Käfergefängnisse" der Kap Honigbienen sich nicht von denen der europäischen Bienen unterscheiden. Allerdings ist das Einsperrverhalten bei Kapvölkern dauerhafter als bei den europäischen. Insgesamt scheint das Einsperren eine allgemeines Abwehrreaktion gegen kleine Eindringlinge im Nest oder nur die erste Verteidigungslinie gegen eindringende Käfer (Hypothesen 2 and 3) und nicht der einzige Grund für die Immunität der Kapbienen gegen den Befall durch den Käfer zu sein, während die europäischen Bienen nicht resistent sind (Hypothese 1). Unsere Ergebnisse lassen deshalb auf zusätzliche Faktoren schließen, die von den Einsperr-Reaktionen unabhängig sind und die wahrscheinlich zu der Immunität der Kapbienen gegen die Käfer führen.

***Aethina tumida* / *Apis mellifera* / Gefängnis / *A. tumida* Verhalten / Kaphonigbienen**

REFERENCES

Breed M.D., Robinson G.E., Page R.E. Jr. (1990) Division of labor during honey bee colony defence, Behav. Ecol. Sociobiol. 27, 395–401.

Ellis J.D. Jr., Pirk C.W.W., Hepburn H.R., Kastberger G., Elzen P.J. (2002) Small hive beetles survive in honeybee prisons by behavioural mimicry, Naturwissenschaften 89, 326–328.

Ellis J.D. Jr., Hepburn H.R., Delaplane K.S., Neumann P., Elzen P.J. (2003a) The effects of adult small hive beetles, *Aethina tumida* (Coleoptera: Nitidulidae), on nests and flight activity of Cape and European honey bees (*Apis mellifera*), Apidologie 34, 399–408.

Ellis J.D. Jr., Hepburn H.R., Ellis A.M., Elzen P.J. (2003b) Social encapsulation of the small hive beetle (*Aethina tumida* Murray) by European honeybees (*Apis mellifera* L.), Insectes Soc. 50, 286–291.

Ellis J.D. Jr., Hepburn H.R., Ellis A.M., Elzen P.J. (2003c) Prison construction and guarding behavior by European honeybees is dependent on inmate small hive beetle density, Naturwissenschaften 90, 382–384.

Elzen P.J., Baxter J.R., Neumann P., Solbrig A.J., Pirk C.W.W., Hepburn R., Westervelt D., Randall C. (2001) Behavior of African and European subspecies of *Apis mellifera* toward the small hive beetle, *Aethina tumida*, J. Apic. Res. 40, 40–41.

Hepburn H.R., Radloff S.E. (1998) Honeybees of Africa, Springer, Berlin, Germany.

Kaiser W. (1988) Busy bees need rest, too, J. Comp. Physiol. 163, 565–584.

Lundie A.E. (1940) The small hive beetle, *Aethina tumida*, South Africa Department of Agriculture and Forestry Entomological Series 3, Sci. Bull. 220.

Moore A.J., Breed M.D., Moor M.J. (1987) The guard honey bee: ontogeny and behavioural variability of workers performing a specialized task, Anim. Behav. 35, 1159–1167.

Moritz R.F.A., Southwick E.E. (1992) Bees as Superorganisms, Springer Verlag, Berlin, Germany, pp. 107–109.

Neumann P., Pirk C.W.W., Hepburn H.R., Solbrig A.J., Ratnieks F.L.W., Elzen P.J., Baxter J.R. (2001) Social encapsulation of beetle parasites by Cape honeybee colonies (*Apis mellifera capensis* Esch.), Naturwissenschaften 88, 214–216.

Schmolke M.D. (1974) A study of *Aethina tumida*: the small hive beetle, Certificate in Field Ecology Project Report, University of Rhodesia.

Solbrig A.J. (2001) Interaction between the South African honeybee, *Apis mellifera capensis* Esch., and the small hive beetle, *Aethina tumida* Murray, Diplomarbeit, Freie Universitt Berlin, Institut fr Zoologie, Berlin, Deutschland.

Statistica (2001) System reference, version 6, StatSoft, Tulsa, Oklahoma, p. 1063.