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The biology of the small hive beetle (*Aethina tumida*, Coleoptera: Nitidulidae): Gaps in our knowledge of an invasive species

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Abstract – Small hive beetles, *Aethina tumida*, are honeybee parasites native to Africa, where they are a minor pest only. In contrast, the beetles can be harmful parasites of European honeybee subspecies. Resistance of African subspecies to infestations is probably due to quantitative differences in a series of behaviours such as absconding, aggression, removal of parasite eggs and larvae and social encapsulation. The beetles use counter-resistance tactics such as defence posture, dropping, hiding, escape, egg laying in small gaps and trophallactic mimicry. Small hive beetles are efficient in long-range transportation (US: 1996, Australia: 2002) and can establish populations in temperate regions due to their overwintering capacity in honeybee clusters. Host shifts to other bee species may also occur. Thus, small hive beetles have the potential to become a global threat to apiculture and wild bee populations. However, our knowledge of the small hive beetle is still limited, creating demand for more research in all areas of its biology.

Apis mellifera / *Aethina tumida* / honeybee / invasive species / small hive beetle

1. INTRODUCTION

In recent decades, the frequency of biological invasions has increased to an unprecedented level, stimulating a multitude of research projects in population biology and community ecology (Hänfling and Kollmann, 2002). The small hive beetle, *Aethina tumida* Murray, a nest parasite of honeybees, *Apis mellifera* L., constitutes a recent example of such an invasive species in populations of European host subspecies. Here we summarize the literature on the biology and the current distribution of the small hive beetle. We will concentrate on examining the more proximate aspects of the biology of the beetle and the host that may contribute to the invasion process. This is particularly important because successful and

sustainable control efforts require a detailed understanding of the invasion dynamics and of the biology of an invasive species.

2. THE SMALL HIVE BEETLE

The small hive beetle was first described by Murray (1867) and is native to Africa (Fig. 1). It belongs to the coleopteran family Nitidulidae, which contains ~2800 described species in 172 genera worldwide (Habeck, 2002). The nitidulid beetles can be distinguished from other similar beetles by their transverse procoxal cavities, grooved metacoxae, dilated tarsal segments, small fourth tarsi and three-segmented antennal club (Habeck, 2002). The nitidulid beetles can feed on fresh, rotten and

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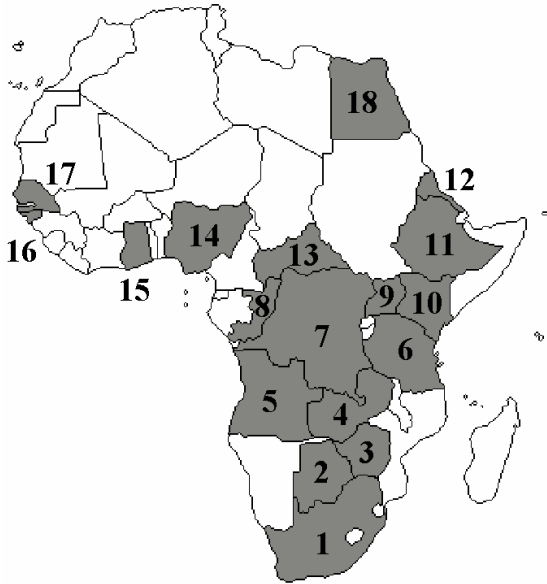


Figure 1. Records of the small hive beetle in Africa (March 2003): 1- South Africa: Walter (1939a, b); Lundie (1940, 1951, 1952a, b); May (1969); Anderson et al. (1983); 2- Botswana: Phokedi (1985); 3- Zimbabwe: Mostafa and Williams (2000); 4- Zambia: Clauss (1992); 5- Angola: Rosário Nunes and Tordo (1960); 6- Tanzania: Smith (1960); Ntenga (1970); Ntenga and Mugongo (1991); 7- Democratic Republic of Congo: Aurelien (1950); Dubois and Collart (1950); 8- Congo Republic: Castagné (1983); 9- Uganda: Roberts (1971); 10- Kenya: Mostafa and Williams (2000); 11- Ethiopia: Mostafa and Williams (2000); 12- Eritrea: Mostafa and Williams (2000); 13- Central African Republic: Lepissier (1968); 14- Nigeria: Mutsaers (1991); 15- Ghana: Gorenz (1964); Adjare (1990); 16- Guinea Bissau: Svensson (1984); 17- Senegal: N'diaye (1974); 18- Egypt: Mostafa and Williams (2000), probably recently introduced (see Chap. 3.2).

dried fruits, plant juices, carrion, crops and on flowers (Lin et al., 1992; Fadamiro et al., 1998; Hepburn and Radloff, 1998; Smart and Blight, 2000; Wolff et al., 2001). The natural history and morphology of *A. tumida* were described by Lundie (1940) and Schmolke (1974).

2.1. Pest status and putative life cycle in Africa (Fig. 2)

Here we focus on the life cycle aspects necessary to understand and control the beetle. Other features are reported in more detail elsewhere (Lundie, 1940, 1951, 1952a, b; Schmolke, 1974; Hepburn and Radloff, 1998; Elzen et al., 2000c; Hood, 2000; Pettis and Shimanuki, 2000; Flügge, 2001; Neumann et al., 2001a, b; Swart et al., 2001; Ellis et al., 2002b, c, d). In its native range, the small hive beetle is usually a minor pest only, because successful reproduction appears most successful in weak, stressed colonies or in recently abandoned honeybee nests and is far less common in strong colonies (Lundie, 1940; Schmolke, 1974; Hepburn and Radloff, 1998; Fig. 2). In Africa, the main problems associated with the beetles are in the destruction of stored bee products (Lundie, 1940; Schmolke, 1974; Fig. 2), which most likely result from a

lack of bee populations to guard against reproduction. However, neither the beekeeping terms “weak/stressed” vs. “strong/unstressed” colonies nor the actual levels of beetle reproduction in such colonies have been rigorously quantified yet. This appears of prime importance to understand the biology of *A. tumida*.

Strong African honeybee colonies, even if heavily infested (Neumann et al., 2001b; Neumann and Härtel, 2004), can usually prevent or postpone successful beetle reproduction (Hepburn and Radloff, 1998; Fig. 2). In such colonies small hive beetles usually have to wait until non-reproductive swarming (= absconding or migration, Hepburn and Radloff, 1998; see 4.8) leads to recently abandoned nests (Fig. 2). Massive aggregations of small hive beetles and/or heavy infestations appear to induce absconding in Africa (Fig. 2). But neither beetle-induced absconding nor the potential effects of colony movements on levels of infestation and parasite population sizes are well understood (see 4.8). This seems highly relevant because parasite population sizes may trigger pest severity. The underlying reasons for the occurrence of beetle aggregations are also unclear (see 4.9).

Host finding (see 4.1) and intrusion into the colony (see 4.2) are most relevant for the invasion process (Fig. 2), but neither the actual

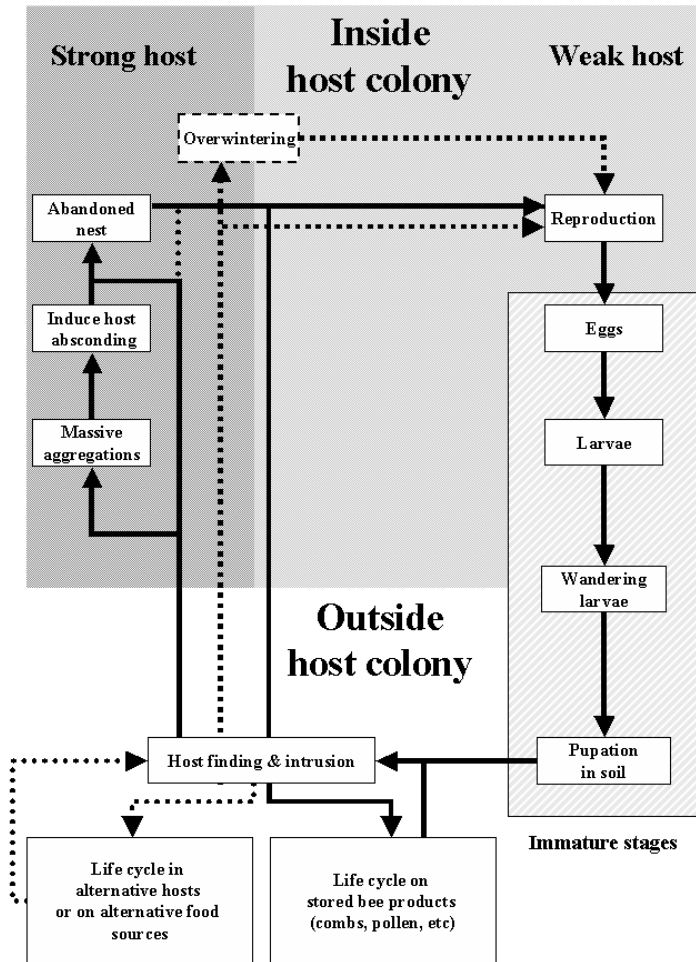


Figure 2. Putative life cycle of the small hive beetle (dotted lines = rare events or unclear; dashed lines and dashed box = colonies of European honeybee subspecies only).

cues nor the underlying mechanisms have been identified yet. Female beetles oviposit in the host colonies (see 4.7). The emerging larvae (see 4.7) develop until the wandering stage and then leave the nest for pupation in the soil (Fig. 2). While the adults have little impact on the colony, the larvae can cause severe damage to combs (Lundie, 1940; Schmolke, 1974), often resulting in the full structural collapse of the nest (Hepburn and Radloff, 1998). Newly emerged adults invade host colonies, thereby completing the life cycle of *A. tumida* (Fig. 2). In the laboratory, the life cycle can also be completed on fruits (see 2.2) and in bumble bee colonies (see 5; Fig. 2). However, the level

of reproduction and feeding on fruits in the wild has not been studied, which seems important to investigate this potential transmission pathway. Likewise, the ability of small hive beetles to infest bumble bee colonies in the field is unknown. This should be investigated to evaluate the potential impact of small hive beetles on wild bumble bee populations.

2.2. Alternative food sources

Small hive beetles may use fruits as alternative food sources (Schmolke, 1974; Eischen et al., 1999; Ellis et al., 2002c) in the absence of honey bee colonies, e.g. following removal

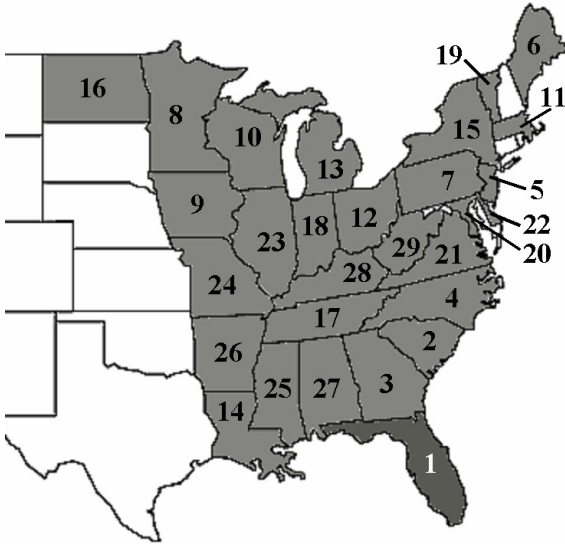


Figure 3. Current distribution of the small hive beetle in the USA (March 2003; J. Pettis [USDA], unpublished data). It has been reported in 29 states so far (year reported in brackets): 1- Florida (1998), 2- South Carolina (1998), 3- Georgia (1998), 4- North Carolina (1998), 5- New Jersey (1999), 6- Maine (1999), 7- Pennsylvania (1999), 8- Minnesota (1999), 9- Iowa (1999), 10- Wisconsin (1999), 11- Massachusetts (1999), 12- Ohio (1999), 13- Michigan (1999), 14- Louisiana (2000), 15- New York (2000), 16- North Dakota (2000), 17- Tennessee (2000), 18- Indiana (2000), 19- Vermont (2000), 20- Maryland (2001), 21- Virginia (2001), 22- Delaware (2001), 23- Illinois (2001), 24- Missouri (2001), 25- Mississippi (2001), 26- Arkansas (2002), 27- Alabama (2002), 28- Kentucky (2002), 29- W. Virginia (2003); dark area = severe damage.

of colonies in migratory beekeeping (Eischen et al., 1999). Moreover, a complete life cycle can be achieved on fruits (Ellis et al., 2002c; Fig. 2). However, although larvae develop normally on avocado, cantaloupe, grapefruit and some other fruit with over 500 beetles observed in one cantaloupe (Eischen et al., 1999), the number of offspring per breeding couple is significantly lower than on bee products such as pollen (Ellis et al., 2002c). Furthermore, small hive beetles have never been observed to reproduce or even feed on fruits in the field in South Africa (M.F. Johannsmeier, unpublished data). Likewise, there are no reports that small hive beetles are a crop pest in Southern Africa (M.F. Johannsmeier, unpublished data). Therefore, reproduction on fruits appears to be rare if not absent in natural populations. This might be related to the different reproductive success on different diets (Ellis et al., 2002c). Although successful reproduction is in principal possible on other diets, small hive beetles should prefer honeybee colonies whenever possible to maximize their reproductive output. However, the actual amount of small hive beetle reproduction on fruits has never been rigorously investigated in the field. Therefore, we cannot completely exclude that the presence of an abundant food source other than honeybee colonies may serve as a refuge for the small hive beetle and as a source of further infestations.

3. CURRENT DISTRIBUTION, PEST STATUS AND PUTATIVE LIFE CYCLE IN POPULATIONS OF EUROPEAN HONEYBEES

3.1. Current distribution and pest status in the USA

The first confirmed detection of small hive beetles in the US was in St. Lucie, Florida in June 1998, as identified by the Florida Department of Agriculture and Consumer Services (Hood, 2000; Sanford, 2002). Earlier, unidentified specimens were collected in Charleston, South Carolina, in November 1996 (Hood, 1999a). The introduction of the small hive beetle into the USA was thought to have been through South Carolina and from there to Georgia and Florida (Hood, 2000). Since then, the small hive beetle has extended its range from 18 states by the end of 2001 (Hood, 2001), over 25 states in April 2002 (Evans et al., 2003), to 29 states in March 2003 (Fig. 3). This rapid spread is likely to result from natural range expansion and movement of infested honeybee colonies, migratory beekeeping, package bees and beekeeping equipment (Delaplane, 1998). Mt-DNA sequence analyses of the small hive beetle from the US and South Africa indicate that the populations on both continents belong to a single species,

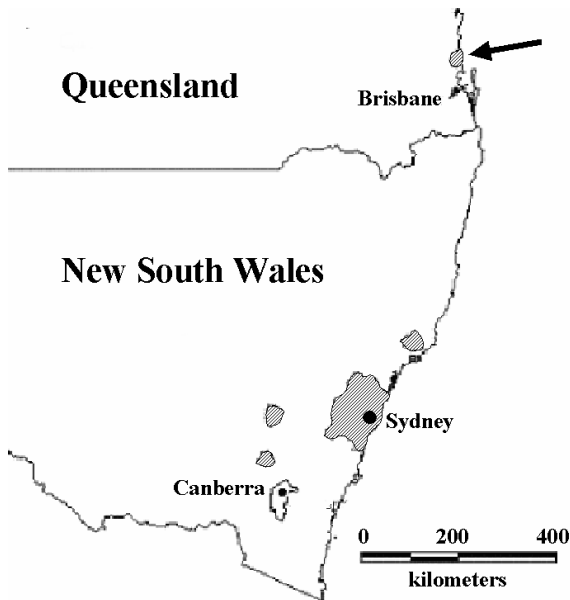


Figure 4. Current distribution of the small hive beetle in Australia (March 2003; shaded areas and arrow = small hive beetle infestations; picture courtesy of P. Boland, modified).

although it is not clear whether a single or multiple introductions occurred (Evans et al., 2000, 2003). Even strong colonies of European honeybee subspecies can be taken over and killed by small hive beetles in the US (Sanford, 1998; Elzen et al., 1999a, b). The state most severely affected by the small hive beetle has been Florida (Elzen et al., 2002; Fig. 3) and the damage to local apiculture can be serious (Elzen et al., 2000b). Indeed, only in 1998 in Florida losses were estimated to be in excess of \$3 million (Ellis et al., 2002c).

3.2. Current distribution and pest status in Australia and Egypt

In July 2002 beetle damage was noticed in a nucleus colony in New South Wales (M. Duncan, unpublished data). The beetles were identified as *A. tumida* in October 2002 (Animal Health Australia, 2003). In March 2003, the small hive beetle is still fairly restricted in its occurrence (D. Anderson [CSIRO], M. Beekman, P. Boland [Biosecurity Australia], L. Cook [NSW Agriculture] and M. Duncan, unpublished data; Fig. 4). At present, the beetle is causing no noticeable losses (D. Anderson [CSIRO], unpublished data). In contrast to the US, strong colonies don't collapse with the beetle (D. Anderson [CSIRO], M. Duncan, unpublished data).

In Egypt, small hive beetles were first detected in Etaie Al-Baroud (~110 km North-West of Cairo) in Summer 2000 (Mostafa and Williams, 2000). Since then, the small hive beetle was also found in other apiaries along the Nile Delta (A.M. Mostafa, unpublished data). *A. tumida* is probably not endemic to Egypt (H.R. Hepburn, A.M. Mostafa and B. Schrickler, personal communications). In order to clarify whether the small hive beetle is native to Egypt or has been introduced, it seems necessary to investigate its distribution in upper Egypt, which is more close to its sub-Saharan endemic region (Fig. 1). At present, reports on the small hive beetle in both Australia and Egypt are largely anecdotal and more detailed studies are urgently required.

3.3. Putative life cycle in colonies of European honeybees (Fig. 2)

There seems to be two differences in the putative life cycle of small hive beetles in colonies of European honeybee subspecies in the US (Fig. 2).

3.3.1. Overwintering capacity (Fig. 2)

European honeybee subspecies form a winter cluster in colder climates to survive longer periods of cold weather conditions (Gates, 1914; Corkins, 1930), a behaviour which is not

expressed in African subspecies (Hepburn and Radloff, 1998). Despite its tropical origin, adult small hive beetles can overwinter within such clusters (Elzen et al., 1999a; Hood, 2000), where >300 beetles have been reported in small clusters (Pettis and Shimanuki, 2000). This is quite surprising, even in light of low aggression levels by the European bees (Elzen et al., 2001). It seems as if small hive beetles have adapted to temperate climates by exploiting the cluster behaviour of European subspecies. Thus, although -12°C for 24 hours is reported to kill all life stages of the beetle (Hood, 1999b), it is obvious that small hive beetles are able to survive in colder climates and have the potential to establish populations across a significant part of the US (Evans et al., 2003). Indeed, there are established beetle populations as far North as Ohio (Evans et al., 2003). More detailed studies are required to understand how small hive beetles can survive in the winter clusters. However, the establishment of beetle populations alone cannot explain the severe effects of infestations in US honeybee populations.

3.3.2. *Life history short-cut (Fig. 2)*

In contrast to African subspecies, even strong colonies of European honeybee subspecies can be taken over and killed by small hive beetles in the US (Sanford, 1998; Elzen et al., 1999a, b; Fig. 2). Weakened and stressed colonies may even succumb within two weeks (Wenning, 2001). Thus, successful reproduction of the parasite seems to be more common in strong European colonies in the US (Fig. 2). It seems as if small hive beetles in European colonies in the US do not have to wait for recently abandoned nests or for favourable time windows (see Mutsaers, 1991). This constitutes a short-cut in the life history enabling successful reproduction more often than in African host populations.

What are the underlying reasons for such a life history short-cut? It might well be that European honeybee subspecies lack behavioural resistance mechanisms and therefore the small hive beetle is a serious threat. Indeed, the presence of large numbers of small hive beetles in African honeybee colonies does not significantly affect adult bee populations, brood area and foraging behaviour although small hive beetle presence significantly low-

ered all of these variables in European colonies (Ellis et al., 2003a). This indicates that behavioural characteristics are important to understand resistance towards small hive beetle infestations. In the following chapters we will address such behaviours in detail.

4. BEHAVIOURAL INTERACTIONS BETWEEN HOST AND PARASITE

4.1. Host finding (Fig. 2)

Adult small hive beetles are active flyers (Elzen et al., 1999b, 2000c) and individuals or occasionally swarms (Tribe, 2000) can infest honeybee colonies. It has been stated (Wenning, 2001), that small hive beetles can detect colonies under stress, e.g. due to disease or management techniques such as splitting, and that they are able to detect such colonies from a distance of about 13–16 km. Detection of stressed colonies might be adaptive in Africa, where reproduction is more likely in such colonies than in unstressed ones (Hepburn and Radloff, 1998). However, the actual mechanism which might allow small hive beetles to detect stressed colonies over large distances is unclear (see 4.9). Baited trap studies show that a combination of honey/pollen and adult bees is highly attractive to flying beetles, whereas adult bees alone are less attractive and brood, hive products and infested combs alone are not attractive (Elzen et al., 1999b). This indicates that an intact honeybee colony with food storage is most likely the preferred breeding place of small hive beetles.

4.2. Host intrusion (Fig. 2)

Honeybee colonies have highly specialized guard bees, that carefully scrutinize incoming individuals (Ribbands, 1953). However, the adult beetles can intrude strong honeybee colonies as well as weak ones with equal impunity (Lundie, 1940). Nevertheless, fewer beetles intruded into colonies with reduced entrances (Ellis et al., 2002a), suggesting that guard bees are capable of preventing intrusion at least to some degree. Beekeeping activities such as frequent inspections appear to facilitate beetle intrusion into host colonies. Some colonies have been reported to collapse after beekeepers have united them with other highly-infested supers (Sanford, 2002).

4.3. Aggression towards adult beetles

4.3.1. Host tactics

A. m. scutellata and *A. m. capensis* protect themselves by active aggression towards both the adults and larvae (Lundie, 1940; Elzen et al., 2001; Neumann et al., 2001b). The bees try to bite or sting the adults but usually with only little success (Lundie, 1940; Elzen et al., 2001; Neumann et al., 2001b; Swart et al., 2001). In the few cases, when the adult beetles are decapitated (Neumann et al., 2001b) or extremities are removed (Schmolke, 1974), they are thrown out of the hive (Lundie, 1952b). Observations that small hive beetles can live for long periods of time even in strong colonies with relative impunity (Lundie, 1940) also suggest that aggression is not very effective in killing the beetles. This may be partly due to the hard exoskeleton (Lundie, 1940) but also due to the following defence tactics of the adult beetles.

4.3.2. Parasite tactics

4.3.2.1. Defence posture

When attacked, the adults can perform a turtle-like defence posture (Lundie, 1940; Schmolke, 1974; Neumann et al., 2001b). While exhibiting this defence posture the beetle stays motionless and tucks its head underneath the pronotum with the legs and antennae pressed tightly to the body (much like withdrawal in a turtle, Neumann et al., 2001b).

4.3.2.2. Running

Beetles usually move very quickly out of the range of bees (Schmolke, 1974; Neumann et al., 2001b).

4.3.2.3. Dropping

The beetles can deliberately drop from the combs to escape pursuit (Schmolke, 1974).

4.3.2.4. Hiding

Inside of the nest cavity, the adults typically hide in small cracks (Schmolke, 1974; Neumann et al., 2001b), under the bottom board of commercial hives (Lundie, 1940) or in cells (Schmolke, 1974; personal observations). While

hiding in cells, small hive beetles usually stay motionless at the bottom (Lundie, 1940; Schmolke, 1974). When field colonies are inspected, the adult beetles are often seen moving from one hiding place to another one nearby (Lundie, 1940; Swart et al., 2001). This also happens on a regular basis in observation hives (Neumann et al., 2001b).

Nevertheless, although aggression is not very effective in killing the beetles, it may contribute to resistance. African honeybees show significantly more investigative contact and aggression behaviour to the adults than European ones (Elzen et al., 2001). About 1/3 of all encounters between African bees and adult beetles resulted in attacks by the workers, whereas this was only 1.4% in European bees (Elzen et al., 2001). Therefore, the adult beetles are probably under constant harassment in an African colony, which may minimize beetle reproduction.

4.4. Social encapsulation

4.4.1. Host tactics

Sometimes the bees succeed in “corralling” (Elzen et al., 2000a, b) or “herding” (Swart et al., 2001) the adult beetles into specific corners, preventing them from moving freely over the combs. When such beetles are corralled, or when they actively hide in small gaps (Schmolke, 1974; Neumann et al., 2001b), they are often encapsulated in propolis confinements (*A. m. scutellata*: Hepburn and Radloff, 1998; *A. m. capensis*: Neumann et al., 2001b; Solbrig, 2001; Ellis et al., 2003b). This is not an artefact of observation hives because social encapsulation also occurs in normal field colonies (Neumann et al., 2001b). Corralling behaviour has never been observed in field colonies or natural nests. While it seems logically to assume that corralling occurs because it is a necessary part of social encapsulation, its occurrence can only be inferred at this point.

During the encapsulation process, workers add propolis around detected hidden or corralled beetles and completely encapsulate most of them (Neumann et al., 2001b). The bees have a sophisticated tactic for limiting beetle escape during encapsulation (Neumann

et al., 2001b). While some workers add propolis, one or more others continuously guard the beetles in both open and closed confinements day and night for up to 57 days (Neumann et al., 2001b). The guard workers continuously attack the beetles when they move to the edges of still open confinements and thus keep them imprisoned (Neumann et al., 2001b). Social encapsulation may be an additional factor for preventing or postponing successful reproduction of the parasite.

However, social encapsulation also occurs in susceptible European honeybee subspecies (Ellis et al., 2003c). Because the use of propolis is more abundant in African subspecies compared to European ones (Hepburn and Radloff, 1998) social encapsulation may be more efficient and/or more common in African honeybee colonies. Indeed, the number of confinements per colony and encapsulated beetles in these prisons were both lower in European colonies (Ellis et al., 2003c) than in African ones (Neumann et al., 2001b). Moreover, European honeybees guard prisons significantly longer than Cape honeybees (Ellis et al., 2003b). However, the underlying reasons for this or its effect on beetle survival and/or colony performance are unknown. African bees are more aggressive towards the small hive beetle (Elzen et al., 2001). Therefore, African prison guards may be more efficient in preventing beetle escape (Neumann et al., 2001b). Clearly, more detailed studies are necessary to evaluate to what extent social encapsulation triggers resistance towards small hive beetle infestations.

4.4.2. Parasite tactics

Some beetles manage to escape encapsulation at night (Neumann et al., 2001b), possibly because honeybees are generally less active at night (Moritz and Kryger, 1994). Matings in prisons and cannibalism among small hive beetles were also observed (Neumann et al., 2001b), which might enhance their survival in large prisons. Despite no access to food in the combs, imprisoned beetles may survive for two months or longer (Neumann et al., 2001b). However, their survival is not due to metabolic reserves, because starved beetles die within a fortnight (Flügge, 2001; Ellis et al., 2002c). The beetles approach the prison guard bees, extend their heads towards and make antennal

contact with the bees thus mimicking normal honeybee trophallaxis (Korst and Velthuis, 1982). Often workers respond with aggression, so it may take several attempts before the bees regurgitate food (Ellis et al., 2002d). Thus, long term survival of small hive beetles in prisons is probably also derived from behavioural mimicry (Ellis et al., 2002d).

4.5. Patrolling

Despite frequent searching, only few small hive beetles can be seen on the combs of strong colonies (Schmolke, 1974). This indicates that such colonies are able to prevent small hive beetle intrusion in the comb area at least to some degree by guarding this area. This comb guarding behaviour (= patrolling; Swart et al., 2001) seems to be more efficient in strong colonies due to the higher density of bees in the nest (Lundie, 1952b; Swart et al., 2001). Lundie (1952a) stated: "Any factor which so reduces the ratio of the population of a colony of bees to its comb surface that the bees are no longer able to protect the comb surface adequately is a precursor to the ravages of both the wax moth and *Aethina tumida*". The patrolling behaviour seems particularly well expressed in the brood area of the colony (Schmolke, 1974; Solbrig, 2001) but less well expressed in the outer frames and honey supers (personal observations). This might explain, why adult beetles may oviposit on outer frames and why larvae can appear on them after transport to the honey house. It appears as if the host becomes alerted by newly intruded beetles (Schmolke, 1974). We conclude that protection of the combs via patrolling/high bee density might contribute to resistance. However, this potential impact needs to be investigated in future studies.

4.6. Worker aggregation and cell content removal

When beetles manage to intrude into the comb area and hide in cells, African workers rapidly aggregate around them (S. Härtel and P. Neumann, unpublished data; W.R.E. Hoffmann, unpublished data). Then, the workers remove the contents of nearby honey, pollen and brood cells to get access to the hidden beetles (Schmolke, 1974; personal observations).

The bees get extremely agitated until the small hive beetle is finally removed from the comb area (personal observations) or deliberately shows the dropping behaviour (Schmolke, 1974). This behaviour may minimize small hive beetle oviposition on the combs.

4.7. Removal of small hive beetle eggs and larvae

4.7.1. Parasite tactics

Female beetles oviposit in batches or irregular clutches (Lundie, 1940; Schmolke, 1974) of up to 210 eggs (mean = 14 ± 20 eggs; S. Härtel and P. Neumann, unpublished data) throughout the hive, but seem to prefer small gaps and the bottom of cells (Lundie, 1940; Schmolke, 1974). At initial stages of infestation, when no larvae are present, females significantly oviposit in cracks rather than on the combs (S. Härtel and P. Neumann, unpublished data). Nevertheless, females can also oviposit on the combs, because super frames of infested colonies quickly show larvae after transport to the honey house (Lundie, 1940). On the combs oviposition seems to preferentially occur in pollen cells (>30 small larvae per cell; Lundie, 1940), probably because reproductive success can be very high on a pollen diet alone (Ellis et al., 2002c). The number of eggs laid per female is high in the first 24 hours after infestation (69 ± 15 eggs; S. Härtel and P. Neumann, unpublished data). Schmolke (1974) estimated about 1000 eggs per female in a three to four month period, after which oviposition declines. Oviposition of many eggs in gaps appears adaptive because survival chances for the offspring are enhanced (Neumann and Härtel, 2004).

4.7.2. Host tactics

4.7.2.1. Eggs

It has been reported that African workers do remove small hive beetle eggs (Swart et al., 2001). This removal was recently studied in *A. m. scutellata* field colonies (Neumann and Härtel, 2004) by introduction of unprotected and protected eggs (laid in gaps). Whereas all unprotected eggs were removed within 24 hours, 66% of the protected eggs remained.

This indicates that unprotected eggs are efficiently removed but also shows that eggs laid in gaps are likely to hatch (Neumann and Härtel, 2004).

4.7.2.2. Larvae (jettisoning behaviour)

Bees which get hold of a larvae can carry it out of the hive at some distance (~20 meters; Lundie, 1940; Schmolke, 1974). Sometimes there is a tug-of-war between two jettisoning workers tearing apart one larvae and resulting in both bees carrying out of the hive what they are holding (Schmolke, 1974). This jettisoning behaviour seems to be efficient (Lundie, 1952b) because all introduced larvae were removed within 24 hours in an observation hive study (Schmolke, 1974). Likewise, all larvae (N = 700) introduced into seven *A. m. scutellata* field colonies were ejected within 24 hours (Neumann and Härtel, 2004). Field observations also indicate that larvae are efficiently ejected by jettisoning workers (Lundie, 1940; Swart et al., 2001).

African workers respond quickly to the presence of small hive beetle offspring because 72% of the non-protected eggs and 49% of the larvae were removed within one hour after introduction (Neumann and Härtel, 2004; see also Schmolke, 1974). The removal was not correlated with colony phenotypes (size, amount of open and sealed brood, pollen and honey area; Neumann and Härtel, 2004). However, Neumann and Härtel (2004) only studied relatively strong, unstressed colonies. Thus, these studies should be repeated with weak/stressed colonies. We conclude that removal behaviour plays an important role for the apparent resistance of African honeybees. However, it is unknown to what extent European bees remove small hive beetle eggs and larvae. Because prevention of beetle reproduction seems crucial, this behaviour should be more deeply investigated in the future.

4.8. Colony mobility: absconding and migration

African honeybee subspecies are much more mobile compared to European bees (Hepburn and Radloff, 1998). One can distinguish between two forms of non-reproductive swarming (Hepburn and Radloff, 1998).

4.8.1. Absconding

Absconding can be induced by severe disturbance, predation, and declining quality of the nest and/or nest cavity as well as by parasites (Hepburn and Radloff, 1998). The African subspecies are prone to absconding, queenright or not, and may abandon open and sealed brood and food stores as well (Hepburn and Radloff, 1998; Hepburn et al., 1999). African honeybee colonies can also respond to heavy small hive beetle infestations by absconding (Hepburn and Radloff, 1998; Fig. 2). However, it has also been shown that strong African colonies can tolerate large infestations with only minor colony level effects (Ellis et al., 2003a). Thus, it seems somehow contradictory that as if at times African colonies can tolerate large populations of small hive beetles, but at other times high infestation rates can induce abandonment of the nest. Several bees are probably involved in small hive beetle resistance (e.g. in prison guarding; Ellis et al., 2003b) when African colonies are heavily infested with hundreds of beetles (Neumann et al., 2001b; Neumann and Härtel, 2004). This might reduce colony efficiency in the long run because large scale infestations are a continuous and major predatory pressure on the honeybee nest (Hepburn and Radloff, 1998) and may favour beetle-induced absconding in Africa. Moreover, the occurrence of small hive beetle larvae and the resulting partial nest destruction and fermentation of the honey (Lundie, 1940) are also likely to play a role for beetle-induced absconding (M. Duncan, unpublished data; P. Neumann, unpublished data). There might be a seasonal pattern for beetle-induced absconding in Africa. Indeed, colony stress can be seasonal (Lundie, 1952b), e.g. it has been reported that small hive beetle damage may occur during the rainy season (Mutsaers, 1991). Finally, there might be an upper limit of infestation that can be tolerated, which is only exceeded in a few colonies due to massive beetle aggregations (see below). In any case, the underlying reasons for beetle-induced absconding are not fully understood yet and need further investigation.

4.8.2. Migration

Migration can be defined as a seasonally predictable phenomenon that may serve as an alternative to massive hoarding given the suit-

able flight temperatures and seasonal flowering of Africa (Hepburn and Radloff, 1998). Large scale migration of colonies without regard to reproduction are well documented for several African subspecies (Hepburn and Radloff, 1998). African colonies seem to prepare for migration by a reduction of egg-laying by the queen, waiting for the hatching of sealed brood, and consumption of stores (Hepburn and Radloff, 1998).

However, the distinction between the two forms is not absolute. There are also cases of “prepared” absconding (Hepburn and Radloff, 1998). This refers to only a few colonies in an apiary, while the majority stays behind, and can be regarded as migration on a small scale (Hepburn and Radloff, 1998). Similar to migration such colonies may also undergo preparation for nest desertion (see above). This behaviour has been recorded for several African subspecies (Hepburn and Radloff, 1998).

What are the effects of colony mobility on small hive beetle infestation levels and on parasite population densities? Any form of colony movement can be assumed to reduce colony levels of infestation with *A. tumida*, because the non-phoretic beetles are left behind. Moreover, the life cycle of the beetle is broken (Lundie, 1940). Reports that stationary hives were more vulnerable than hives that were moved on a regular basis (Lundie, 1940) point in that direction. On the other hand, recently abandoned nests after absconding, prepared absconding or migration are a breeding opportunity for small hive beetles because food stores and brood are not protected anymore. However, in such cases small hive beetles can be in strong competition with ants, which also exploit the recently abandoned nests (P. Neumann, personal observations). While both absconding and seasonal migration may interrupt the small hive beetle’s life cycle, it seems that migration (in which food stores are consumed before departure) would have a much more serious limiting effect on beetle populations than disturbance induced absconding, in which large food reserves can be left behind. Thus, beetle population densities in Africa, where host colonies migrate seasonally, might be smaller compared to populations of European honeybee subspecies. This may partially explain different pest severities. However, not a single study has compared small hive beetle

population sizes between the endemic and new ranges.

Although absconding is rare in European bees (Ruttner, 1986), it is also induced in infested European colonies (Ellis et al., 2003a). Because African subspecies are more prone to absconding than European bees (Hepburn and Radloff, 1998), another reason for better small hive beetle resistance/less pest severity may be that African bees are somehow more efficient in preparation for absconding and/or respond earlier with nest abandonment. We recommend more detailed studies on the effects of absconding and seasonal migration in future studies.

4.9. Small hive beetle aggregation pheromone?

Long range host finding of adults (Wenning, 2001) requires efficient cues. Furthermore, small hive beetle swarms can be occasionally observed in South Africa (Tribe, 2000). Massive aggregations of adult small hive beetles prior to the absconding of such heavily infested colonies can be found in Africa (Neumann et al., 2001b; Neumann and Härtel, 2004) and in the US (Elzen et al., 2002; Ellis et al., 2003a). In European honey bee hives, *A. tumida* infestations may consist of as many as 1000 adults and several hundred larvae per hive (Elzen et al., 1999b). In a single *A. m. scutellata* colony 491 adult beetles were found (Neumann and Härtel, 2004), while all other colonies at the same apiary show low infestation levels ($N = 7$ colonies; mean infestation level = 14 ± 12 beetles; S. Härtel and P. Neumann, unpublished data). These colonies with large numbers of beetles are neither particularly weak nor have massive food stores (Neumann et al., 2001b), indicating that cues other than simple host colony size and food stores are responsible for their attractiveness. Indeed, aggregation pheromones have been described for a variety of Nitidulidae species and are widely used as control agents (Petroski et al., 1994; James et al., 2000). Such pheromones are produced by exceptional large specialized cells within the body cavity of nitidulid beetles (Nardi et al., 1996). We consider it very likely that a similar pheromone plays a role for long range host finding and aggregations of small hive beetles. Observations that males tend to infest before females (Elzen

et al., 2000c) indicate that the aggregation pheromone might be male produced as in *Carpophilus obsoletus* and is attractive to both sexes (Petroski et al., 1994). Synergistic effects between food odours and aggregation pheromones for attracting small hive beetle might also play a role as shown for *Carpophilus lugubris* (Lin et al., 1992). However, in another nitidulid beetle, *Prostephanus truncatus*, the absence of upwind flight to food volatiles, or any synergism between pheromone and food volatiles suggests that the male-produced pheromone is the only known semiochemical for long-range host finding (Fadamiro et al., 1998). More research is needed to identify and evaluate the potential impact of different compounds such as aggregation pheromones, food volatiles, or any synergism between pheromone and food volatiles on the short and long-range dispersal and host selection of *A. tumida*.

5. ALTERNATIVE HOSTS (FIG. 2)

Bumblebees do not occur in sub-Saharan Africa but are native to North America (Michener, 2000). Recent laboratory studies indicate that a host shift of *A. tumida* to bumblebees may occur in its new range (Stanghellini et al., 2000; Ambrose et al., 2000). Bumblebee colonies, *Bombus impatiens*, artificially infested with small hive beetles had fewer live bees, more dead adult bees and greater comb damage than controls (Stanghellini et al., 2000; Ambrose et al., 2000). The bees did not show any aggression either towards the adult beetles or to the larvae (Stanghellini et al., 2000), indicating a lack of behavioural resistance. However, nest defence of bumblebees against small intruders has been described and species vary in their reactions (Michener, 1974). For example, *B. atratus* (Sakagami et al., 1967; Sakagami, 1976) and *B. (Robustobombus) melaleucus* (Hoffmann et al., 2004) tend to be more aggressive than other species.

Small intruders are stung and carried outside by bumblebee workers (Michener, 1974) similar to the jettisoning behaviour of honeybees (Lundie, 1940; Schmolke, 1974). Moreover, social encapsulation of small intruders in wax or propolis confinements has also been

described (Michener, 1974), but it is not known whether live intruders are also encapsulated. Colony defensiveness seems to be correlated with colony size, with smaller colonies being less defensive (Michener, 1974). Therefore, there might be considerable variance between bumblebee species and nests also with respect to small hive beetle resistance. More detailed studies on a variety of species and on a range of colony sizes are required to evaluate the susceptibility of bumblebees towards small hive beetle infestations.

Nevertheless, a new generation of small hive beetle was produced from adult to adult in each of the *B. impatiens* units which were held on soil (Stanghellini et al., 2000; Ambrose et al., 2000). Therefore, small hive beetles are in principle able to complete an entire life cycle in association with bumblebees. However, it is unclear whether adult beetles are able to find bumblebee colonies in the wild. We suggest bait trap studies (Elzen et al., 2000c) and studies of adjacent honeybee and bumblebee colonies (Whitfield and Cameron, 1993) to evaluate whether bumblebee colonies are attractive for adult beetles.

6. DISCUSSION

The introduction of *A. tumida* in areas as far from its endemic range as North America and Australia illustrates the high anthropogenic transportation potential of this parasite. However, it appears difficult to trace back the actual transport mechanism into specific areas, especially if introduction is only detected after secondary spread. The small hive beetle is thought to have been transported to the USA aboard ship in 1996 (Wenning, 2001), because it first appeared near a major harbour (Hood, 2000). Successful alternate feeding on fruits suggests that the beetles may be transported on fruits (Ellis et al., 2002c). However, fruit shipments are usually subject to intensive quarantine and small hive beetles have not yet been detected in such shipments. It seems plausible to assume that the import of package bees, honeybee and bumblebee colonies, queens, hive equipment and or even soil (Brown et al., 2002) constitute potential invasion pathways of the small hive beetle. Nevertheless, at the

current state of evidence it is still unclear how small hive beetles actually reached Australia and the US. The migratory nature of beekeeping is probably the greatest contributor of small hive beetle transmission within its new ranges (US: Delaplane, 1998; Australia: M. Duncan, personal communication). Nevertheless, natural dispersal mechanisms may also considerably contribute. Thus, the small hive beetle most likely constitutes an example of a biological invasion that involves multiple dispersal processes such as long-range transport, migratory beekeeping and natural dispersal abilities. The pattern of small hive beetle spread is probably dominated by long-distance jump dispersal as in Argentine ants (Suarez et al., 2001). Detailed data and comparative studies on the invasion dynamics in the new ranges seem necessary to evaluate the contribution of individual processes to the spread of *A. tumida* and to improve the predictive power of future modelling efforts. Such studies are however still lacking.

The environmental requirements of the small hive beetle are readily met within a large range of the distribution of *A. mellifera* both in terms of survival and completion of its life cycle (Brown et al., 2002). Indeed, small hive beetles can establish populations in temperate regions (e.g. Ohio, Evans et al., 2003) due to their overwintering capacity. The requirement for lighter sandy soils during pupation can also be met within many areas (Brown et al., 2002). Thus, it is likely that, if introduced, the small hive beetle would swiftly become established in most of the range of the Western honeybee with major implications for apiculture. Also, the ability of small hive beetles to heavily infest the protected environment of honey houses may allow severe economic damage in any location worldwide.

A variety of control methods has been developed and discussed (e.g. Baxter et al., 1999; Ellis et al., 2002a; Elzen et al., 1999b; Hood, 1999b, 2000; Lafrière, 2000; Mostafa and Williams, 2000; Park et al., 2002 among others). They range from prevention through sanitation in apiaries and honey houses (Thomas, 1998), over trapping of larvae using fluorescent lights and adult beetles using nucleus hives (Sanford, 1998; Elzen et al., 1999b) to chemical control in the hive (Elzen et al., 1999b) and insecticide treatment of soil (Baxter et al.,

1999; Lafrèniere, 2000). However, as in the case of *Varroa destructor* Trueman and Anderson, resistant strains may develop (Spreafico et al., 2001). Thus, the development of sustainable control methods seems desirable to avoid resistance to chemical treatments in the long run (e.g. pheromone trapping, biological control agents or breeding of resistant strains). In general, small hive beetle control should not overlook the control of other honeybee pests and vice versa. For example, grease/antibiotic patties used to control American foulbrood seem to worsen small hive beetle infestations because larvae readily accept the patties as food (Westervelt et al., 2001; Elzen et al., 2002).

The development of efficient control methods is likely for managed honeybees sooner or later, but appears difficult for wild bee populations. Thus, once established, small hive beetles may also pose a serious threat to wild bee populations with potential drastic ecological consequences. Several nitidulid species have a close association with social insects other than honeybees (Morse, 1998), e.g. Lundie (1940), reported about *Brachypeplus* species (*B. autitus*, *B. planus*, and *B. meyricki*) associated with stingless bees of the genus *Trigona*. Given that bumblebees may actually serve as an alternative host in nature and resistance is low (Stanghellini et al., 2000; Ambrose et al., 2000), small hive beetles may cause severe damage to bumblebee populations. Other bee species may also serve as alternative hosts (e.g. *Apis cerana*). Indeed, the reciprocal host shift of parasitic *V. destructor* mites from *A. cerana* to *A. mellifera* has already proven to cause a global problem for apiculture and wild *A. mellifera* populations. However, there are differences when comparing *V. destructor* and the small hive beetle. In case of *V. destructor* an interspecific host shift has occurred between two species showing clear differences in their behaviour (e.g. hygienic behaviour) and nesting biology (e.g. drone cell construction). In case of the small hive beetle an intraspecific host shift has occurred between sympatric and non-sympatric host subspecies. Thus, rather quantitative differences seem to trigger resistance to this parasite (see Elzen et al., 2001) and breeding programs towards resistance may be more rewarding than in the case of *V. destructor*.

Several potential reasons may be responsible for the difference between pest severity in Africa, in the US and in Australia.

6.1. Different beekeeping techniques

There are differences in beekeeping practices which may contribute to the damage caused by the small hive beetle. For example, African beekeepers tend to minimize the amount of honey stored in hives. However, no comparative data is available yet.

6.2. Differences between introduced small hive beetle populations

The Australian small hive beetle populations seem to be genetically different from those in the US and so may not cause the same problems as in the US (D. Anderson, unpublished data). In this case one might expect a different beetle behaviour and/or reproductive potential in the US and Australia. Against this, small hive beetle behaviour appears to be very similar in the US and in Africa (Elzen et al., 2000b). Moreover, the small hive beetles found in North America are genetically very similar to beetles from Southern Africa (Evans et al., 2003). Thus, differences between beetle populations may explain divergent pest severity between Australia and the US but not between the US and Africa. However, detailed comparative studies on the behaviour and/or reproductive potential of small hive beetles in Africa and its new ranges are lacking.

6.3. Enemy release hypothesis

Invasive species such as the small hive beetle might have escaped from important parasites, predators or pathogens that limit populations in their native ranges (Keane and Crawley, 2002) and release from such enemies has been implicated in the success of invasive species (Huffaker and Messenger, 1997). Indeed, an average invasive species has more parasites in its native region than in the new range (Torchin et al., 2003). This point is entirely unclear because neither small hive beetle parasites nor pathogens have been found yet.

6.4. Climatic differences

The number of beetle generations per year in temperate regions is likely to be smaller than in South Africa (five generations; Lundie, 1940) because temperature has an effect on beetle developmental time (Schmolke, 1974; Neumann et al., 2001a). Thus, pest severity may be less too due to smaller beetle population sizes (see 6.6. below). However, this has not been investigated yet. Very dry conditions may also limit beetle reproduction in its new ranges (Australia: M. Duncan, personal communication; Egypt: A.M. Mostafa, personal communication). Thus, similar to Africa, where successful reproduction of the small hive beetle can be enhanced by hot and humid conditions (Swart et al., 2001), climatic differences may play a key role in damage because small hive beetle population growth is smaller (see 6.6. below). This point may explain differences in pest severity between the US and Australia/Egypt but not between the US and Africa. However, the underlying reasons are still unclear and need further investigation.

6.5. Different strains of honeybees

Differences in African vs. European honeybee subspecies are numerous (see above). Therefore, we regard it as most likely that this is the major factor contributing to the different impact of small hive beetles on populations of African honeybees in Africa and European honeybees in the US. However, the bees which are apparently less affected in Australia are *A. m. ligustica* (M. Duncan, personal communication), one of the predominant subspecies in the US (Schiff and Sheppard, 1995). Unless there are differences between Australian and US *A. m. ligustica* strains with respect to beetle resistance, this points in the direction that other factors are important for the apparent differences in beetle damage between Australia and the US.

In the US, the invasion of the Africanized honeybee may prove to be an advantage at least with regard to small hive beetle resistance because Africanized bees are likely to be resistant towards the small hive beetle. However, to our knowledge, the small hive beetle is not yet found in South America. Thus, Africanized bees have not encountered this para-

site since their introduction to South America in 1956 (Kerr, 1957) and some resistance might have been lost.

Managed European honeybee populations are under strong selection pressures due to intense breeding over the past centuries. Traits such as absconding, aggression and abundant propolis usage have been selected against, which are undesirable from a beekeeping perspective but may trigger small hive beetle resistance. Therefore, the low resistance of managed European honeybees may not necessarily reflect actual susceptibility of wild European honeybee populations. It is possible that the susceptibility of managed European honeybees in the US, is a result of efficient breeding efforts in the past. This hypothesis remains to be tested with feral/wild colonies of European honeybee subspecies.

6.6. Different densities of small hive beetle populations

One potential reason, why Australia have had little small hive beetle damage so far, might be that it has only been there long enough to establish moderate numbers of adults in hives (M. Duncan, personal communication). So, it might well be that the beetle populations will need some time to build up to a certain size before serious damage occurs (D. Anderson [CSIRO], M. Duncan, personal communications). In this case one might expect more severe problems in Australia in the nearby future when small hive beetle populations have build up. The higher mobility of African bees, in particular seasonal migration (see above), may also contribute to smaller parasite population sizes and consequent minor pest severity in Africa.

We conclude that at the current state of evidence it appears premature to decide which of these factors is important for the differences between beetle damage in the US and Australia. However, the differences between the US and Africa most likely result from behavioural differences between African and European subspecies, unless massive host shifts occur in the new range or unless important small hive beetle pests/parasites have not been identified yet. The known behaviours, which are probably involved in small hive beetle resistance of African bees, such as absconding (Hepburn et al.,

1999), aggression (Elzen et al., 2001) and social encapsulation (Neumann et al., 2001b) also occur in susceptible populations of European honeybees (Ellis et al., 2003a, b, c). Therefore, it is obvious that the susceptibility of European bees is not due to a lack of behavioural resistance mechanisms. Resistance of African bees is probably due to quantitative differences in a series of behaviours such as absconding, aggression, removal of beetle eggs and larvae and social encapsulation. It is likely that general adaptations to higher predation and parasite loads are responsible for the apparent resistance of African honeybees rather than specific adaptations towards the small hive beetle. For example, African bees are in general more aggressive than European subspecies (Hepburn and Radloff, 1998). However, many of the behavioural mechanisms have only been qualitatively described, have not been tested in comparative studies between African and European bees or may even simply be unknown. Moreover, very important basic features like the number of beetle offspring per colony in the US and Africa and levels of infestation of African and European host populations have not been rigorously quantified yet. Therefore, more comparative studies between parasite and host populations in Africa, Australia and in the US are urgently required. In general, we still have a fragmentary knowledge of the small hive beetle, creating demand for more research in all areas of its biology. Joint research efforts of the scientific community seem necessary in the nearby future, because *A. tumida* has the potential to become a serious global problem for apiculture and natural bee populations.

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Résumé – Biologie du Petit Coléoptère des ruches (*Aethina tumida*, Coleoptera : Nitidulidae) : lacunes dans nos connaissances sur cette espèce invasive. Le Petit Coléoptère des ruches (PCR), parasite relativement anodin des abeilles domestiques africaines, est indigène en Afrique sud-saharienne (Fig. 1). Dans son aire naturelle de répartition la reproduction du PCR se limite principalement aux colonies faibles ou malades et aux nids récemment abandonnés. (Fig. 2). Il est par contre capable de se reproduire dans des colonies européennes fortes (Fig. 2) et peut alors causer de gros dégâts dans les populations des sous-espèces européennes, comme c'est le cas par exemple aux États-Unis depuis 1998 (Fig. 3). Il a même été trouvé en Égypte (2000) et en Australie (2002, Fig. 4). En Australie les dégâts semblent jusqu'à présent limités, mais les raisons de cet état de fait restent obscures. Le PCR peut hiverner dans le grappe d'abeilles et donc s'établir sous des latitudes de climat tempéré. Il peut utiliser les fruits comme source alternative de nourriture, ce qui n'a été pourtant à ce jour montré qu'au laboratoire. La résistance des abeilles africaines à l'infestation par le PCR repose probablement sur des différences quantitatives dans de nombreux types de comportements, tels que l'agression, l'élimination des œufs et des larves du coléoptère, l'encapsulation sociale ainsi que l'essaimage non lié à la reproduction. Le PCR présente une gamme de contre-mesures telles que se laisser tomber du rayon, s'enfuir, se cacher, prendre des postures de défense et mimer la trophallaxie. Mais de nombreux mécanismes de défense ne sont pas encore suffisamment étudiés. Le PCR se propage avec efficacité (cf. son extension aux États-Unis, Fig. 3) et est susceptible d'utiliser dans les nouvelles régions des hôtes alternatifs (par ex. les bourdons en Amérique du Nord). Il a donc le potentiel de devenir un problème global pour l'apiculture et les populations naturelles d'abeilles. Nos connaissances actuelles étant encore très restreintes, il semble donc nécessaire de mener d'autres études comparatives sur les populations de petits coléoptères des ruches et d'abeilles domestiques en Afrique, en Australie et aux USA.

Apis mellifera / *Aethina tumida* / espèce invasive / Petit Coléoptère des ruches

Zusammenfassung – Die Biologie des kleinen Beutenkäfers (*Aethina tumida*, Coleoptera: Nitidulidae): Unsere Wissenslücken über eine invasive Art. Der kleine Beutenkäfer ist ein relativ harmloser Parasit afrikanischer Honigbienen, der in Afrika südlich der Sahara heimisch ist (Abb. 1). Im natürlichen Verbreitungsgebiet ist die erfolgreiche Vermehrung des Käfers meist auf schwache oder kranke Völker und kürzlich verlassene Nester beschränkt (Abb. 2). Im Gegensatz dazu kann sich der Käfer auch in starken europäischen Völkern erfolgreich vermehren (Abb. 2). Er kann daher große Schäden in Populationen europäischer Unterarten

verursachen, wie z.B. seit 1998 in den USA (Abb. 3). Der kleine Beutenkäfer wurde ebenfalls in Ägypten (2000) und Australien (2002, Abb. 4) gefunden. In Australien scheinen die Schäden bisher nur gering zu sein. Die Gründe hierfür sind jedoch bislang unklar. Der Beutenkäfer kann in der Wintertraube überwintern und somit in gemäßigten Breiten Populationen etablieren. Früchte können als alternative Nahrung dienen, was jedoch bisher nur in Laborversuchen gezeigt werden konnte. Die Resistenz afrikanischer Bienen gegenüber Infektionen mit dem Beutenkäfer beruht vermutlich auf quantitativen Unterschieden in mehreren Verhaltensweisen, wie z.B. Aggression, Entfernen von Eiern und Larven des Käfers, soziale Einkapselung sowie nicht reproduktivem Schwärmen. Die Käfer zeigen eine Reihe von Gegenmaßnahmen wie z.B. Fallenlassen von der Wabe, Flüchten, Verstecken, Verteidigungshaltung und trophallaktische Mimikry. Jedoch sind viele Resistenzmechanismen noch nicht ausreichend untersucht worden. Der kleine Beutenkäfer ist effizient in der Verbreitung (s. Ausbreitung in den USA, Abb. 3) und kann möglicherweise auch alternative Wirte in den neuen Verbreitungsgebieten nutzen (z.B. Hummeln in Nordamerika). Von daher hat der kleine Beutenkäfer das Potential, ein globales Problem für die Imkerei und natürliche Bienenpopulationen zu werden. Jedoch ist unser bisheriges Wissen über diesen Parasiten noch sehr gering. Weitere vergleichende Untersuchungen an Käfer- und Bienenpopulationen in Afrika, Australien und den USA erscheinen daher dringend notwendig.

***Apis mellifera* / *Aethina tumida* / Honigbiene / invasiver Art / kleiner Beutenkäfer**

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