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Review article

Behavioural basis for social parasitism of Cape honeybees (*Apis mellifera capensis*)

Peter NEUMANN[a]*, Randall HEPBURN[b]

[a] Martin-Luther-Universität Halle-Wittenberg, Institut für Zoologie,
Kröllwitzerstr. 44, 06099 Halle/Saale, Germany
[b] Rhodes University, Department of Zoology and Entomology,
61440 Grahamstown, Republic of South Africa

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Abstract – Cape honeybee workers show important pre-adaptations for social parasitism and can cause the dwindling colony syndrome of host colonies. Parasitic workers may drift or actively disperse into host colonies. They may also join absconding swarms, which can merge with host colonies. After transmission, parasitic workers have to establish themselves in the host, which is probably promoted by their spatial distribution, their readiness to gain trophallactic dominance and their ability to survive worker-worker aggression. Established parasitic workers have to evade egg removal by other workers in host colonies. The resulting offspring is preferentially fed, can be expected to be highly virulent and may show different behaviour in the course of infestation. It is unknown why and how the host queen is lost. High numbers of parasitic workers are reared until the host colony dies or absconds. This offspring can infest new host colonies, thereby completing the social parasitic life cycle.

***Apis mellifera capensis* / *Apis mellifera scutellata* / honeybee / social parasitism / worker reproduction**

1. INTRODUCTION

The invasion of distant host colonies of *Apis mellifera ligustica* Spinola by *Apis mellifera capensis* Escholtz laying workers was first described by Onions (1912), but was only recently recognised as social parasitism (Velthuis et al., 1990). When colonies of the neighbouring subspecies *Apis mellifera scutellata* Lepeletier and other subspecies were transported into the region of *A. m. capensis* (Moore, 1911; Guy, 1975; Tribe, 1981; Moodie, 1983) or vice versa (Lundie, 1954; Johannsmeier, 1983), this resulted in the widespread take over by *A. m. capensis* laying workers (Hepburn

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* Correspondence and reprints
E-mail: p.neumann@zoologie.uni-halle.de

and Allsopp, 1994). This was amplified by orders of magnitude when many *A. m. capensis* colonies were transferred into the area of *A. m. scutellata* (Allsopp, 1992; Johannsmeier, 1992; Lear, 1992; Allsopp and Crewe, 1993). An estimated 30 000 *A. m. scutellata* colonies were usurped by *A. m. capensis* laying workers in the Highveld of South Africa, resulting in the so-called "*capensis* calamity" for beekeepers (Allsopp, 1993; Allsopp and Crewe, 1993). These events established two important points: 1. Laying workers of *A. m. capensis* are facultative social parasites and 2. Colonies of *A. m. scutellata* are highly susceptible host colonies, because they apparently lack efficient resistance mechanisms to prevent the establishment of laying *A. m. capensis* workers.

Social parasitism by *A. m. capensis* laying workers is expressed at the level of the host colony phenotype by the dwindling colony syndrome (Allsopp, 1995). This dwindling is characterized by an initial reduction in foraging, then fighting at the hive entrance and inside of the colony between host workers and *A. m. capensis* workers, the appearance of worker-laid brood, the loss of the host queen and finally the eventual (at least in the case of *A. m. scutellata* inevitable) death of the host colony and its replacement by *A. m. capensis* (Allsopp, 1995; Magnuson, 1995). This process lasts up to four months (Swart and Kryger, unpublished data; cited in Martin et al., 2002b), some nine weeks on the average and may be even faster in the region of *A. m. scutellata* (Kryger, 2001b).

Over a very large area of *A. m. scutellata* in north-eastern South Africa all parasitic Cape honeybee workers apparently belong to a single so-called pseudo-clone (Kryger, 2001a,b; Kryger et al., 2002), because with the exception of a few mutational events all DNA microsatellite loci studied showed a maximum of two alleles (Solignac et al., 2001) indicating that they are progeny of a single founder worker (Kryger, 2001a,b; Solignac et al., 2001; Radloff et al., 2002).

The present review is focussed on what is known of the biology of *A. m. capensis* in its native fynbos region in South Africa (Hepburn and Jacot-Guillarmod, 1991) and the naturally occurring hybrid zone between *A. m. capensis* and the neighbouring subspecies *A. m. scutellata* (Hepburn and Radloff, 2002) but will draw parallels to the current situation of the *capensis* calamity and the *A. m. capensis* pseudo-clone population in the northern parts of South Africa where information has very recently become available. Here we will present a general pattern of the social parasitism by laying Cape honeybee workers. However, this does not imply that there are no differences with respect to certain aspects of this social parasitic pathway due to biological variations among different populations of laying *A. m. capensis* workers and/or their respective host colonies. Indeed, laying worker populations of *A. m. capensis* appear to show considerable differences with respect to social parasitism (Neumann et al., 2001b). For example, the *A. m. capensis* pseudo-clone population invading *A. m. scutellata* in its native range (Kryger, 2001a,b) seems to be more virulent compared to a laying worker population from the native range of the Cape honeybee (Port Elizabeth, Neumann et al., 2001b). This might be a result of severe selection processes between different strains of parasitic *A. m. capensis* workers which occurred in the *A. m. scutellata* population (Neumann et al., 2001b; Wossler, 2002). Such variability in *A. m. capensis* with respect to traits related to worker reproduction is well documented (Hepburn, 1994; Hepburn and Radloff, 1998).

Obviously, social parasitism by worker honeybees could have potentially evolved in all honeybee subspecies, because in principle they are able to reproduce parthenogenetically either via arrhenotoky (the production of drones; Ruttner, 1992;

Crozier and Pamilo, 1996) or via thelytoky (the production of diploid females; Onions, 1912; Crozier and Pamilo, 1996). However, it seems more likely that social parasitism would evolve when individual workers have the opportunity to maximise their reproductive success. Indeed, individual fitness can be extremely high as shown by the wide spread of the *A. m. capensis* pseudoclone (Kryger, 2001a,b; Kryger et al., 2002). Moreover, *A. m. capensis* laying workers generally contribute considerably to population fitness in South African honeybee populations, because an *A. m. capensis* mitochondrial DNA type introgressed far into the *A. m. scutellata* population (Moritz et al., 1998). The latter observation indicates that worker reproduction in *A. m. capensis* is also very important in the native range of the Cape honeybee and is not only an artefact of migratory beekeeping as in the case of the *capensis* calamity.

Cape honeybee workers show a unique series of traits that reflect important physiological and genetic pre-adaptations for intraspecific social parasitism: high fecundity (ovarial development; Hepburn and Crewe, 1990; high number of eggs laid; Velthuis et al., 1990 soon after queen loss; Ruttner and Hesse, 1981; Hepburn and Radloff, 1998), longevity (3–5 months Velthuis et al., 1990; up to five months and more Tribe and Allsopp, 2001b), high and fast pheromonal development (Hepburn, 1994; Simon et al., 2001; Wossler, 2002, this issue) and thelytoky (Onions, 1912; Hepburn and Crewe, 1991).

Thelytoky appears to predispose for the evolution of aggressive worker reproduction (Greeff, 1996, 1997) and consequently for social parasitism of workers (Neumann et al., 2001c), because self-replicating thelytokous laying worker offspring can immediately infest new host colonies, without an intervening sexual generation. Moreover, worker egg-laying (Pirk et al., 2002, this issue) and even successful worker reproduction (Pettey, 1922; Moritz et al., 1999) is common in queenright colonies of *A. m. capensis.* This indicates that the effects of brood and queen pheromones on worker ovary inhibition is reduced (Wossler, 2002, this issue) and that *A. m. capensis* laying workers are able to evade the removal of worker-laid eggs in queenright honeybee colonies (Martin et al., 2002a; Pirk et al., 2002; Neumann, Pirk, Hepburn and Moritz, unpublished data). Both ovary activation and escape of worker policing are essential features to explain the successful reproduction of laying *A. m. capensis* workers in queenright colonies of their own and of other subspecies. The high incidence of successful parasitized host colonies (Allsopp and Crewe, 1993) appears as unequivocal evidence that both aspects happen on a regular basis at least in *A. m. scutellata* host colonies.

The pheromonal development of *A. m. capensis* workers can become much more queen-like (Crewe and Velthuis, 1980; Velthuis et al., 1990; Wossler, 2002, this issue) and the onset of pheromonal development more rapid (Hepburn, 1992; Simon et al., 2001; Wossler, 2002, this issue) than in European subspecies. Of particular importance is that ovarial and pheromonal development covary in *A. m. capensis* workers (Hepburn, 1992). Although all combinations of reproductive traits are possible in laying *A. m. capensis* workers (Hepburn, 1994), many more of them show the combination of both high ovarial development and a queenlike pheromonal bouquet (Hepburn and Radloff, 1998) than other subspecies of *A. mellifera* (Velthuis, 1970; Crewe and Velthuis, 1980; Hepburn and Radloff, 1998). Such workers have been termed surrogate (Hepburn, 1992) or pseudoqueens (Crewe et al., 1990; Wossler, 2002, this issue).

Taking into account the above mentioned pre-adaptations it seems not surprising that the adoption of *A. m. capensis* laying workers in host colonies of other honeybee subspecies *A. m. ligustica* (Onions, 1912), *A. m. mellifera* (Woyke, 1995, personal communication), *A. m. scutellata* (Guy, 1975; Lundie, 1954; Johannsmeier, 1983) often results in their usurpation (Hepburn and Allsopp, 1994; Hepburn and Radloff, 1998). Since migratory beekeepers repeatedly moved *A. m. capensis* colonies from their native fynbos region (a macchia-like biome in the Eastern and Western Cape provinces of South Africa, Hepburn and Jacot-Guillarmod, 1991) across the natural hybrid zone into *A. m. scutellata* populations in the Highveld of South Africa (Allsopp, 1995) parasitic workers have spread widely throughout the summer rainfall regions of South Africa (Allsopp, 1993). This strongly suggests that there is also a behavioural basis for social parasitism by Cape honeybees. Here we give an overview on the relevant literature dealing with behavioural traits of *A. m. capensis* related to social parasitism.

2. SOCIAL PARASITIC LIFE CYCLE OF CAPE HONEYBEE LAYING WORKERS

The social parasitic life cycle of *A. m. capensis* laying workers involves a series of critical steps and events associated with the two major aspects: transmission and virulence (Fig. 1). Transmission is the transfer of parasites from one host to another. Virulence is usually defined as the mortality caused by a parasite in a standard host (Schmid-Hempel, 1998). In the context of social parasitism by Cape honeybee laying workers virulence is associated with the speed of host colony death by dwindling. The speed of colony dwindling is probably caused by a variety of factors such as the degree of reduction in foraging by host workers (Allsopp, 1995), the chance of invaded parasitic workers to survive worker-worker aggression, the extent of intracolonial fighting (Allsopp, 1995), the degree of losses of host workers (Allsopp, 1995), the speed and extent of reproduction by parasitic laying workers and finally the timing of the loss of the host queen. Concomitantly there are substantial numbers of parasitic offspring that mainly focus on reproduction and which participate to a lesser extent in normal hive duties such as brood rearing (Hillesheim et al., 1989) or foraging (Martin et al., 2002b). If a given strain of social parasitic workers causes a host colony to die quicker, these workers can be considered to be more virulent. Detailed knowledge of both transmission and virulence is crucial to understand social parasitism of laying Cape honeybee workers because higher transmission increases parasite fitness, whereas higher virulence decreases parasite fitness because it damages the parasites' food supply. In the context of transmission and virulence two major questions emerge with respect to the behaviour of Cape honeybees: (1) What are potential behavioural mechanisms for the transmission of social parasitic workers? (2) What behavioural factors govern the virulence of social parasitic workers and consequently the resistance of host colonies?

We will now give a very brief overview of the reproductive life cycle of social parasitic laying *A. m. capensis* workers, which is shown in Figure 1. Transmission may occur within one (horizontal) or between (vertical) generations (Schmid-Hempel, 1998). Horizontal transmission of *A. m. capensis* workers may occur at the individual and at the colony level. Individual workers may spread into neighbouring hives by passive drifting (step 1 in Fig. 1; Neumann et al., 2000b, 2001c) or actively disperse into distant colonies (step 2 in Fig. 1; Neumann et al., 2001c). Both drifted and dispersed individual workers have to bypass the host colony's guard force (Lindauer, 1952; Ribbands, 1953) to successfully invade the host colony. Workers of *A. m. capensis* may also join absconding swarms (step 3 in Fig. 1; Hepburn et al., 1999), which can subsequently merge with other colonies (step 4 in

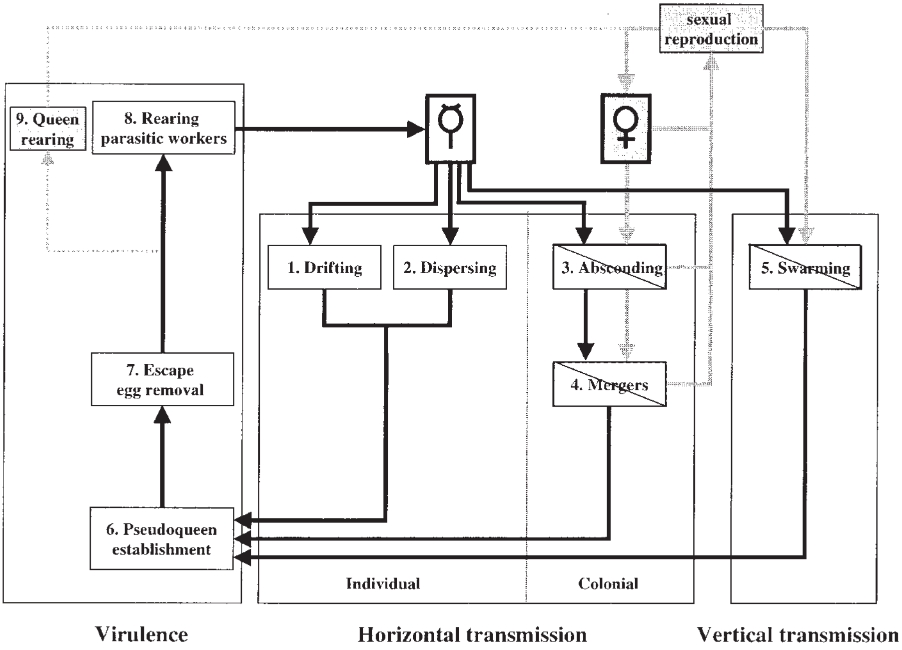

Figure 1. Minimum configurations for the reproductive cycle of social parasitic Cape honeybee workers. Shaded boxes and grey lines represent the normal sexual reproductive pathway of *A. m. capensis*. Blank boxes and black lines represent the social parasitic pathway of laying workers. Shaded/blank boxes represent steps, which are involved in both the sexual reproductive and parthenogenetical laying worker pathway. Dotted lines represent rare events (see Swart et al., 2001 and Martin et al., 2002b). For simplicity all behavioural interactions between individual steps have been omitted.

Fig. 1; Hepburn and Radloff, 1998; Hepburn et al., 1999; Neumann et al., 2001a). For vertical transmission *A. m. capensis* workers may join reproductive swarms (step 5 in Fig. 1). To successfully reproduce, *A. m. capensis* workers, which have successfully invaded a host colony must establish themselves as pseudoqueens (step 6 in Fig. 1; Hepburn, 1992). Established pseudoqueens have to evade the removal of their eggs in host colonies (step 7 in Fig. 1; Ratnieks and Visscher, 1989; Miller and Ratnieks, 2001; Martin et al., 2002a; Pirk et al., 2002, this issue; Neumann, Pirk, Hepburn and Moritz, unpublished data). The resulting parasitic offspring is preferentially fed by the host workers (step 8 in Fig. 1; Beekman et al., 2000; Calis et al., 2002, this issue), resulting in highly developed progeny. Occasionally an *A. m. capensis* queen may be reared (step 9 in Fig. 1; but see Swart et al., 2001 and Martin et al., 2002b). In the following sections, each of these points will be discussed in detail.

3. TRANSMISSION OF SOCIAL PARASITIC CAPE HONEYBEE WORKERS

Efficient transmission through beekeeping activity, or via the individual and/or colonial pathways is essential because a host colony of another subspecies that is taken over by *A. m. capensis* laying workers cannot remain alive on its own and eventually dwindles and dies (Swart et al., 2001; Martin et al., 2002b; Moritz, 2002). These observations evoke a number of considerations. For example, the more virulent parasitic workers are and the faster host colonies die, the more efficient transmission must be in order to maintain such parasitic strains. Because the *A. m. capensis* pseudo clone (Kryger et al., 2002) inevitably spreads like a "disease" in the region of *A. m. scutellata* (Swart et al., 2001; A. Schehle personal communication) and *A. m. scutellata* host colonies die rather rapidly (Kryger, 2001b; Martin et al., 2002b) transmission of the parasite is apparently very efficient. In light of these observations two questions emerge: (1) What are potential mechanisms for individual workers or whole colonies (either pure *A. m. capensis* colonies or infested host colonies) to find and to successfully invade new host colonies? (2) To what extent is such transmission influenced by the development of the *A. m. capensis* workers? In the following sections we will address in detail these questions related to the potential transmission pathways at the level of the individual parasitic workers and at the colony level.

3.1. Pathway of horizontal transmission of individual workers

Drifting and dispersing (steps 1 and 2 in Fig. 1)

What potential mechanisms allow individual workers to find new host colonies? It is well established that honeybee workers often join neighbouring colonies by accidental drifting (Rauschmayer, 1928; Free, 1958; Jay, 1966a,b, 1968; Neumann et al., 2000b). Drifting is caused by slight orientation errors of young workers during their orientation flights and sometimes by returning foragers (Rauschmayer, 1928; Free, 1958) and also requires adoption of these workers by the guard force of the host colonies. The amount of drifting strongly depends on a variety of factors such as age of the bees (Ribbands, 1953), race (Ruttner, 1992) and the apiary layout (Jay, 1966a,b, 1968). Long-range drifting of workers also rarely occurs to colonies far away from their maternal nests (Renz and Rosenkranz, 2001; Neumann et al., 2001c).

Onions (1912) reported that *A. m. capensis* laying workers invaded colonies of *A. m. ligustica* far out of the range of young workers on their orientation flights. Likewise, Johannsmeier (1983) described a pattern of invasion by laying workers of *A. m. capensis* of an *A. m. scutellata* apiary, which was difficult to explain by simple drifting. When keeping colonies of *A. m. capensis* in areas of other honeybees (e.g. Germany), it was suggested that the Cape honeybee colonies be separated by 300 m from other colonies to prevent "drifting" (Koeniger and Wurkner, 1992). Such a distance is difficult to explain by simple orientation errors, supporting the idea that *A. m. capensis* workers may actively seek host colonies over large distances.

Recently, the impact of queenstate (presence or absence of the queen) and taxon of both mother and host colonies on short-range drifting and long range dispersing of workers and on the hosting of these workers in colonies of *A. m. capensis*, *A. m. scutellata* and their natural occurring hybrids was investigated in a mark-recapture experiment (Neumann et al., 2001c). Six colonies each of *A. m. capensis*, *A. m. scutellata* and their natural occurring hybrids were split into queenless and queenright parts and arranged in three circular micro-apiaries (Neumann et al., 2001c). 12034 workers of the same age cohort were colony specific labelled and reintroduced into their respective mother colonies. After 10 days all labelled workers were recaptured from either their mother colony or from foreign host colonies. 579 workers (~ 4%) drifted into other colonies within their apiary and 89 workers were recaptured in other apiaries than their home apiary (= dispersers, Neumann et al., 2001c).

It was established that drifting and dispersing represent entirely different behaviours (Neumann et al., 2001c) because: (1) Significantly more *A. m. capensis* workers dispersed into another apiary than expected from the distribution of the drifted workers. (2) Dispersers did not only leave their own apiary but also did not prefer the same sector of the new apiary, as expected from simple orientation errors involved in drifting. (3) There were significant differences in the distribution patterns of drifters and dispersers among the tested groups. Although the hybrids drifted significantly more often than *A. m. capensis* and *A. m. scutellata*, they dispersed less often than the other groups. Moreover, *A. m. capensis* workers dispersed more often than the hybrids and *A. m. scutellata* combined. If drifting and dispersing constituted the same behaviour, one would expect a similar trend. (4) Whereas drifted *A. m. capensis* workers from queenright mother colonies were predominantly found in queenright host colonies (as opposed to drifted workers from other subspecies), dispersers from queenright *A. m. capensis* colonies were more often found in queenless host colonies and vice versa.

Were drifting and dispersing the same phenomenon, one would expect far fewer *A. m. capensis* workers to leave their home apiaries and no differences between the tested groups (Neumann et al., 2001c). Thus, it is very likely that drifting is a result of slight orientation errors into closely neighbouring colonies whereas dispersing constitutes active host finding by *A. m. capensis* workers over large distances (from > 40 m up to c. 1 km, Neumann et al., 2001c). It is of course very difficult to distinguish drifting and dispersing in the case of closely neighbouring colonies unless detailed behavioural studies reveal e.g. different flight patterns in front of the hive. It would be of prime interest to evaluate whether the predisposition for reproductive dominance in Cape honeybee workers (Moritz and Hillesheim, 1985; Moritz et al., 1996) is linked with a high predisposition for invading other colonies.

Neumann et al. (2001c) found that a high proportion of dispersed *A. m. capensis* workers (> 80%) originated from a single colony only. This suggests a high inter colony variability for this trait among *A. m. capensis* and may contribute to our understanding of the apparent differences between populations of *A. m. capensis* laying workers with respect to social parasitism, e.g. between the pseudo-clone invading *A. m. scutellata* (Kryger, 2001a,b) and from the native range of the Cape honeybee (e.g. Port Elizabeth; Neumann et al., 2001c). When comparing these two populations of *A. m. capensis* laying workers with respect to transmission, Neumann et al., (2001b) found that pseudo-clone workers from the Transvaal are less efficient in spreading compared to laying workers from Port Elizabeth. This might be related to the higher virulence, particularly to the more “queen-like” behaviour of the pseudo-clone workers, which tend to stay on the combs when colonies are inspected (Magnuson, 1995) and are less likely to leave their maternal colonies, e.g. during foraging (Martin et al., 2002b).

Breaking into a defended fortress (Schmid-Hempel, 1998) not only requires host finding by potential social parasitic workers (either via “serendipitous” orientation errors or via active host finding) but also bypassing the host colony’s guard force which carefully scrutinises incoming individuals (Lindauer, 1952; Ribbands, 1953). Thus, one might expect behavioural adaptations of social parasitic workers to facilitate the bypassing of guard bees. For example, drifted workers may facilitate the entrance to new colonies by offering droplets of food to the guard bees (Ribbands, 1953; Free, 1958). Recently, *A. m. scutellata* discriminator colonies that were split into queenright and queenless parts were used to test whether invading workers of *A. m. capensis* have special mechanisms to circumvent the *A. m. scutellata* guards compared to *A. m. scutellata* workers (M. Beekman, personal communication). Queenstate may play a role in this perspective because queenless colonies are more prone to infestations by laying *A. m. capensis* workers (Woyke, 1995), which may related to different guarding behaviour. However, neither race of the introduced bee nor presence or absence of the queen in the guarding colony affected the proportion of introduced workers accepted (M. Beekman, personal communication). Nonetheless, Tribe (1983) reported that invading *A. m. capensis* workers may be severely mauled by *A. m. scutellata* guard bees, but invariably are allowed to enter the hive. Mauling intensity of guard bees of other races towards intruding *A. m. capensis* workers has not been quantitatively investigated yet. Tribe (1983) further suggested that incidents of successfully intruding Cape workers may be related to their more queen-like pheromonal bouquet. So, one special way of *A. m. capensis* might be a fast pheromonal development (Simon et al., 2001) before the onset of ovarial development.

Guard bees may have different conspecific acceptance-thresholds (Reeve, 1989) for workers with respect to their reproductive status. For example, recent data suggest that *A. m. capensis* colonies are able to prevent workers with developed ovaries from entering the colony (Reece, 2002, this issue). This seems plausible because workers with developed ovaries can be discriminated against because they are attacked by other workers (Velthuis, 1976; Visscher and Dukas, 1995). This may form the behavioural basis for a queenstate-discriminating guarding mechanism, which was indicated by the hosting of drifted (Reece, 2002) and dispersed *A. m. capensis* workers (Neumann et al., 2001c). However, the reproductive status of *A. m. capensis* workers actually invading host colonies is not yet known. Whether dispersing *A. m. capensis* workers also show alternative behavioural tactics to facilitate admission into the host colony is simply not known. However, if only very few workers are needed to initiate infestations it may well be that no special mechanisms are actually needed for *A. m. capensis* workers to get into host colonies.

We conclude that two basic mechanisms enable individual *A. m. capensis* workers to find new host colonies. Individual *A. m. capensis* workers may invade host colonies via passive drifting due to simple orientation errors. This appears to be the prevalent mode of individual host finding in apiaries with closely neighbouring hives but is unlikely in the wild population due to the low population density (Neumann et al., 2001c). Alternatively, but not mutually exclusive, *A. m. capensis* workers may also actively seek host colonies (Johannsmeier, 1983; Neumann et al., 2001c) and spread individually between apiaries and into the wild population. Whether invading workers show behavioural tactics to facilitate their invasion is not known. Likewise is not yet clear how the state of development of such workers affects their acceptance by the guard force of host colonies. Thus, more quantitative data are needed to evaluate the relative chance of invasion of *A. m. capensis* workers with or without developed ovaries and the pre- and post-invasion ovarial and pheromonal development of such workers.

An admittedly speculative interpretation would suggest that workers with undeveloped ovaries and worker-like pheromones are unlikely to enter other colonies. Workers with developed ovaries and worker-like pheromones would be most unlikely invaders (Visscher and Dukas, 1995; Reece, 2002). Workers with queen-like pheromones seem to be likely to enter (Tribe, 1983). Workers with developed ovaries and queen-like pheromones (pseudoqueens) are also likely to successfully invade but are less likely to leave their host colonies because once they have developed into pseudoqueens and are also behaviourally queen-like do not fly up but rather stay on the combs in contrast to the *A. m. scutellata* host workers, when infested colonies are inspected (Magnuson, 1995). This clearly indicates that already established pseudoqueens are less likely to spread. Thus, the combination of developed ovaries and queenlike pheromonal bouquet is likely to develop after a less queen-like worker has invaded another colony.

3.2. Pathway of colonial horizontal transmission

3.2.1. Absconding (step 4 in Fig. 1)

Absconding, a form of non-reproductive swarming (Hepburn, 1988; Hepburn et al., 1999), is commonplace in colonies of African honeybees and can be triggered by a host of stimuli (Hepburn and Radloff, 1998). In a natural population of Cape honeybees 20% of unmanaged colonies absconded (Allsopp and Hepburn, 1997). Queen loss appears to promote absconding, which is extremely important with respect to the reproductive predisposition of queenless *A. m. capensis* workers (Hepburn, 1994; Reece, 2002). Indeed, queenless colonies of the Cape honeybee abscond twice as readily as queenless colonies of *A. m. scutellata* and their naturally occurring hybrids (Hepburn et al., 1999).

Moreover, the mode of worker reproduction may also play a role because colonies with predominantly thelytokous laying workers (*A. m. capensis*: Onions, 1912; Hepburn and Crewe, 1991; natural occurring hybrids: Neumann et al., 2000a) abscond significantly more often than *A. m. scutellata* colonies with arrhenotokous laying workers (Hepburn et al., 1999). Also *A. m. scutellata* colonies, which are highly infested with *A. m. capensis* laying workers in the Highveld of South Africa, frequently send out absconding swarms (Magnuson, 1995). Since foraging activity is reduced by the host workers when infestations are initiated (Allsopp, 1995; Swart et al., 2001), this may promote absconding of infested host colonies. Likewise, *A. m. capensis* remnants from recently collapsed *A. m. scutellata* host colonies also readily abscond (Allsopp, 1998).

Johannsmeier (1983) reported that swarms of *A. m. scutellata* (1 queenless, two queenright) infested with *A. m. capensis* laying workers were caught 1 and 3 km away from an apiary where every colony infested with *A. m. capensis* laying workers had been destroyed. Moore (1911) reported an *A. m. capensis* swarm migrating over 28 km, which fits well with estimates on the winter dispersal capacity of swarms in the fynbos region (Hepburn et al., 1993). A whole apiary of *A. m. scutellata* on an previously honeybee-free island, about 6 km away from the mainland and used as an *A. m. scutellata* island mating apiary similar to those of Europe (Neumann et al., 1999), was taken over by *A. m. capensis* (Anderson, 1965). In light of the speed of dwindling observed in the Transvaal (Kryger, 2001b) it is very unlikely that the *A. m. capensis* bees were introduced with the mating colonies because the problems with *A. m. capensis* laying workers occurred only after several months (Anderson, 1965). This strongly indicates that a migrating swarm of *A. m. capensis* reached this island despite 6 km of open sea. Moreover, Hannabus (1945) reported that a migrating *A. m. capensis* swarm flew 11 km over open water. These observations clearly indicate that absconding and migration may be important mechanisms for the long-range transmission of parasitic *A. m. capensis* workers at the colony level. However, no qualitative assessments have been made so far regarding the importance of absconding in the spread of laying *A. m. capensis* workers (e.g. between apiaries and into the wild population).

3.2.2 Mergers (step 5 in Fig. 1)

After absconding, swarms may subsequently merge with each other in mid-air (Hepburn, personal observations), on tree congregations (up to 57 queenright swarms, Herman, 1922; 11 queenright swarms, Hepburn and Whiffler, 1988) or with established colonies (Walter, 1939; Hepburn, 1993; Hepburn and Radloff, 1998; Neumann et al., 2001a). Such natural mergers require recruitment of colony parts or of a whole colony via scout workers to find a new nest site and/or host colony, just as in reproductive swarming (Seeley, 1985), clearly constituting a colony phenomenon. With the exception of mergers in the open (mid-air or tree branches), the colony initiating the merger must subsequently invade the host colony, which might be associated with severe fighting at the host nest entrance (Anderson, 1963; Neumann et al., 2001a) or not (Kigatiira, 1988). The intensity of aggression, associated with invasion of the host colony appears to depend on food sources of the host and on size differences between the merging colonies (Kigatiira, 1988). Surplus queens are usually eliminated within a short period of time after merger (Hepburn et al., 1988; but see Herman, 1922 for the co-existence of two queens for a period of several years).

Such natural mergers of honeybee colonies are commonplace in tropical Africa (Hepburn and Radloff, 1998), but their consequences on organisational structure of a colony and behaviour are largely unknown. The only reported study on this phenomenon strongly suggests that the origin of merging bees may matter, because task shifts in worker bees differed substantially between the colonies before and after they merged (Neumann et al., 2001a). Possibly, workers changed tasks as a result of different behavioural thresholds and task specialisation (Moritz and Page, 1999). The task shifts and worker distribution observed in this study suggest that many bees responded to a different colony environment in the new unit. Depending on which reproductives dominate after such mergers, either the host and/or the invading workers are unrelated to the new offspring. In cases of successful invading and suppression of reproduction by the host, this constitutes a case of "slave making", analogous to that of some ant species (Hölldobler and Wilson, 1990).

Thus, colonies which are well adapted to mergers and the resulting conflicts are predisposed to spread their genes (Kigatiira, 1988). This has been claimed as one of the factors favouring the spread of *A. m. scutellata* in the Americas (Vergara et al., 1993). Since, mergers are particularly common among *A. m. capensis* (Herman, 1922; Walter, 1939; Hepburn, 1988; Hepburn, 1993; Hepburn et al., 1993), queens and workers of this subspecies should be well adapted in this regard. However, *A. m. scutellata* also shows frequent mergers (Silberrad, 1976; Kigatiira, 1988). Given that the fighting abilities of queens and queen-worker aggressive encounters are the same in both subspecies, worker-worker interactions with respect to reproductive dominance come into play. Because *A. m. capensis* workers are distinct gainers in this respect (see virulence below), they can be expected to become dominant after intersubspecific mergers with *A. m. scutellata* hosts.

We conclude that transmission at the colonial level may be important with respect to long range transmission between apiaries, introgression of parasitic workers into the wild population and the speed of colony dwindling because many parasitic host workers may enter simultaneously host colonies. Against this, *A. m. capensis* pseudoqueens appear to lack the ability to maintain swarm cohesion to the same extent as true queens, when placed with *A. m.*

scutellata (Hepburn, 1988). Moreover, mainly *A. m. capensis* workers were left behind, when artificially infested *A. m. scutellata* colonies absconded (Hepburn, 1988; H.M.G. Lattorff, personal communication). Therefore, more data especially on the mergers of highly infested *A. m. scutellata* host colonies or of *A. m. capensis* remnants (Allsopp, 1998) with non-infested host colonies are needed to further evaluate the importance and efficiency of absconding and colony mergers for the long-range transmission of *A. m. capensis* laying workers at the colonial level.

3.3. Pathway of colonial vertical transmission (step 6 in Fig. 1)

It is simply unknown whether parasitic *A. m. capensis* workers that have invaded *A. m. scutellata* or other subspecies join reproductive swarms cast out by their hosts at early stages of infestation or not. What is known from the fynbos region is that reproductive swarms frequently merge with each other (Hepburn, personal observations; Hepburn and Whiffler, 1988), suggesting that this may also constitute a potential pathway for the transmission of parasitic *A. m. capensis* workers. However, this potential pathway is unlikely when the speed of host colony dwindling is fast (Martin et al., 2002b).

3.4. Beekeeping assisted transmission

Beekeeping assisted transmission appears to play a major role for the spread of parasitic *A. m. capensis* workers. Indeed, without human intervention the natural occurring hybrid zone appeared to be stable and “problems” with laying *A. m. capensis* workers were only reported after migratory beekeeping activities (Johannsmeier, 1983; Allsopp, 1992). Repeated observations that fixed site hobby beekeepers have lower infestation rates than migratory commercial beekeepers are numerous (Magnuson, 1995; Swart et al., 2001). Large-scale beekeepers initiated the “*capensis* calamity” by transmission of colonies across the natural hybrid zone between *A. m. capensis* and *A. m. scutellata* (see above). Moreover, hobby beekeepers often keep a very small number of colonies only and beekeeping scale probably also affects transmission because large-scale beekeepers more frequently move their hives than do hobby beekeepers.

In particular, hive management within apiaries, e.g. when colonies are inspected (Swart et al., 2001), may facilitate the invasion of *A. m. scutellata* colonies by social parasitic workers of *A. m. capensis* because the guard bees can be evaded. Indeed, invasion by *A. m. capensis* workers may successfully occur, when *A. m. scutellata* colonies are smoked during hive inspections (Tribe, 1983) and colonies which were frequently inspected seem to show the signs of the “dwindling colony” syndrome faster than other colonies (A. Schehle, personal communications). Moreover, the splitting of colonies, moving brood frames from one hive into another, transport and increasing the number of colonies for pollination purposes obviously facilitate the transmission of *A. m. capensis* workers. The dramatic differences of scale are reflected in the reports of Johannsmeier (1983) for small-scale apiaries and of Steinhobel (1977) for large-scale beekeeping by orders of magnitude. Whereas only 8 *A. m. capensis* colonies from Cape town were moved into an *A. m. scutellata* apiary with 40–50 colonies (Johannsmeier, 1983), migratory beekeepers moved and opened at least 2000 colonies for making increase during pollination services (Steinhobel, 1977).

We conclude that transmission of social parasitic Cape honeybee workers may occur via drifting and dispersing at the individual level and via absconding and colony mergers at the colony level. Very few data are currently available to evaluate the relative importance of these different transmission pathways for the actual spread of Cape honeybees among *A. m. scutellata* colonies. However, beekeeping activities seem to be crucial for transmission at least in the case of the highly virulent *A. m. capensis* pseudo clone because mainly large scale beekeepers are affected by the *capensis* calamity. Infestation data for the wild population are urgently needed to evaluate the efficiency of long transmission of the social parasite besides migratory beekeeping.

4. VIRULENCE OF CAPE HONEYBEE LAYING WORKERS

It is well known, that when *A. m. capensis* workers are placed in queenright and or queenless *A. m. scutellata* colonies they readily adopt pseudoqueen status (induce retinue behaviour etc., Crewe and Velthuis, 1980; Tribe, 1983; Wossler, 1991) which is related to the pheromonal status of such workers (Wossler, 2002, this issue). Thus, *A. m. capensis* workers are apparently not reproductively regulated by the *A. m. scutellata* queen or by the host brood (Allsopp and Crewe, 1993; see Wossler, 2002 for a review). But which behavioural factors govern the virulence of *A. m. capensis* workers and consequently the susceptibility and the dwindling of host colonies?

We will now give a brief outline of the events following the successful invasion of an *A. m. capensis* worker into a host colonies and which are associated with virulence (see above for a definition) of the social parasites and the dwindling host colony syndrome (Fig. 2). When *A. m. capensis* workers have successfully invaded colonies either via drifting, dispersing, swarm mergers, joining of reproductive swarms or simply stayed in their host colonies they have to (further) develop their ovaries and establish themselves as pseudoqueens in the host colonies (Fig. 2). Such workers may or may not already show some pre-host development (see above). Due to the high variability for traits related to worker reproduction in *A. m. capensis* (Hepburn, 1994), virulent laying workers may show two different phenotypes: high ovarial development and no queenlike pheromonal bouquet and a fully developed pseudoqueen phenotype with both high ovarial development and a queenlike pheromonal bouquet.

Pseudoqueen establishment (step 1 in Fig. 2) is based on a series of behavioural and pheromonal interactions between the host (queen and workers), invaded workers and their parasitic offspring. Inside of the host colony, *A. m. capensis* workers tend to avoid the host queen (step 2 in Fig. 2; Moritz et al., 2001a,b, 2002) and are prone to gain trophallactic dominance over host workers (step 3 in Fig. 2; Velthuis et al., 1990). These two mechanisms predispose the invaded workers to (further) develop their ovaries. However, workers with developed ovaries are attacked by other workers (Velthuis, 1976; Visscher and Dukas, 1995) and also *A. m. capensis* workers are attacked by host workers inside of the colony (Allsopp, 1995). Thus, workers have to evade worker-worker aggression to successfully establish themselves as pseudoqueens (step 4 in Fig. 2; Tribe, 1981; Allsopp, 1995). *A. m. scutellata* host workers counter pseudoqueen establishment by aggressive behaviour towards *A. m. capensis* workers (step 5 in Fig. 2; Allsopp, 1995; Magnuson, 1995); but they also promote pseudoqueen establishment by being trophallactically subordinate (step 6 in Fig. 2; Velthuis et al., 1990). The host queen tends to pheromonally suppress the development of invaded *A. m. capensis* workers (Wossler, 2002, this issue) and enhances the removal of worker-laid eggs, because egg removal eventually vanishes in queenless honeybee colonies (Miller and Ratnieks, 2001).

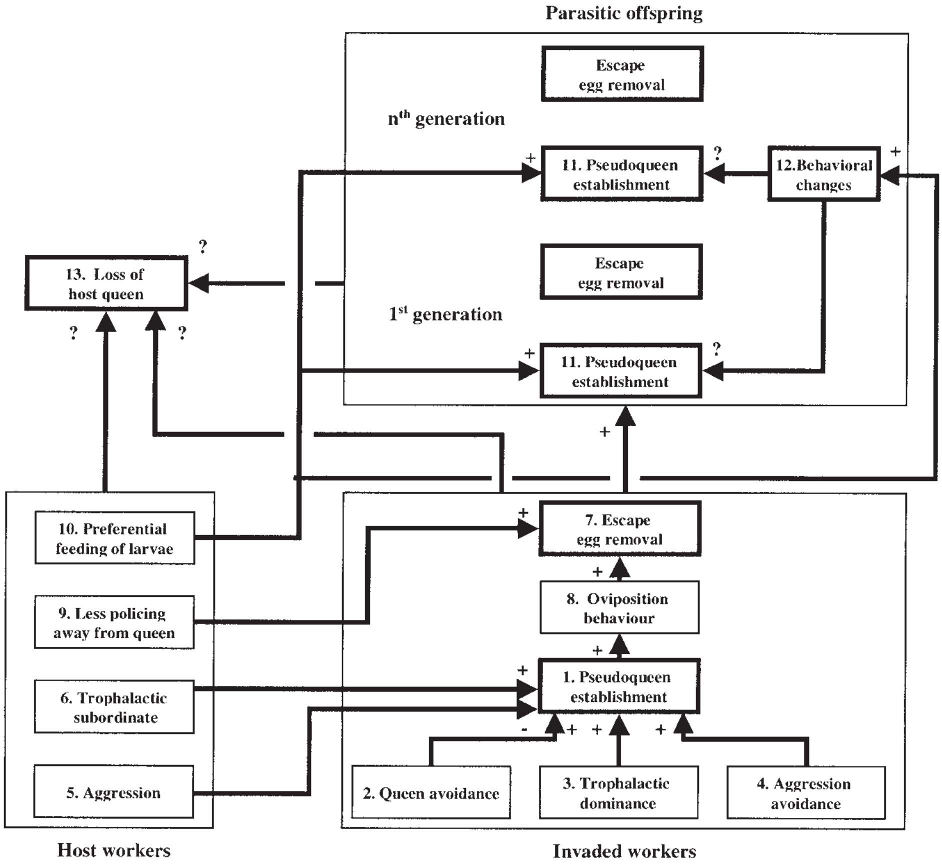

Figure 2. Virulence of social parasitic Cape honeybee workers following successful invasion, associated with parasitic pseudoqueen establishment and the "dwindling colony" syndrome of host colonies. The minimum number of behavioural interactions between host workers, invaded workers and parasitic offspring are shown. Positive and negative interactions are indicated with "+" and "–" respectively, unknown interactions with "?". The nth generation of parasitic offspring represents progeny reared after the loss of the host queen and is variable. For simplicity behavioural interactions related to the laying worker/pseudoqueen establishment and escape of egg-removal of parasitic offspring have been omitted.

Those workers surviving worker-worker aggression have successfully established themselves as parasitic pseudoqueens but have to evade the removal of worker-laid eggs in queenright host colonies (step 8 in Fig. 2) by preferentially laying eggs with low removal rates (Martin et al., 2002a) in parts of the hive where the removal of worker-laid eggs seems to be reduced (step 7 in Fig. 2, Neumann, Pirk, Hepburn and Moritz, unpublished data). Host workers promote this by removing fewer *A. m. capensis* worker-laid eggs above the queen excluder (step 9 in Fig. 2, Neumann, Pirk, Hepburn and Moritz, unpublished data).

The resulting parasitic offspring is preferentially fed by the host workers (step 10 in Fig. 2; Beekman et al., 2000; Calis et al., 2002, this issue) leading to highly developed progeny. Thus, parasitic offspring can be expected to be predisposed for further reproduction (step 11 in Fig. 2; Calis et al., 2002, this issue). This preferential feeding by the host workers (step 10 in Fig. 2) may also be responsible for the more "queen-like" behaviour of later generations of parasitic offspring compared to workers which have initially invaded the host (step 12 in Fig. 2; Magnuson, 1995); especially when the host queen is lost (step 13 in Fig. 2; Allsopp, 1995; Swart et al., 2001) and their pheromonal suppression vanishes in the course of infestation (Magnuson, 1995). It is unknown which group (host workers, invaded workers or parasitic offspring) is responsible for the loss of the host queen (step 13 in Fig. 2).

Replacement queen rearing from the host queen offspring, recently after queenloss and the rearing of an *A. m. capensis* queen at later stages of infestation is pheromonally suppressed by the already established parasitic *A. m. capensis* pseudoqueens (Anderson, 1968; Wossler, 2002, this issue). Finally, *A. m. capensis* workers may infest new host colonies via the different transmission pathways, thereby completing the social parasitic pathway of laying *A. m. capensis* workers. In the following sections, these steps are discussed in detail.

4.1. Pseudoqueen establishment: how to gain reproductive dominance in host colonies (step 1 in Fig. 2)

After queen loss only a few pseudoqueens monopolize reproduction in queenless Cape honeybee colonies (Moritz et al., 1996), indicating strong competition for reproductive dominance among workers. Pheromones may play a key role in obtaining the position of a pseudoqueen since workers compete for producing the strongest pheromonal signal (Moritz et al., 2000). However, behavioural influences are also clearly shown to influence pseudoqueen status.

4.1.1. Queen avoidance (step 2 in Fig. 2)

Worker avoidance of queen pheromonal suppression may be crucial to establish or maintain high pheromonal and ovarial development (Moritz et al., 2001a,b, 2002). Indeed, *A. m. capensis* workers tend to avoid the queen, while *A. m. scutellata* workers are more often found in their close vicinity (Moritz et al., 2001a). Workers with a queen-like pheromonal bouquet avoid the queen more than workers with a more worker-like pheromonal bouquet, which should reduce the suppressing effect on ovary development (Moritz et al., 2002). It is unclear whether the avoidance behaviour causes the more queen-like pheromonal bouquet or whether the queen-like pheromonal bouquet is associated with avoidance behaviourally. Moreover, there seems to be a spatial separation of pseudoqueens in queenless Cape honeybee colonies (Lattorff et al., 2001). Thus, workers may also avoid other highly developed workers to gain or maintain reproductive dominance. Alternatively, but not mutually exclusive, such a spatial distance between pseudoqueens is needed to allow for more than one of such workers with a queen-like pheromonal bouquet. Since invading workers join a foreign host colony, the new colony environment may predispose them for gaining reproductive dominance. Indeed, even drifted workers participate less in hive duties (*A. m. carnica*: Pfeiffer and Crailsheim, 1998; *A. m. capensis*: Neumann, Hepburn and Radloff, unpublished data) and tend to avoid the queen more than native control workers from the same age cohort (Neumann, Hepburn and Radloff, unpublished data). Thus, it appears as if foreign workers exhibit queen avoidance behaviour more readily, which probably predisposes them for gaining reproductive dominance in their host colonies.

4.1.2. Trophallactic dominance (step 3 in Fig. 2)

It is well established that workers of *A. m. capensis* are prone to gain trophallactic dominance when caged with workers of other subspecies (Velthuis et al., 1990). Unless *A. m. capensis* workers do not feed themselves from pollen stores, which is unknown, this appears to be essential for ovary activation.

4.1.3. Avoidance of worker-worker aggression (step 4 in Fig. 2)

Honeybee workers with developed ovaries are attacked by other workers (Velthuis, 1976; Visscher and Dukas, 1995). Severe fighting occurs in some Cape honeybee colonies after queenloss (Stuart-Findlay, 1953; Lundie, 1954; Anderson, 1963, 1968, 1977; Tribe, 1981). Dead *A. m. capensis* workers can be found in large numbers in front of *A. m. capensis* colonies which recently lost their queens (Anderson, 1977; up to one-third of the colony, Tribe and Allsopp, 2001a,b). Also, *A. m. scutellata* workers in infested host colonies of *A. m. scutellata* show aggressive behaviour towards invaded *A. m. capensis* workers (Allsopp, 1995). Indeed, severe fighting can be observed at the hive entrance of infested colonies (Swart et al., 2001). Thus, dead workers can be frequently found in front of infested *A. m. scutellata* colonies and can be used diagnostically to identify infestations with *A. m. capensis* laying workers at early stages (Allsopp, 1995).

Clearly, only those workers surviving worker-worker aggression can successfully infest and reproduce in host colonies. Rapid development of a queenlike pheromonal bouquet (Simon et al., 2001) as indicated by observations of Tribe (1981) is one probable mechanism. When workers approach an *A. m. capensis* worker with a queenlike pheromonal bouquet, they may back away from her as much as from a queen (Tribe, 1981). Alternatively, but not mutually exclusive, social parasitic workers may show behavioural traits to avoid aggressive encounters with host workers, such as hiding in small cracks in the nest (Tribe, personal communication). However, not a single study has been published in this regard. Interestingly, aggressive interactions among *A. m. capensis* laying workers have not been reported and laying *A. m. capensis* queens and laying pseudoqueens can be seen side by side (Tribe, 1981). In contrast to *A. m. scutellata* workers, a high proportion of *A. m. capensis* pseudo-clone workers survived which were artificially introduced into host colonies (50% Martin et al., 2002b). This shows good abilities to survive worker-worker aggression in host colonies and further indicates a high virulence of this particular strain.

Alternatively, *A. m. capensis* workers which have already a queen-like pheromonal bouquet and/or high ovarial development may enter host colonies (see above). This seems plausible in light of the fast ovarial and pheromonal development of *A. m. capensis* workers (Simon et al., 2001). In this case, trophallactic dominance can be easily established and worker-worker aggression inside of the colony easily avoided. Because almost all combinations of reproductive status are possible in *A. m. capensis* workers (Hepburn, 1994), such workers with developed pheromones may have developed ovaries or not. In case of invading workers with already developed pheromones and ovaries, all steps leading to reproductive dominance can be omitted. It is likely, that such workers can immediately start egg laying within the host colonies. Initially most invaded *A. m. capensis* workers surviving worker-worker aggression should be able to develop the full pseudoqueen phenotype due to the inability of the *A. m. scutellata* queen and the host brood to suppress their development (Wossler, 2002). At later stages it is likely that not all workers can develop into pseudoqueens because they are suppressed pheromonally by the already established *A. m. capensis* pseudoqueens.

4.2. Evasion of worker policing (step 7 in Fig. 2)

Eggs laid by workers are removed by other workers in queenright and in recently queenless colonies of European honeybees (worker policing, Ratnieks and Visscher, 1989; Miller and Ratnieks, 2001). Because both *A. m. capensis* and *A m. scutellata* are also able to police worker-laid eggs of their own and of the other subspecies (Neumann, Pirk and Ratnieks, unpublished data), policing of worker-laid eggs constitutes a host resistance mechanism and consequently parasitic *A. m. capensis* workers have to evade worker policing in queenless and queenright host colonies to successfully reproduce. Thus, the question emerges how *A. m. capensis* workers are able to evade worker policing.

Worker policing in the Cape honeybee is reduced during unfavourable weather conditions (Pirk et al., 2002, this issue; C.W.W. Pirk, unpublished data). So, one potential tactic of *A. m. capensis* laying workers, to achieve successful reproduction despite the presence of the host queen, could be to lay eggs when worker policing is reduced (Pirk et al., 2002). However, egg-removal and worker egg-laying are positively correlated in queenright Cape honeybee colonies, strongly indicating that laying workers do not use such a tactic (Pirk et al., 2002, this issue).

One mechanism seems to actually involve evasion of the queen and the brood nest of the host colonies by laying *A. m. capensis* workers (Neumann, Pirk, Hepburn and Moritz, unpublished data). Workers of *A. m. capensis* preferentially lay eggs above the queen excluder in queenright colonies, where worker policing is reduced (Neumann, Pirk, Hepburn and Moritz, unpublished data). Frequent field observations strongly indicate that this is expressed at the level of the host colony’s phenotype as parasitic worker brood initially appearing at the extreme outside frames (Lundie, 1954; Allsopp, 1995; Martin et al., 2002b), followed by parasitic worker brood frames close to the actual brood nest of the host queen and finally flanking the brood frames of the host queen (Allsopp, 1995). The eggs laid by pseudoqueens can escape policing and young nurse workers of the host colony are attracted by brood pheromones to the hatching larvae.

The second mechanism seems to be the removal rates of eggs laid by parasitic workers. Eggs laid by highly virulent parasitic workers of the *A. m. capensis* pseudo clone (Kryger, 2001a,b; Kryger, Solignac, Lubbe, unpublished data), which are invading *A. m. scutellata* colonies in the Highveld of South Africa, seem to have lower removal rates than laying workers of *A. m. scutellata* (Martin et al., 2002a) and intermediate between *A. m. capensis* queen-laid eggs and worker-laid eggs from the native range of the Cape honeybee (Port Elizabeth, Neumann et al., 2001b).

4.3. Oviposition behaviour (step 8 in Fig. 2)

In the Cape honeybee worker egg-laying (Pirk et al., 2002, this issue) and successful worker reproduction in the presence of a queen (Pettey, 1922; Moritz et al., 1999) is much more common than in European subspecies of *A. mellifera* (Ratnieks, 1993; Visscher, 1996). Moreover, laying worker colonies of *A. m. capensis* can persist for long periods without raising a new queen (up to 8 months, Hepburn, personal observations). These observations indicate that *A. m. capensis* laying workers may show specific adaptations for how many eggs are laid per cell, how and where eggs are laid in an individual brood cell and in which brood cell type workers preferentially oviposit (drone or worker cells), because inappropriate oviposition would cause drastic losses in the colony worker population within a short period of time causing a shorter life span of *A. m. capensis* laying worker colonies.

Indeed, thelytokous *A. m. capensis* workers preferentially lay eggs in worker cells (Neumann et al., 2000a), which have the appropriate cell size for rearing female offspring. Moreover, it is often very difficult to distinguish the brood nest of *A. m. capensis* pseudoqueens from that of a laying queen, because a single egg is laid at the bottom of the cell in a regular pattern (Tribe, 1981; Tribe and Allsopp, 2001b, personal observations). Such provisioning behaviour (in terms of number of eggs laid and how and where they are laid) might considerably enhance the longevity of queenless *A. m. capensis* colonies and the reproductive output of individual parasitic workers in the initial phase of infestation because only one larva per cell can be reared to adulthood and surplus offspring in one cell is cannibalised. Indeed, during usurpation of *A. m. scutellata* colonies by *A. m. capensis* pseudo clone workers, single worker-laid eggs appeared in worker cells (Martin et al., 2002b). This is in contrast to laying workers of other *A. mellifera* subspecies, which lay multiple eggs per cell (Hastings, 1989; up to several dozens eggs in one cell in *A. m. scutellata*, personal observations) and may accidentally kill or even deliberately remove previously laid eggs.

4.4. Rearing of parasitic offspring (Fig. 2)

The resulting parasitic offspring is preferentially fed by host colony workers of other *A. mellifera* subspecies (step 10 in Fig. 2, European *A. mellifera*: Beekman et al., 2000; *A. m. scutellata*: Calis et al., 2002, this issue). This results in highly developed workers (Calis et al., 2002, this issue), which can be expected to be highly virulent and predisposed for pseudoqueen establishment in the host (step 11 in Fig. 2). Thus, although such a preferential feeding may not be really needed for the social parasitic cycle to work it appears to clearly promote the dwindling of host colonies. The queenstate of the host colony may also play a role in this regard, because *A. m. capensis* workers reared in colonies headed by laying workers are bigger and have more ovarioles than those reared in a queenright colony (Woyke, 1979).

However, in queenright (Hepburn et al., 1991) and queenless (Tribe, 1981) *A. m. capensis* colonies only a few workers can actually develop the pseudoqueen phenotype, which might indicate that not all of these workers will establish themselves as pseudoqueens in the host colony. Although parasitic brood is preferentially fed by the host workers (Beekman et al., 2000; Calis et al., 2002), this picture might change in the course of infestation because the reduction in foraging causes a decrease in stored food. Moreover, fewer host workers have to nurse more and more hatching parasitic larvae. Finally, with the passage of time the size of the nursing cohort with developed hypopharyngeal glands quickly diminishes as well. Thus, the relative low ovarial development of *A. m. capensis* pseudo-clone workers (Martin et al., 2002b) might not only be caused by pheromonal suppression of already established parasitic pseudoqueens but also a result of less efficient nutrition at later stages of infestation. Nevertheless, high numbers of adult *A. m. capensis* workers can be reared in an *A. m. scutellata* host colony (~3 000–10 000, Martin et al., 2002b).

Laying worker colonies of *A. m. capensis* in the fynbos region occasionally requeen from laying worker offspring (c. 7% of all colonies, Allsopp and Hepburn, 1997). However, this has not been reported yet from the colonies of *A. m. scutellata* which have been infested with *A. m. capensis* laying workers (Swart et al., 2001; Martin et al., 2002b). Indeed, recent genetic data also strongly indicates that there is no *A. m.*

capensis queen rearing in infested colonies (Kryger et al., 2002). Such a lack of queen rearing in infested colonies (both of a new host queen recently after queenloss and of an *A. m. capensis* queen) is probably due to the pheromonal suppression by established *A. m. capensis* pseudoqueens (Anderson, 1968).

4.5. Behavioural changes in the course of infestation (step 12 in Fig. 2)

Field observations indicate, that there might be considerable differences between generations of parasitic workers reared in host colonies with respect to behaviour (Magnuson, 1995). For example, in contrast to the *A. m. scutellata* host workers behaviourally "queen-like" parasitic workers of *A. m. capensis* do not fly up but rather stay on the combs when infested colonies are inspected (Magnuson, 1995). Moreover, it has been reported that the pseudo clone bees are not capable of caring for themselves, because they are too queen-like in behaviour (Kryger, 2001b). Especially after the loss of the host queen, when pheromonal suppression vanishes and parasitic offspring is reared in great numbers in the absence of the host queen, such "queen-like" behaviour may be even more readily expressed (Magnuson, 1995). Likewise, oviposition behaviour changes in the course of infestation. Initially single eggs are laid per cell by parasitic workers (Martin et al., 2002b) but at later stages of infestation multiple eggs can be regularly found per cell (Allsopp, 1995; Martin et al., 2002b).

There is severe competition for reproductive dominance among *A. m. capensis* workers (Moritz et al., 1996; Moritz et al., 2000), resulting in just a few pseudoqueens monopolising reproduction in a laying worker colony of *A. m. capensis* (c. 14 in a colony of 2000 bees, Tribe, 1981). The pheromonal bouquet of pseudoqueens is apparently able to suppress queen rearing and development in other workers (Hepburn et al., 1988) and may also influence the behaviour of other parasitic workers. Therefore, it is likely that the traits "queen-like" behaviour and high ovarial and pheromonal development are not expressed by all *A. m. capensis* workers in a host colony at late stages of infestation (Hepburn and Allsopp, 1994), even if they are all genetically predisposed for such a development (Moritz and Hillesheim, 1985). This may be particularly interesting with respect to transmission to new hosts, assuming that workers with developed ovaries have fewer chances to invade host colonies (Reece, 2002) and taking into account that pseudoqueens are unlikely to leave the hive (Tribe, 1981). However this must be further investigated. For example, few *A. m. capensis* workers may even participate in foraging at later stages of infestation (Martin et al., 2002b), which is not expected from reproductive dominant workers.

4.6. Loss of the host queen (step 13 in Fig. 2)

The host queen seems to play an important role in the context of social parasitism by laying workers (Tribe, 1983; Woyke, 1995; Neumann et al., 2001). However, given the current state of evidence, it is simply unclear what factors and which of the various groups in an infested colony (invaded *A. m. capensis* workers, *A. m. capensis* laying worker offspring reared in the host, *A. m. scutellata* host workers) actually cause the loss of the host queen and whether agonistic encounters are involved or not. Because, queen pheromone production in honeybees is associated with egg-laying (e.g. laying queens produce a stronger queen signal than virgin queens; Wossler, 2002, this issue, and queens approaching supersedure; Allsopp and Hepburn, 1997) a potential reduction in queen pheromone production resulting from reduced egg-laying by the host queen in the course of infestation may be relevant. This seems plausible in light of the massive egg laying by the parasitic *A. m. capensis* workers, simply resulting in less available space in the brood nest (see above Allsopp, 1995). Alternatively, but not mutually exclusive a reduced nutrition of the host queen may also play a role (Kryger, 2001). Finally the rapid loss of the host queen in some cases (Martin et al., 2002) indicates that immediate agonistic interactions should also be considered. However, not a single study has addressed this question to date.

We conclude that the spatial distribution of *A. m. capensis* workers in host colonies, their readiness to gain trophallactic dominance, the high chance of surviving worker-worker aggression and their oviposition behaviour are essential behavioural aspects for the virulence of social parasitic workers.

5. RESISTANCE AND SUSCEPITIBILITY OF HOST COLONIES

Queenless and queenright colonies of *A. m. scutellata* are highly susceptible hosts for invasion by Cape honeybees (Hepburn and Allsopp, 1994). Likewise, queenless colonies of European subspecies are also susceptible (Woyke, 1995). In general, queenless colonies are more prone to invasion by laying workers than queenright colonies (Tribe, 1983; Woyke, 1995), e.g. *A. m. scutellata* colonies may be successfully taken over when the virgin *A. m. scutellata* host queen departs on a mating flight or during swarming, when only sealed queen cells are left in a colony (Tribe, 1983). In an apiary, where both *A. m. mellifera* and *A. m. capensis* were kept, problems occurred with queenless *A. m. mellifera* colonies rearing queens because *A. m. capensis* workers invaded such colonies, and the queen cells were destroyed (J. Woyke, personal communication). However, it also happened that *A. m. mellifera* queens disappeared and laying *A. m. capensis* workers took over the colonies (J. Woyke, personal communication). Nevertheless, queenright colonies of other subspecies than *A. m. scutellata* seem to be somehow resistant (*A. m. ligustica*, *A. m. carnica*, *A. m. caucasica* and *A. m. mellifera*; Woyke, 1995). Moreover, the "dwindling colony" syndrome due to laying workers has never been reported from *A. m. capensis* colonies and there are reports that natural hybrid colonies between *A. m. capensis* and *A. m. scutellata* are somewhat resistant to *A. m. capensis* infestations (Greeff, 1997; but see Reece, 2002).

These observations strongly indicate that queenstate and race are important factors to explain the resistance of colonies towards infestations with *A. m. capensis* laying workers. So, why are *A. m. scutellata* colonies highly susceptible hosts, whereas queenright colonies of other subspecies seem to be somehow resistant and why was the natural hybrid zone between *A. m. capensis* and *A. m. scutellata* stable without human intervention?

5.1. Susceptibility of *A. m. scutellata* host colonies

If *A. m. capensis* workers are not able to break into the fortress (Schmid-Hempel, 1998) infestations cannot be initiated. Thus, efficient guarding by host colonies might constitute an important behavioural resistance mechanism in the context of social parasitism by *A. m. capensis* laying workers. However, although *A. m. scutellata* colonies may scrutinise incoming foreign workers more carefully than do *A. m. capensis* colonies, because *A. m. scutellata* colonies hosted fewer drifted and dispersed workers than did *A. m. capensis* colonies (Neumann et al., 2001c) nonetheless they are readily taken over by laying *A. m. capensis* workers (Hepburn and Allsopp, 1994). This clearly indicates that efficient guarding behaviour is not a particular important aspect for host colony resistance.

Although the basic pattern of worker policing (worker-laid eggs are removed faster than queen-laid eggs) can be observed in queenright *A. m. scutellata* and *A. m. capensis* colonies, the actual number of remaining worker-laid eggs after 24 hours is much higher compared to European subspecies (~20% Neumann, Pirk and Ratnieks, unpublished data). This suggests that either policing is reduced and/or workers lay eggs which have lower removal rates compared to European subspecies. Given policing in *A. m. scutellata* is truly reduced, this might explain why queenright *A. m. scutellata* colonies may be more susceptible towards infestations by *A. m. capensis* laying workers compared to queenright colonies of European subspecies. Unfortunately, the relative importance of queenstate of *A. m. scutellata* host colonies and worker policing efficiency compared to queenright European host colonies for the success rate of *A. m. capensis* parasitic workers has not yet been investigated quantitatively.

The rejection of developed workers in queenless colonies seems to be more readily expressed in *A. m. capensis* than in *A. m. scutellata* (Anderson, 1977). Clearly, this further contributes to our understanding of the susceptibility of *A. m. scutellata* host colonies to infestations by *A. m. capensis* laying workers because the more developed workers are rejected the fewer remain to successfully reproduce.

The high incidents of successful infestations of queenright *A. m. scutellata* colonies by social parasitic *A. m. capensis* workers (Allsopp and Crewe, 1993) clearly indicate that *A. m. scutellata* queens are not able to suppress the development of invaded *A. m. capensis* workers. Thus, it is very likely that race specific ratios of compounds in the pheromonal bouquet of queens (see Wossler, 2002 for a review on this particular issue) may play a key role in determining whether queens can suppress *A. m. capensis* laying workers or not. For example, virgin queens of *A. m. scutellata* were killed by *A. m. capensis* workers when kept in transport cages (Buys, 1984) indicating that the workers did not accept the queens.

5.2. Stability of the natural hybrid zone between *A. m. capensis* and *A. m. scutellata*

Worker reproduction is an important feature in the natural occurring hybrid zone between *A. m. capensis* and *A. m. scutellata* (Moritz et al., 1998). Although there is a morphometrically clearly defined zone of natural hybrid colonies, thelytoky has introgressed into the region (Hepburn and Radloff, 2002). Since the hybrid zone appeared to be stable, one could expect hybrid colonies to have behavioural features, explaining their resistance and/or the stability of the natural hybrid zone. Indeed, the natural hybrids do not behave in an intermediate matter, but instead exhibit unique behavioural characteristics at worker and colony levels which are highly suggestive of a buffering capacity in the hybrid zone (Hepburn and Radloff, 1998; Neumann et al., 2001c).

First, hybrid workers disperse less often than either *A. m. capensis* or *A. m. scutellata* (Neumann et al., 2001c). Given that dispersing represents a host finding mechanism for social parasitic laying workers outside of apiaries, clearly fewer hybrid workers spread than do workers of *A. m. capensis*. However, why do the hybrids lack this behaviour? One possible explanation might be the general clinal structure of the hybrid zone in which characteristics of *A. m. capensis* are gradually replaced by those of *A. m. scutellata* (cf. Hepburn and Radloff, 1998; Hepburn and Radloff, 2002). As a result, hybrid colonies may simultaneously consist of both arrhenotokous and thelytokous laying workers (Pettey, 1922; Moritz et al., 1999; Neumann et al., 2000a). Since the population density in the drier parts of the hybrid zone is sparse and much lower than in *A. m. capensis* populations (Hepburn et al., 1994), the chance of successful transmission may be low. Moreover, thelytokous laying workers are more likely to become reproductively dominant in queenless hybrid colonies than arrhenotokous ones (Neumann et al., 2000a). Thus, the low dispersal frequency of the natural occurring hybrids may reflect a trade-off for thelytokous laying workers between a low chance of successful transmission into a host colony against a high chance of successful reproduction in the mother colony after queenloss.

Second, different hosting mechanisms of dispersed workers by hybrid colonies may also play a role (but see above). In contrast to *A. m. capensis*, hybrid colonies host proportionally more drifters than dispersers (Neumann et al., 2001c). Moreover, queenless hybrid colonies host significantly fewer drifters than their queenright counterparts; and the former also host significantly fewer dispersers than queenright or queenless *A. m. capensis* colonies (Neumann et al., 2001c). If fewer dispersers were accepted by hybrid host colonies, especially by queenless ones, the chance of their usurpation should be smaller (Hepburn and Allsopp, 1994). However, against this the hybrid colonies appeared unable to suppress post-drifting development of drifted *A. m. capensis* workers (Reece, 2002), suggesting that they are not resistant with respect to infestations by laying *A. m. capensis* workers.

We conclude that a combination of worker policing inefficiency, less efficient rejection of developed workers in recently queenless colonies and queen inability to suppress worker development governs the susceptibility of *A. m. scutellata* host colonies to social parasitic *A. m. capensis* workers. In particular, race specific abilities of queen and or brood pheromones seem to play the key role to suppress the development and establishment of *A. m. capensis* workers in host colonies (Wossler, 2002). However, colonies of other subspecies may have not yet encountered highly virulent strains of social parasitic *A. m. capensis* workers, such as the pseudo clone invading the Northern regions of South Africa. Thus, it remains to be tested whether other subspecies than *A. m. scutellata* are resistant against that particular strain or not. The lack of dispersal in the hybrids (Neumann et al., 2001c) and the very low population density in the hybrid zone (Hepburn et al., 1994) might have been responsible for the apparent stability of the natural occurring hybrid zone between *A. m. capensis* and *A. m. scutellata* before the *capensis* calamity occurred.

6. GENERAL CONCLUSIONS

A. m. capensis shows several behavioural traits favouring both transmission (e.g. dispersing behaviour, ready absconding of queenless units, frequent mergers) and virulence (e.g. queen avoidance, trophallactic dominance, oviposition behaviour, evasion of worker policing, “queen-like” behaviour) of social parasitic workers. However, while some behavioural aspects are well understood (e.g. trophalactic dominance), other factors associated with social parasitism by *A. m. capensis* laying workers are still unclear (e.g. loss of the host queen). Thus, although the *A. m. capensis* calamity occurred 10 years ago (Allsopp, 1992; Johannsmeier, 1992; Lear, 1992) the behavioural aspects still need deeper investigation.

Here we suggest the reproductive cycle for social parasitism by laying Cape honeybee workers. *A. m. capensis* workers with undeveloped ovaries are predisposed to initially infest a potential host colony and to successfully establish themselves as pseudoqueens in host colonies when the host queen is still alive. Then, the first generation of highly developed parasitic workers emerges without the suppression of an *A. m. capensis* queen and/or pseudoqueens. This effect is probably amplified when the host queen dies. These workers are predisposed for pseudoqueen establishment (because they have better developed ovaries; Calis et al., 2002, this issue) and can take over a host colony until the host colony's queen dies. The high frequency of parasitic pseudoqueens in the host at later stages of infestation suppresses queen rearing and the development and gaining pseudoqueen status of newly hatching *A. m. capensis* workers. Such undeveloped *A. m. capensis* workers are more likely to successfully infest new host colonies via the individual or the colonial transmission pathways.

A recent model (Moritz, 2002) indicates that infestations are likely to be fatal for apiary populations irrespective of beekeeping activities compensating for colony losses due to parasitation. Wild *A. m. scutellata* populations are however less likely to be affected by parasitic laying workers and stable equilibria between host and parasite occur over a wide range of the parameter space (Moritz, 2002). Although it is unlikely that the parasitic pseudo clone represents a threat to the conservation of biodiversity, even low frequencies of parasitic *A. m. capensis* workers in wild honeybee population can cause a permanent threat to beekeeping activities (Moritz, 2002).

It remains open whether social parasitism by laying workers is purely an artefact of beekeeping activity or a regular part of the life history of the Cape honeybee. Due to the high virulence of the *A. m. capensis* pseudo clone host colonies die quickly (Martin et al., 2002b). However, the transmission capacity appears to be reduced (Neumann et al., 2001b) and the problem is mainly restricted to large scale beekeepers. Thus, it appears as if the *capensis* calamity is probably maintained by large scale beekeeping. We conclude that more studies are needed to evaluate whether social parasitism by laying *A. m. capensis* workers is a peculiar sideline of reproduction reflecting a man-made problem or a general/regular lifestyle of the Cape honeybee.

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Résumé – Base comportementale du parasitisme social chez l'abeille du Cap (*Apis mellifera capensis*). Les ouvrières pondeuses de l'abeille du Cap (*Apis mellifera capensis* Escholtz) sont des parasites sociaux facultatifs et conduisent au syndrome du dépérissement de la colonie chez les colonies hôtes. Les ouvrières d'*A. m. capensis* présentent une gamme de pré-adaptations importantes pour ce parasitisme social (par exemple, le nombre élevé d'œufs pondus par jour, la longévité, la parthénogenèse thélytoque) et peuvent se transformer en pseudo-reines, qui possèdent un développement ovarien fort et un bouquet phéromonal semblable à celui de la reine. Le cycle de reproduction des ouvrières pondeuses parasites sociales (Fig. 1) nécessite néanmoins une base comportementale aussi bien pour la transmission que pour la virulence. La transmission horizontale (au sein d'une même génération) peut s'effectuer sur le plan individuel et sur le plan de la colonie (Fig. 1). Sur le plan individuel les ouvrières du Cap peuvent soit atteindre des colonies hôtes passivement par dérive (étape 1 de la Fig. 1), soit les rechercher activement (étape 2 de la Fig. 1). On ne sait pas si les ouvrières d'*A. m. capensis* présentent des comportement spécifiques à ce sujet. Sur le plan de la colonie les

ouvrières d'*A. m. capensis* peuvent se joindre à des essaims non reproducteurs (désertion, étape 4 de la Fig. 1). Le fait que la colonie soit orpheline et le mode de reproduction des ouvrières ne semblent pas favoriser les essaims non reproducteurs. Chez l'abeille du Cap cet essaim non reproducteur peut se déplacer sur de grandes distances. Les colonies d'*A. m. scutellata* Lepeletier infestées par des ouvrières du Cap pondeuses et les ouvrières du Cap qui restent dans la colonie hôte après son effondrement essaiment souvent. Les essaims non reproducteurs peuvent chez l'abeille du Cap fusionner avec d'autres colonies et infester ainsi de nouveaux hôtes (étape 5 de la Fig. 1). Les fusions d'essaims se produisent souvent chez les abeilles africaines, en particulier chez *A. m. capensis.* La transmission verticale peut avoir lieu lorsque les ouvrières du Cap se joignent à des essaims reproducteurs des colonies hôtes aux stades initiaux de l'infestation (étape 6 de la Fig. 1). Mais cela n'a pas encore été étudié. Après une transmission réussie les ouvrières du Cap doivent s'établir comme pseudo-reines dans les colonies hôtes (étape 7 de la Fig. 1 ; étape 1 de la Fig. 2). La répartition spatiale des ouvrières dans les colonies hôtes semble dans ce contexte revêtir une importance. Les ouvrières du Cap ont tendance à éviter les reines hôtes (étape 2 de la Fig. 2), ce qui peut être décisif pour le développement des phéromones et des ovaires. En outre les ouvrières d'*A. m. capensis* sont dominantes dans les échanges trophallactiques par rapport aux ouvrières des autres sous-espèces (étape 3 de la Fig. 2), ce qui peut être également important pour l'activation des ovaires. Puisque les ouvrières à ovaires développés sont attaquées par les autres ouvrières, les ouvrières du Cap doivent éviter les agressions (étape 4 de la Fig. 2). On ignore si les ouvrières du Cap présentent des comportements particuliers à cet égard ou si simplement elles développent rapidement leur bouquet phéromonal. Les ouvrières hôtes d'*A. m. capensis* attaquent bien les ouvrières du Cap dans les colonies infestées (étape 5 de la Fig. 2), mais en même temps elles les nourrissent plus (étape 6 de la Fig. 2). Les ouvrières du Cap établies comme pseudo-reines dans la colonie hôte doivent échapper à l'élimination de leurs propres œufs par les ouvrières hôtes (maintien de l'ordre par les ouvrières ou « worker policing », étape 8 de la Fig. 1, étape 7 de la Fig. 2). Les ouvrières pondeuses du Cap pondent de préférence au-dessus de la grille à reine dans les colonies qui possèdent une reine (étape 8 de la Fig. 2). Là l'élimination des œufs pondus par les ouvrières du Cap est moindre (étape 9 de la Fig. 2). Les œufs des ouvrières du Cap très virulentes ont un taux d'élimination plus faible que les œufs des ouvrières pondeuses d'*A. m. scutellata* et intermédiaire entre les œufs des reines d'*A. m. capensis* et des œufs des ouvrières pondeuses du Cap moins virulentes. Puisqu'une seule ouvrière peut être élevée par cellule, le grand nombre d'œufs pondus par cellule peut réduire le succès reproducteur des ouvrières parasites. Les pseudo-reines *A. m. capensis* pondent souvent un œuf sur le fond de la cellule, si bien que le nid à couvain résultant se différencie peu de celui d'une reine. Les larves parasites d'*A. m. capensis,* qui éclosent dans les colonies hôtes, reçoivent la nourriture des ouvrières de la colonie hôte qui les nourrissent préférentiellement (étape 10 de la Fig. 2). De ce fait des ouvrières du Cap très développées sont élevées dans la colonie hôte et prédisposées à devenir des ouvrières pondeuses (étape 11 de la Fig. 2). Le nourrissement préférentiel pourrait expliquer aussi les différences de comportement entre les diverses générations d'ouvrières du Cap dans la colonie hôte (étape 12 de la Fig. 2). Ces différences de comportement n'ont pas été jusqu'à présent étudiées en détail. Il y a perte de la reine hôte au cours de l'infestation (étape 13 de la Fig. 2). On ignore quels en sont les facteurs décisifs et quel rôle y jouent les ouvrières du Cap. Aux stades ultérieurs de l'infestation, de nombreuses ouvrières d'*A. m. capensis* sont élevées (mais pas de reines ou

très rarement, étape 10 de la Fig. 1), de nouvelles colonies hôtes peuvent être infestées et le cycle de reproduction du parasite social est ainsi bouclé.

***Apis mellifera capensis / Apis mellifera scutellata* / reproduction des ouvrières / parasitisme social**

Zusammenfassung – Verhalten der Kaphonigbiene (*Apis mellifera capensis*) für Sozialparasitismus. Legende Arbeiterinnen der Kaphonigbiene (*Apis mellifera capensis* Escholtz) sind fakultative Sozialparasiten und führen das „dwindling colony syndrome“ in Wirtsvölkern herbei. *A. m. capensis* Arbeiterinnen zeigen eine Reihe wichtiger Präadaptationen für diesen Sozialparasitismus (z.B. hohe Anzahl an gelegten Eiern pro Tag, Langlebigkeit, Thelytokie) und können sich zu Pseudoköniginnen entwickeln, die eine starke ovarielle Entwicklung und ein der Königin ähnliches Pheromonbouquet aufweisen. Der sozialparasitische Reproduktionszyklus legender Kaparbeiterinnen (Abb. 1) erfordert jedoch auch eine Verhaltensgrundlage sowohl für die Transmission als auch für die Virulenz. Horizontale Transmission (innerhalb einer Generation) kann auf der individuellen und der kolonialen Ebene erfolgen (Abb. 1). Auf der individuellen Ebene können Kaparbeiterinnen entweder passiv durch Verflug zu Wirtsvölkern gelangen (Schritt 1 in Abb. 1) oder aber aktiv Wirtsvölker aufsuchen (Schritt 2 in Abb. 1). Diese Arbeiterinnen müssen als Individuen in das Wirtsvolk eindringen (Schritt 3 in Abb. 1). Es ist unbekannt, ob *A. m. capensis* Arbeiterinnen in diesem Zusammenhang spezielle Verhaltensweisen aufweisen. Auf der kolonialen Ebene können sich *A. m. capensis* Arbeiterinnen nicht reproduktiven Schwärmen anschließen (absconding, Schritt 4 in Abb. 1). Weisellosigkeit und der Modus der Arbeiterinnenreproduktion scheinen nicht reproduktives Schwärmen bei *A. m. capensis* zu fördern. Dieses nicht reproduktive Schwärmen kann bei der Kaphonigbiene über große Distanzen erfolgen. Auch von legenden Kaparbeiterinnen infizierte *A. m. scutellata* Völker und die nach dem Zusammenbruch der Wirtsvölker übriggebliebenen Kaparbeiterinnen schwärmen häufig. Nicht reproduktive Schwärme mit Kaparbeiterinnen können mit anderen Völkern fusionieren und somit neue Wirte infizieren (Schritt 5 in Abb. 1). Schwarmfusionen sind häufig in afrikanischen Bienen, insbesondere bei *A. m. capensis*. Vertikale Transmission kann erfolgen, wenn Kaparbeiterinnen sich reproduktiven Schwärmen der Wirtsvölker in frühen Infektionsstadien anschließen (Schritt 6 in Abb. 1). Dies ist jedoch noch nicht untersucht worden. Nach erfolgreicher Transmission müssen sich die Kaparbeiterinnen als Pseudoköniginnen in den Wirtsvölkern etablieren (Schritt 7 in Abb. 1, Schritt 1 in Abb. 2). Die räumliche Verteilung von Arbeiterinnen in den Wirtsvölkern scheint hierbei von Bedeutung zu sein. Kaparbeiterinnen haben die Tendenz, Wirtsköniginnen zu meiden (Schritt 2 in Abb. 2), was für die Entwicklung von Pheromonen und Ovarien entscheidend sein kann. Darüber hinaus sind *A. m. capensis* Arbeiterinnen trophallaktisch dominant gegenüber Arbeiterinnen von anderen Unterarten (Schritt 3 in Abb. 2), was ebenfalls für die Aktivierung der Ovarien wichtig sein kann. Da Arbeiterinnen mit entwickelten Ovarien von anderen Arbeiterinnen attackiert werden, müssen die Kaparbeiterinnen in der Lage sein diese Aggressionen zu vermeiden (Schritt 4 in Abb. 2). Es ist nicht bekannt, ob Kaparbeiterinnen hierfür spezielle Verhaltensweisen aufzeigen oder lediglich eine schnelle pheromonale Entwicklung durchführen. *A. m. scutellata* Wirtsarbeiterinnen attackieren zwar Kaparbeiterinnen in infizierten Völkern (Schritt 5 in Abb. 2), füttern diese aber auch bevorzugt (Schritt 6 in Abb. 2). Kaparbeiterinnen, die intrakoloniale Auseinandersetzungen überlebt haben und als Pseudokönigin im Wirtsvolk etabliert sind, müssen der Entfernung ihrer gelegten Eier durch die Wirtsarbeiterinnen in den Wirtsvölkern entgehen (worker policing, Schritt 8 in Abb. 1, Schritt 7 in Abb. 2). Legende Kaparbeiterinnen legen in

weiselrichtigen Völkern bevorzugt oberhalb des Königinnenabsperrgitters (Schritt 8 in Abb. 2). Dort ist die Entfernung von Eiern legender Kaparbeiterinnen erniedrigt (Schritt 9 in Abb. 2). Darüber hinaus zeigen die Eier hochvirulenter Kaparbeiterinnen geringere Ausräumraten als Eier von legenden *A. m. scutellata* Arbeiterinnen, intermediär zwischen Eiern von *A. m. capensis* Königinnen und von weniger virulenten legenden Arbeiterinnen. Da nur eine Arbeiterin pro Zelle aufgezogen werden kann, können viele gelegte Eier pro Zelle den Reproduktionserfolg parasitischer Arbeiterinnen reduzieren. *A. m. capensis* Pseudo-Königinnen legen häufig ein Ei auf den Boden der Zelle, so dass das resultierende Brutnest nur schwer von dem einer Königin zu unterscheiden ist. Die parasitischen *A. m. capensis* Larven, die in den Wirtsvölkern schlüpfen, werden von den Arbeiterinnen des Wirtsvolkes bevorzugt gefüttert (Schritt 10 in Abb. 2). Dies führt dazu, dass hochentwickelte Kaparbeiterinnen im Wirtsvolk herangezogen werden, die für die Etablierung zur legenden Arbeiterin prädisponiert sind (Schritt 11 in Abb. 2). Das bevorzugte Füttern könnte auch Verhaltensunterschiede zwischen den verschiedenen Generationen der Kaparbeiterinnen im Wirtsvolk erklären (Schritt 12 in Abb. 2). Diese Verhaltensunterschiede wurden jedoch bisher noch nicht eingehend untersucht. Im Laufe der Infektion geht die Wirtskönigin verloren (Schritt 13 in Abb. 2). Welche Faktoren hierbei entscheidend sind und welche Rolle die parasitischen Kaparbeiterinnen dabei spielen ist nicht bekannt. In späten Infektionsstadien werden viele *A. m. capensis* Arbeiterinnen aufgezogen (jedoch keine oder nur sehr selten Königinnen, Schritt 10 in Abb. 1), die neue Wirtsvölker infizieren können und somit den sozialparasitischen Reproduktionszyklus legender Kaparbeiterinnen schließen.

***Apis mellifera capensis* / *Apis mellifera scutellata* / Arbeiterinnenreproduktion / Honigbiene / Sozialparasitismus**

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