Apidologie 33 (2002) 139–163

DOI: 10.1051/apido:2002006

Review article

Pheromone mimicry by *Apis mellifera capensis* social parasites leads to reproductive anarchy in host *Apis mellifera scutellata* colonies

Theresa Clair WOSSLER*

Department of Zoology and Entomology, University of Pretoria, Pretoria, 0002, South Africa

(Received 1 November; revised 12 December 2001; accepted 19 December 2001)

Abstract – Queen mandibular, tergal, tarsal and Dufour's gland secretions, as well as brood pheromones regulate worker reproduction in honeybees. In South Africa two contiguous populations of honeybees exist, *Apis mellifera capensis* and *A. m. scutellata*. Queenless *A. m. capensis* workers are reproductively distinct from workers of other races, in that they readily develop into pseudoqueens with rapid ovary and signal development. *A. m. capensis* queens are pheromonally competent in regulating reproduction in the resident workers. Recently however Cape honeybee workers have successfully invaded queenright *A. m. scutellata* colonies and simultaneously escaped reproductive suppression from the resident queen and brood. These "social parasites" rapidly develop into reproductives, lay acceptable eggs and mimic a series of queen pheromones. This pheromone mimicry by invading *A. m. capensis* workers causes a breakdown in reproductive regulation, resulting in reproductive anarchy.

***Apis mellifera* / worker reproduction / caste plasticity / pheromones / social parasite**

1. INTRODUCTION

The control of reproduction in the honeybee (*Apis mellifera* L.) colony hinges largely on pheromones; namely queen mandibular gland secretions, tergal gland secretions, tarsal gland secretions, Dufour's gland secretions and brood pheromones. In these large social insect colonies, reproductive dominance can no longer be achieved by physical interactions and therefore pheromone signals have evolved to regulate colony reproduction. These so-called primer pheromones (Blum, 1974; Winston and Slessor, 1992) signal queen presence and fecundity, and workers respond to these signals in such a way as to increase their own inclusive fitness (Visscher, 1989, 1998; Keller and Nonacs, 1993; Naumann et al., 1993; Seeley, 1985, 1995). Honest

---

* Correspondence and reprints
E-mail: tcwossler@zoology.up.ac.za

signalling is an alternate hypothesis to the original concept of queen signals being controlling (Keller and Nonacs, 1993). Nonetheless, direct empirical data to distinguish between these two ideas has as yet not been developed; consequently the idea of queen repression pheromones cannot be ruled out. What is more, the worker caste is also in an important position to maintain colony reproductive hierarchies, ultimately through the regulation of worker reproduction by mutual worker policing (Keller and Nonacs, 1993; Ratnieks and Visscher, 1989). However cheating does occur, as is evident in anarchistic honeybees and in *A. m. capensis* workers (Johannsmeier, 1983; Allsopp and Crewe, 1993; Hepburn and Allsopp, 1994; Oldroyd et al., 1994; Martin et al., 2002a; Neumann and Hepburn, 2002; Pirk et al., 2002).

Worker reproduction in the honeybee is not solely regulated by pheromones. Other factors, such as environmental, physiological and genetic aspects also play a role. Some of these are nonetheless indirectly related to pheromones and their functions. An important environmental factor is protein availability. This needs to meet the colony's demands firstly and only if this exceeds the demands will the protein necessary for worker oogenesis be available (Jay, 1968, 1970, 1972; Velthuis, 1970a; Korst and Velthuis, 1982; van der Blom, 1991; Wheeler, 1996). Physiological factors expressed at the level of the individual, such as age and ovariole number, influences the reproductive output of the worker. Ovariole number and age have been shown to be positively and/or negatively correlated to reproductive advantage (Velthuis, 1970a; Leonardo, 1985; Delaplane and Harbo, 1987; Allsopp, 1988; Harris and Harbo, 1991; Hepburn et al., 1991; van der Blom and Verkade, 1991; van der Blom et al., 1994). Also, genetic variability among subfamilies, due to the polyandrous nature of honeybee queens (Fuchs and Moritz, 1999; Palmer and Oldroyd, 2000), results in certain individuals being genetically dominant and predisposed to reproduction (Moritz and Hillesheim, 1985; Robinson et al., 1990; Page and Robinson, 1994; Moritz et al., 1996). Genetic variance in developing queen-like signals by workers is high (degree of heritability = 0.89 ± 0.007), with certain patrilines expressing pheromone dominance, and as a consequence reproductive dominance (Moritz and Hillesheim, 1985; Moritz et al., 2000; Simon et al., 2001). Similarly, ovariole number is determined during larval development. Patrilines producing a more attractive brood pheromone elicit more and/or better quality larval food and as a result emerge with increased ovariole number contributing to a higher reproductive potential (Beetsma, 1979; Beekman et al., 2000; Calis et al., 2002). At the level of the individual, a dominant worker will enjoy a greater reproductive success than a subordinate worker; this success is primarily related to pheromone production. At the level of the colony, however, these workers are in turn exposed to queen and brood pheromones that subsequently impinge on their reproductive output.

The nature and mode of action of queen signals on ovary development is not fully understood. The signals involved in reproductive regulation are probably more persistent signals and therefore not affected by those factors affecting the propagation of short-lived signals (Velthuis, 1985; Winston and Slessor, 1998). As early as 1954, De Groot and Voogd showed that a mated queen, a virgin queen and parts of a queen almost completely inhibited ovarian development in workers. Later Butler showed that queen head extracts, specifically 9-keto-(E)-2-decenoic acid (9ODA), inhibited worker ovary development (Butler 1957, 1959; Butler et al., 1962). To date, the effects of queen head extract and 9ODA on worker reproductive regulation has been contentious, with only partial or no inhibition being demonstrated for queen head extracts and/or the 5-component queen mandibular pheromone (QMP) blend (Pain, 1961; Butler and Fairey, 1963; Velthuis, 1970b; Slessor et al., 1988; Willis et al., 1990). Still, the mandibular glands of queens are the major source of pheromone production with the first primer pheromone, 9ODA, identified in honeybee queens (Winston and Slessor, 1992). The physiological effects of 9ODA on colony regulation cannot be disregarded (Butler, 1957, 1959; Butler et al., 1962; Winston and Slessor, 1992; Pettis et al., 1995). More recently the role of queen tergal gland secretions on reproductive regulation has been investigated. These secretions have been shown to inhibit ovary development of caged workers (Wossler and Crewe, 1999a).

Besides the regulation of worker reproduction, the rearing of new female reproductives in the colony also has to be controlled. Queen rearing appears to be regulated both through mandibular gland as well as tarsal gland secretions (Boch and Lensky, 1976; Lensky and Slabezki, 1981; Pettis et al., 1995). The effects of tergal gland secretions, brood pheromones and other glandular secretions on rearing new reproductives still need to be established. Another important facet is the dissemination of queen and brood pheromones for the successful maintenance of colony organization and the regulation of worker and/or queen cell construction. Many mandibular components are of low volatility, some being perceived as odours (Moritz and Crewe, 1988). Others however are thought to act only as contact semiochemicals that are distributed by messengers leaving the retinue. Queen attendance is therefore essential to the dissemination of her pheromones throughout the colony (Velthuis, 1972; Seeley, 1979; Ferguson and Free, 1980; Naumann et al., 1991; Winston and Slessor, 1992; Pankiw et al., 1994). However, *Apis mellifera capensis* Escholtz workers are inclined to avoid the queen (Moritz et al., 2001), this behaviour both diminishes the efficient transmission of queen pheromones and allows these workers to escape queen repression pheromones.

This paper centres on the pheromone production between honeybee castes, reproductive state and brood. Race differences in pheromone biosynthesis, an important factor in *A. m. capensis* worker reproductive control (Hepburn and Radloff, 2002), are also addressed. Lastly, the unique characteristics of *A. m. capensis* workers in their natural environment, cross-fostered with other honeybee races and their recent invasion of the savanna *Apis mellifera scutellata* Lepeletier population are discussed. The invading *A. m. capensis* workers express a mosaic of characteristics responsible for perpetuating the so-called "*capensis*" problem (Moritz, 2002).

2. CASTE-SPECIFIC PHEROMONES

2.1. Mandibular gland secretions

Caste specificity in pheromone composition was thought to be the rule in honeybees, however, accumulating evidence points to caste plasticity in biosynthetic pathways. Both castes can produce the major component of the other, differing only in the selectivity of their biosynthesis. Specificity is however maintained among adults by various factors such as queen and brood pheromones, but certain elements of this caste differentiation can be modified in the adult stage (Sakagami, 1958; Sasaki et al., 1989; Plettner et al., 1993, 1995, 1996, 1997; Robinson, 1996; Katzav-Gozansky et al., 1997, 2000). Queens and workers preferentially synthesize C10 mandibular gland compounds that differ only in the position of the functional group, via disparate pathways, fitting their respective reproductive and non-reproductive roles (Butler et al., 1962; Crewe, 1982; Crewe et al., 1990; Plettner et al., 1995, 1996, 1997).

Table I. Comparison of the mean percentage composition of six mandibular gland compounds in queens and workers, related to reproductive state and colony environment, for selected honeybee races. Pseudoqueens were obtained by introducing an *A. m. capensis* worker into queenless *A. m. scutellata* colonies Abbreviations are as follows; 9ODA = 9-keto-(E)-2-decenoic acid, 9HDA = 9-hydroxy-(E)-2-decenoic acid, 10HDAA = 10-hydroxy-decanoic acid, 10HDA = 10-hydroxy-(E)-2-decenoic acid, HOB = methyl p-hydroxybenzoate, HVA = 4-hydroxy-3-methoxyphenylethanol, • = trace quantities undetectable, * = data not on hand for these compounds/races (Data from Crewe, 1988; Crewe and Velthuis, 1980; Crewe et al., 1990).

		% composition of the major compounds					
Group	N	9ODA	9HDA	10HDAA	10HDA	HOB	HVA
Mated *scutellata* queens	15	65.4	14.4	3.6	8.1	*	*
Virgin *scutellata* queens	5	38.9	13.1	6.7	31.9	*	*
Mated *mellifera* queens	5	36.1	32.2	7.9	12.1	2.3	2.4
Virgin *mellifera* queens	7	26.5	7.0	1.8	61.8	0.6	•
Mated *capensis* queens	6	84.8	9.8	0.5	1.0	*	*
Virgin *capensis* queens	27	80.1	11.1	•	3.8	*	*
Queenless *capensis* workers	17	33.9	6.8	3.0	42.4	•	•
Capensis+mellifera workers	3	76.2	7.7	0.5	5.5	•	•
Capensis pseudoqueens	18	88.4	6.1	0.6	1.6	•	•
Queenless *mellifera* workers	15	•	2.0	9.5	88.5	•	•

Queens secrete a signal dominated by 9ODA and 9HDA (9-hydroxy-(E)-2-decenoic acid), while worker-signals are dominated by 10HDAA (10-hydroxydecanoic acid) and 10HDA (10-hydroxy-2-decenoic acid). However, depending on the social milieu of the colony and the age of the workers, they can produce 9ODA and 9HDA while queens produce 10HDAA and 10HDA (Tab. I). Hence the mandibular components of caste are not mutually exclusive. Queens are distinct however in that they produce a range and quantity of compounds greater than workers (Crewe, 1982; Plettner et al., 1995). Switching from worker pathway synthesis to a queen's biosynthetic pathway is relatively easy for *A. m. capensis* workers who readily secrete queen-like mandibular gland secretions (Fig. 1), dominated by 9ODA (Ruttner et al., 1976; Hemmling et al., 1979; Crewe and Velthuis, 1980; Plettner et al., 1993). Honeybee workers belonging to other races can produce 9ODA, but it is always in much lower proportions than 10HDA. This automatically gives *A. m. capensis* a pheromone advantage over other races and this leads to a reproductive advantage. Reproductively dominant individuals frequently produce 9ODA which seems to precede ovary activation (Crewe and Velthuis, 1980; Sasaki et al., 1989), however workers with activated ovaries can and do secrete very worker-like signals, so the relationship between signal development and ovary activation is inconsistent (Hemmling et al., 1979; Hepburn et al., 1988; Hepburn and Allsopp, 1994). On a developmental pheromone continuum, the biosynthetic capabilities of the mandibular glands begins with mated queens, followed by virgin queens together with *A. m. capensis* pseudoqueens,

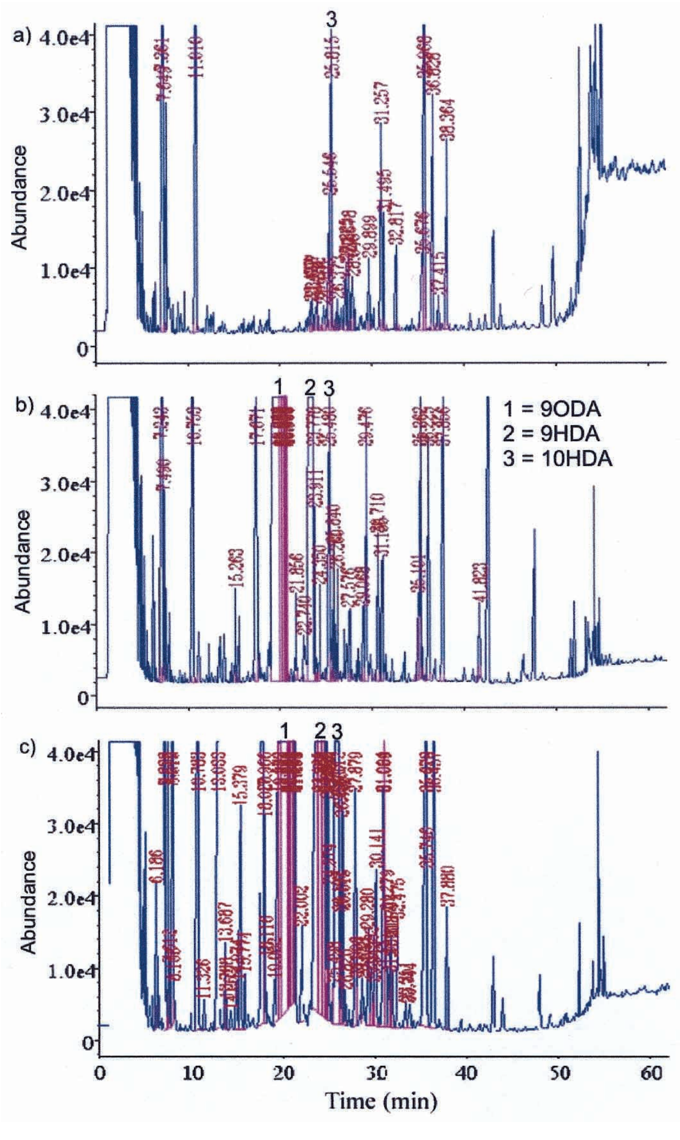

Figure 1. Chromatograms (FID plots) of head extracts of (a) an *A. m. scutellata* worker from a colony with *A. m. capensis* pseudoqueens, (b) an *A. m. capensis* pseudoqueen from the same colony and (c) an *A. m. ligustica* mated queen. The pseudoqueen secretes a very queen-like mandibular gland signal, dominated by 9ODA, that inhibits signal development in the resident *A. m. scutellata* workers. Identified peaks are 9ODA = 9-keto-(E)-2-decenoic acid, 9HDA = 9-hydroxy-(E)-2-decenoic acid, 10HDA = 10-hydroxy-(E)-2-decenoic acid.

pseudoqueens of other races, then laying workers, dominant workers and finally subordinate workers (Plettner et al., 1993).

2.2. Tergal gland secretions

Tergal gland components contribute as much as mandibular gland components to composite queen signals (Moritz and Crewe, 1991). Tergal gland profiles of various test groups of *A. m. scutellata* and *A. m. capensis* differ significantly (Tab. II; Wossler and Crewe, 1999b). Tergal gland secretions separate honeybees according to caste and the reproductive state of queens and workers (Espelie et al., 1990; Wossler and Crewe, 1999b). *A. m. capensis* workers possess well-developed tergal glands compared to *A. m. mellifera* and *A. m. scutellata* workers (Billen et al., 1986; Wossler et al., 2000). In addition, their tergal signals also differ from those of *A. m. scutellata* workers ($P = 0.001$, Tab. II) and may assist them in readily becoming pseudoqueens and regulating dominance hierarchies within colonies. However, the findings suggest that it is more likely for tergal gland secretions to act synergistically with mandibular gland secretions (Velthuis, 1970b, 1985; Vierling and Renner, 1977; Saiovici, 1983; Wossler and Crewe, 1999b).

2.3. Dufour's gland secretions

The biosynthetic capabilities of the Dufour's gland within castes are also totipotent (Katzav-Gozansky et al., 1997, 2000; Sole, 2000). Queen secretions are characterised by many esters besides the hydrocarbons, while workers on the other hand have secretions dominated by hydrocarbons. These signals however change when the worker becomes reproductive, with a number of esters appearing in the secretion, suggesting that these glands are responsible for a potential egg marking pheromone (Ratnieks, 1995; Katzav-Gozansky et al., 2000). Katzav-Gozansky et al. (2000), after having looked at the biosynthesis of these Dufour's compounds in vitro, are of the opinion that the queen suppresses ester production in workers and only on her removal does the gland start synthesising queen-specific esters. These worker-laid eggs, when transferred into discriminator colonies, are however successfully policed (Ratnieks and Visscher, 1989; Ratnieks, 1995; Martin et al., 2002a).

Table II. Comparisons of the tergal gland secretion profiles of *A. m. capensis* and *A. m. scutellata* test groups. The tergal gland profiles are significantly different from each other. Probability values significant at the table-wide α value of $P < 0.05$ using the Bonferroni sequential correction.

Test Groups	*P*
Apis mellifera scutellata virgin/mated queen	0.0001
Apis mellifera scutellata mated queen/worker	0.0001
Apis mellifera capensis virgin/mated queen	0.0001
Apis mellifera capensis virgin queen/worker	0.0001
Apis mellifera capensis mated queen/worker	0.0001
Apis mellifera capensis virgin queen/pseudoqueen	0.0001
Apis mellifera capensis worker/pseudoqueen	0.001
Apis mellifera capensis/scutellata mated queens	0.0001
Apis mellifera capensis/scutellata workers	0.001

This implies that workers are capable of secreting some of the esters but they are not mimicking the full queen bouquet (Katzav-Gozansky et al., 1997), which would offer full protection to their eggs. Queen-specific Dufour's esters have been found on queen eggs and worker eggs treated with queen Dufour's extracts are significantly more attractive (Ratnieks, 1995; Katzav-Gozansky et al., 2000), this therefore supports the idea of the Dufour's glands being the likely source of a possible egg marking pheromone.

The evidence that queens secrete a wider range of esters may prove to be important in worker policing behaviour (Katzav-Gozansky et al., 1997; Sole, 2000). Two specific esters, namely tetradecyl octadecenoate and hexadecyl hexadecenoate, found in the Dufour's secretions of *A. m. scutellata* queens and laying *A. m. capensis* pseudo-clone social parasites (see Kryger, 2001, also explained later in this text) but not in laying *A. m. scutellata* workers may be linked to policing (Sole, 2000). Theory predicts that there would be no selective advantage for worker policing in thelytokous workers since sisters and nieces are related to them by the same magnitude, regardless of the level of polyandry, and so one should not be preferred above the other (Greeff, 1996; Moritz et al., 1999). Moritz et al. (1999) did show that *A. m. capensis* workers produce brood in queenright colonies, up to 33% of offspring can originate from workers, demonstrating that workers do not police (Moritz et al., 1999). Lack of working policing is also found in anarchistic workers of *Apis mellifera ligustica* Spin. origin (Oldroyd et al., 1994, 1999; Montague and Oldroyd, 1998). Brood production in *A. m. capensis* colonies appears to be a behavioural response. *A. m. capensis* colonies show less discrimination towards worker-laid eggs (Oldroyd and Ratnieks, 2000) rather than *A. m. capensis* laying workers mimicking queen egg-marking pheromone. *A. m. capensis* eggs transferred into *A. m. scutellata* discriminator colonies are removed successfully and are not "masked" in any way (Neumann et al., in prep.). However, this does not hold for the *A. m. capensis* pseudo-clone social parasites invading *A. m. scutellata* colonies which lay acceptable eggs that escape detection by the resident *A. m. scutellata* workers (Martin et al., 2002a).

2.4. Tarsal gland secretions

At the level of colony reproduction, the rearing of female reproductives is regulated through pheromones. Queen extract and 9ODA only partially inhibit queen cell construction (Gary and Morse, 1962; Butler, 1954; Boch and Lensky, 1976; Free et al., 1985; Pettis et al., 1995). The tarsal gland "footprint" pheromones and "fecundity signals" from brood, together with the successful transmission of queen pheromone prevent queen rearing (Lensky and Slabezki, 1981; Naumann et al., 1991; Winston et al., 1991; Pettis et al., 1997). Caste specificity and/or plasticity in tarsal gland secretions has to date not been reported on, but the castes do differ in their secretion rates, with queens having a 13 times higher secretion rate than workers (Lensky and Slabezky, 1981). The *A. m. scutellata* usurped colonies initiate the construction of a large number of queen cells, none of which are successfully reared. It is likely that these invading *A. m. capensis* workers do not mimic queen tarsal secretions as they do mandibular gland secretions, and therefore queen cell construction is only partially suppressed. The lower rates of tarsal gland pheromone secretion by workers should however not influence the construction of queen cells since there are a large number of *A. m. capensis* workers secreting "footprint" pheromone simultaneously. However, the dynamics of colony organisation during usurpation, particularly the changes in pheromone dissemination and worker response thresholds, are not understood and so the regulation of rearing queens in these colonies remains unclear.

3. REPRODUCTIVE STATE

3.1. Queens

Virgin queens not only produce significantly lower quantities of queen mandibular pheromone components (Tab. I) but the proportions of these components are significantly different from mated queens (Pankiw et al., 1996). The bouquet and nature of virgin queens' signals change with age and become dominated by 9ODA and 9HDA (Crewe, 1982; De Grandi-Hoffman and Martin, 1993; Plettner et al., 1995; Pankiw et al., 1996). Mating induces additional changes to the signal bouquet with increases in the aromatic compounds and the appearance of 4-hydroxy-3-methoxyphenylethanol (HVA) (Slessor et al., 1990; Pankiw et al., 1996). The progressive change in mandibular gland secretions with age is evident in *A. m. scutellata*, *A. m. mellifera* and *A. m. intermissa* virgin queens but not *A. m. capensis* queens (Pain et al., 1960, 1967; Pain and Roger, 1976; Crewe, 1988; Crewe and Moritz, 1989) which produce large amounts of 9ODA at emergence (Fig. 2; Tab. I), a necessity in establishing queen-worker relationships (Crewe, 1982, 1987, 1988). Also, *A. m. capensis* queens produce stronger signals, secreting the highest proportion of 9ODA (Tab. I), compared to queens of other races (Crewe, 1982, 1988). Most of the variation in mandibular gland secretions hinge on a quantitative difference in the relative proportions making up the mixture. The ratio of 9ODA: 10HDA in queen mandibular gland secretions is race specific, with *A. m. scutellata* mated queens having a ratio of 8:1, while *A. m. capensis* queens have a ratio of 84.8:1 (Tab. I; Crewe, 1988). These almost "super" queen signals in *A. m. capensis* may be linked to the rapid development of laying workers in this population and necessary to control worker reproduction

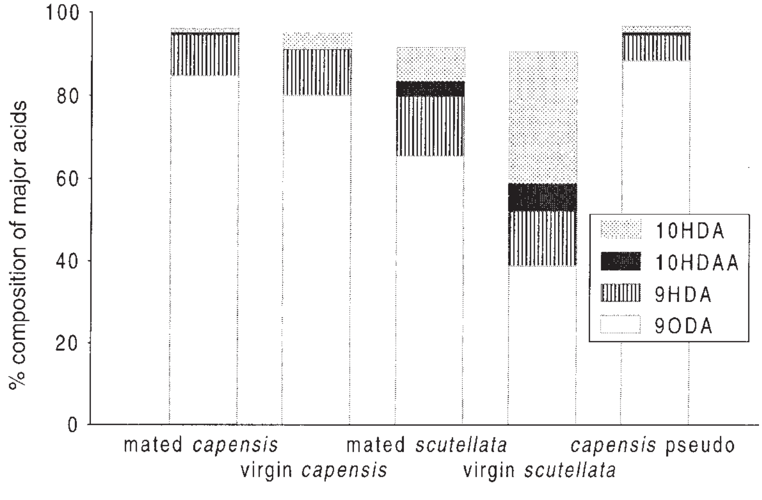

Figure 2. The mean percentage composition of the major mandibular gland acids, for the two African populations, in relation to reproductive state. Both mated and virgin *A. m. capensis* queens, as well as *A. m. capensis* pseudoqueens, secrete a signal dominated by 9ODA. Pseudoqueens were obtained by introducing an *A. m. capensis* worker into queenless *A. m. scutellata* colonies (data taken from Crewe, 1988; Crewe et al., 1990). Sample sizes are as in Table I.

(Crewe, 1982, 1984). This factor has proven to be critical in the usurpation of *A. m. scutellata* colonies by *A. m. capensis* workers.

3.2. Workers

The dynamics of the development of worker signals and reproductive state is more distinct. In *A. m. mellifera* and *A. m. scutellata*, workers produce a mandibular gland signal dominated by 10HDA and if these workers find themselves queenless, the proportions of 9HDA and 10HDAA rise in relation to 10HDA. Some individuals that become egg layers though may produce small and variable quantities of 9ODA, with 9ODA comprising up to 10% of the mandibular gland secretion (Ruttner et al., 1976; Saiovici, 1983; Crewe, 1984, 1988; Crewe and Moritz, 1989; Hepburn, 1992a). However, 9ODA production is not unique to queenless workers, with detectable quantities of 9ODA recorded in queenright *A. m. intermissa* workers (Crewe and Moritz, 1989). The relationship between behaviour and chemical composition of a secretion is not clear cut. Both laying workers and pseudoqueens are reproductively active but unlike most laying workers, pseudoqueens behave as queens, are also treated as queens and produce very queen-like mandibular gland signals (Fig. 2; Tab. I; Butler, 1956; Sakagami, 1958). Plettner et al. (1993) demonstrated that the degree of ovarian development was not statistically different between pseudoqueens and laying workers but their mandibular gland secretions differed greatly, with laying workers showing varying degrees of queen signal mimicry but not synthesising as queen like signals as pseudoqueens. In *A. m. mellifera* workers, pseudoqueens produce 100 times more 9ODA than laying workers (Plettner et al., 1993).

A. m. capensis workers show rapid changes in relative quantities of 9ODA and 9HDA, the precursor of queen substance, within the first four days of queenlessness (Fig. 4; Simon et al., 2001). A week later the *A. m. capensis* workers can produce 50 µg of 9ODA which can rise to as much as 300 µg at 80 days, a concentration comparable to that found in queens (Hemmling et al., 1979). Not only do some queenless

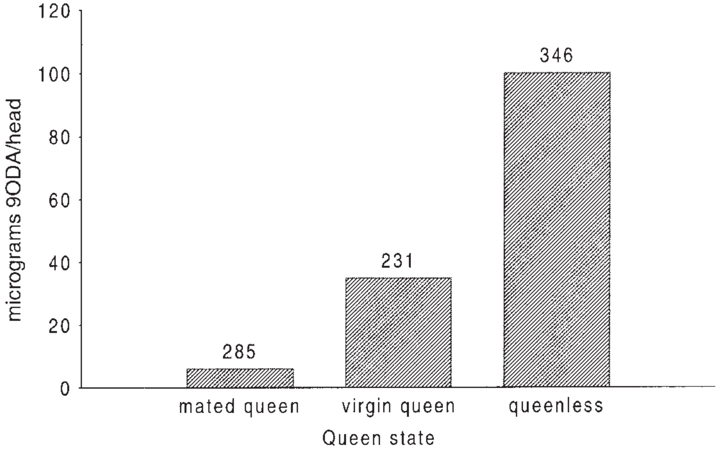

Figure 3. The effect of queen state on the production of 9ODA (mean absolute amounts) by *A. m. capensis* workers in field colonies. Sample sizes are indicated above the bars (modified from Hepburn, 1992a).

A. m. capensis workers produce very high proportions of 9ODA but they also synthesise a composite signal that has almost the full range of queen compounds which assists them in establishing themselves as pseudoqueens (Figs. 1, 3; Ruttner et al., 1976; Crewe and Velthuis, 1980; Crewe, 1984, 1988; Velthuis and van der Kerk, 1988; Crewe et al., 1990; Hepburn, 1992a). What is more, these pseudoqueens can have approximately 75% 9ODA in their secretions (Saiovici, 1983; Free, 1987). Besides the quantitative differences in the relative proportions of the acids produced by *A. m. capensis* when compared with *A. m. scutellata*, there also appears to be a qualitative difference in the aromatic compounds secreted by these two races. *A. m. capensis* are more queen-like on a scale of progressive pheromone development (Crewe, 1993). Therefore, the swift development of these queen-like signals by *A. m. capensis* workers may be an important characteristic of the *A. m. capensis* pseudoclone sustaining its parasitic lifestyle (Simon et al., 2001).

Workers with activated ovaries, *A. m. capensis* in particular, not only suffer increased bouts of aggression by non-reproductive workers but also lose large quantities of high value proteins through trophallaxis, slowing down further ovary development (Anderson, 1963; Fletcher, 1975; Velthuis, 1976; Korst and Velthuis, 1982; Velthuis et al., 1990; van der Blom, 1991; Visscher and Dukas, 1995). Workers developing their ovaries and signals fastest have the best survival chance because aggressors change their behaviour towards them as they become more queen-like (Crewe, 1984). This reproductive differentiation in signal production is particularly obvious when *A. m. capensis* are kept together with bees from other races (Tab. I). Among themselves, however, this reproductive dominance is not as pronounced and their secretion has equal proportions of 9ODA and 10HDA (Tab. I) and they inhibit each other from becoming pseudoqueens (Velthuis, 1976; Crewe and Velthuis, 1980; Crewe, 1981; Free, 1987; Moritz et al., 2000). The uniqueness of *A. m. capensis* and their signals will be discussed in more detail in the following sections.

On queen loss, workers compete for pheromone and reproductive dominance and this is modulated by the presence of brood and queen cells in the colony (Jay, 1970; Moritz et al., 2000). The establishment of reproductive hierarchies does not result from nepotistic discrimination in interactions between workers because there is no difference in a worker becoming reproductive when surrounded by related or unrelated nestmates (van der Blom and Verkade, 1991), but rather from individuals inheriting genes for dominance (Moritz and Hillesheim, 1985; Page and Robinson, 1994; Moritz et al., 1996). Inconsistent results have been obtained for the link between pheromone and reproductive dominance during the establishment of these hierarchies. Appropriate mandibular gland secretions may precede ovary development but are not correlated with the presence or amount of any specific compound but rather with having a relative advantage over others in the range of fatty acids produced and the ratio of compounds involved (Velthuis, 1985; Velthuis et al., 1990). More often than not, a positive relationship between pheromone bouquet and ovary development is evident in *A. m. capensis* workers competing for reproduction (Crewe and Velthuis, 1980; Moritz and Hillesheim, 1985; Crewe, 1987; Allsopp 1988; Velthuis and van der Kerk, 1988; Velthuis et al., 1990; Hepburn 1992a). The first differentiation in ovary development coincides with the production of 8-hydroxyoctanoic acid (8HOA) and 9HDA. Further ovary development is linked to 9ODA (Velthuis and van der Kerk, 1988), but this is not a strict rule (Hemmling et al., 1979; Saiovici, 1983; Velthuis, 1985; Hepburn et al., 1988). On the other hand, the pheromone composition of workers belonging to other races is rarely related to ovary development (Crewe, 1987; Plettner et al., 1993; Hepburn and Allsopp, 1994). It would appear that pheromone production and ovary development are genetically independent characteristics allowing for many combinations of ovary development and mandibular gland pheromone to exist (Hepburn, 1992a), with these two traits simultaneously and more frequently co-induced in *A. m. capensis* workers than other honeybee workers.

4. BROOD PHEROMONES

Besides behaving as primer pheromones in regulating worker reproduction, brood pheromones are also releasers in soliciting food from nurse honeybees (Le Conte et al., 1995). Those larvae that produce stronger signals will be fed more often and higher quality food. This gives them a reproductive head start at an early age. Beekman et al. (2000) have demonstrated that *A. m. capensis* larvae reared by hybrid workers of *A. m. mellifera* and *A. m. carnica* in queenright *A. m. mellifera* colonies are treated "royally" compared to *A. m. capensis* larvae reared in their own colonies. This is also true for *A. m. capensis* larvae reared in *A. m. scutellata* colonies where *A. m. capensis* worker-queen intermediates emerge in these host *A. m. scutellata* colonies (Calis et al., 2002). It would appear as if these larvae can influence the caste fate by secreting more, or more attractive, pheromones. This results in being fed queen-like larval food and in turn more queen-like *A. m. capensis* workers emerge (Tab. III). Rate of larval food intake regulates corpora allata activity and high juvenile hormone levels (JH) results in a reduction in ovary regression and therefore increased ovariole numbers (Beetsma, 1979).

The other role played by brood pheromones is one of regulating worker, as well as colony reproduction. It is likely that brood pheromones, as previously stated, act as "fecundity signals" of queen productivity and when these signals decrease below a certain threshold, workers begin rearing new reproductives (Pettis et al., 1997). With regard to worker ovary development, brood esters have been shown to suppress worker reproduction (Jay, 1968, 1970, 1972; Arnold et al., 1994; Mohammedi et al., 1998). There is a breakdown in brood pheromone suppression in anarchistic workers with anarchistic brood not having the same inhibitory effect as wild type brood (Barron and Oldroyd, 2001). This ineffectiveness of brood signals on worker ovary suppression has been corroborated in *A. m. capensis* colonies, where the presence of brood does not inhibit worker reproduction after queen loss, at which time workers rapidly oviposit despite the presence of brood (Anderson, 1963, 1981). However, Hepburn and his coworkers have shown that the fate of egg laying by queenless *A. m. capensis* workers is partly restricted by the presence of a relatively large amount

Table III. Developing *A. m. capensis* larvae, fed by queenright nurse bees of European origin compared to those fed by queenright *A. m. capensis* nurse bees, are more queen-like and have a higher reproductive potential than normal *A. m. capensis* workers. Weight of the emerging bee, ovariole number and development time (median and ranges) are traits promoting reproductive advantage (data from Beekman et al., 2000).

Origin of nurse bees	Sample size	Emerging weight (g)	Ovariole number	Post-capping time (days)
capensis nurse bees	23	0.112 (0.097–0.123)	14 (10–19)	11.08 (10.63–11.25)
European nurse bees	16	0.125 (0.124–0.126)	25 (16–34)	10.58 (10.25–10.75)

of young brood (Hepburn, 1992b, 1994; Hepburn et al., 1988, 1991). In contrast, the *A. m. capensis* pseudo-clone invaders are not restricted from developing their ovaries by large amounts of queen-laid host *A. m. scutellata* brood. They probably enjoy higher response thresholds (Naumann et al., 1993) to brood pheromone, a trait promoting their parasitic way of life, as well as their individual interests. Additionally, under heavy feeding conditions, the inhibitory effects of brood pheromone are reduced with the rapid development of laying workers (Anderson, 1963; Hepburn et al., 1988). A situation paralleling that of the pseudo-clone social parasites who are most prolific on the high quality pollen and nectar flows of *Aloe greatheadii davyana*.

5. THE CAPE BEE IN HER NATURAL ENVIRONMENT

5.1. What makes *A. m. capensis* unique?

Literature on the Cape bee has covered many of the unique *A. m. capensis* traits, but those traits relating to reproductive dominance are of particular interest – thelytoky, synthesis and secretion of very queen-like pheromones, increased ovariole number and rapid reproductive development time (Onions, 1912, 1914; Anderson, 1963; Ruttner and Hesse, 1981; Ruttner et al., 1976; Hemmling et al., 1979; Crewe, 1982, 1984, 1988, 1993; Crewe and Velthuis, 1980; Tribe, 1983; Hepburn, 1992a; Hepburn and Crewe, 1991; Hepburn et al., 1991; Hepburn and Radloff, 2002). First, thelytoky predicts more conflict between workers over reproductive dominance than arrhenotoky, particularly in queenless situations (Greeff, 1996; Neumann et al., 2000). The asymmetry relatedness is much greater for nieces than nephews of the same and different patrilines and selects for the effective elimination of laying workers of other patrilines (Greeff, 1996, 1997). Excessive fighting after queen loss does occur in *A. m. capensis* as dominance hierarchies are established with the appearance of pseudoqueens (Tribe, 1981, 1983). This reproductive conflict leads first to pheromone exploitation by *A. m. capensis* workers which produce a pheromone bouquet similar to that of a queen (Figs. 1, 2) and in much larger amounts than other races (Crewe and Velthuis, 1980; Crewe, 1984, 1988, 1993; Velthuis et al., 1990; Plettner et al., 1993). Greeff (1996) suggests that *A. m. capensis* selfishly use the pheromone to deceive workers to act altruistically against their own interests which Keller and Nonacs (1993) contend cannot be stable. Greeff (1996) argues however that this coercive use of the pheromone can be stable because it reflects an honest signal more often than not. The nature of the chemical signalling system of *A. m. capensis* workers indicates why it is possible for them to adopt pseudoqueen status and deceive workers with their signals (Figs. 1, 2; Tab. I). These *A. m. capensis* workers are nevertheless still at the worker end of the developmental spectrum, but show a mosaic of worker and queen traits (Crewe et al., 1990). The *A. m. capensis* pseudo-clone invaders may have moved further along the developmental continuum, expressing more and/or more advanced queen characteristics.

Second, the egg laying adaptations of increased ovariole number, and rapid reproductive development is evident in *A. m. capensis* workers after queen loss (within 4 days). This suggests that workers have well-developed ovaries in queenright colonies and simply wait for the chance to lay, gaining a reproductive advantage (Anderson, 1963; Ruttner and Hesse, 1981; Hepburn et al., 1988).

5.2. Queenright colonies

The importance of pheromones in colony organization/behaviour is best portrayed in *A. m. capensis*. *A. m. capensis* queens are capable of regulating and coordinating the activities of *A. m. capensis* workers, as well as worker reproduction (Prince and Gunson, 1992). These queens, as mentioned earlier, have signals that have extremely high concentrations of 9ODA and are quantitatively dominant. This appears to be necessary for the regulation of *A. m. capensis* reproduction (Crewe, 1982, 1988). Both mated and virgin *A. m. capensis* queens repress ovary development and 9ODA production in workers (Fig. 3). Hepburn et al. (1991) have shown that mated *A. m. capensis* queens have a strong effect on worker ovary development with only approximately 1% of the workers showing activated ovaries, while colonies headed by virgin queens have 2–5% of the workers reproductively active. *A. m. capensis* workers in queenright colonies, however, do show higher levels of ovary development than workers of other races (Anderson, 1963). It is likely that these dominant workers, who do not follow an age polyethism, are waiting for the chance to reproduce, and on queen loss they would have a head start in egg laying (Moritz and Hillesheim, 1985; Hillesheim et al., 1989). *A. m. capensis* workers placed in colonies where the queen is isolated will avoid the side of the frame she is on significantly more than *A. m. scutellata* and hybrid workers. So by distancing themselves from queen repression pheromones, genetically dominant individuals increase their chances for early reproduction on queen loss (Moritz et al., 2001).

5.3. Queenless *A. m. capensis* colonies

Reproductive dominance is genetically determined in *A. m. capensis*. Dominant workers have more developed ovaries, oviposit sooner, produce more 9ODA, lay more eggs and there is a positive correlation between dominance and trophallactic advantage (Korst and Velthuis, 1982; Moritz and Hillesheim, 1985). In general, only one or a few dominant subfamilies produce offspring in honeybees, and within these dominant subfamilies there is individual competition for dominance since only a few workers develop into laying workers/pseudoqueens (Robinson et al., 1990; Oldroyd et al., 1994; Moritz et al., 1996). Approximately 5% of the workers will lay and as the duration of the queenless state increases, there is a significant increase in ovary development, but not necessarily in the number of laying workers (Hepburn et al., 1991). These laying workers/pseudoqueens regulate the initiation of ovary development in the other workers (Velthuis et al., 1965; Velthuis, 1970a; Crewe and Velthuis, 1980; Crewe, 1984, 1988). *A. m. capensis* workers placed in pairs compete to produce the strongest queen-like signal and the production of 9ODA (which inhibits 9ODA production in subordinate workers) may therefore be an important signal in pseudoqueen selection (Moritz et al., 2000). Chemical signals change rapidly (Hemmling et al., 1979) with reproductive differentiation and workers will compete for the production of the strongest queen signal, rather than produce signals independent of each other (Hillesheim and Moritz, 1987; Hillesheim et al., 1989; Moritz et al., 2000).

Hepburn (1992a) identified four classes of queenless *A. m. capensis* workers; (1) pheromonally and reproductively worker-like, (2) egg layers with worker-like pheromones, (3) pheromonally queen-like but reproductively worker-like and (4) pheromonally and reproductively queen-like. These workers are not separate categories but points along a developmental continuum. The duration of queenlessness and behavioural interactions go hand in hand in becoming pheromonally and reproductively queen-like. The expression of these two traits are co-induced and not co-dependent (Saiovici, 1983; Velthuis, 1990; Hepburn, 1992a). Pseudoqueens belong to the last class, are rare in most races except in *A. m. capensis*, produce large quantities of 9ODA (Figs. 1, 2; Tab. I), elicit retinue behaviour and repress both ovary and chemical development in the other workers (Ruttner et al., 1976; Velthuis, 1976, 1985; Hemmling et al., 1979; Crewe and Velthuis, 1980; Tribe, 1983; Velthuis et al., 1990; Plettner et al., 1993).

Queenless *A. m. capensis* either rear new queens from queen brood, or worker brood, or they continue as laying workers. The path chosen by queenless *A. m. capensis* probably depends on the extent of ovary and chemical development of the residents which is dependent on brood conditions, the presence of which seems to stimulate queen cell construction. This in turn delays the development of laying workers, but once the former brood is capped, repression is lifted and workers develop reproductively, partially suppressing further queen cell construction and destroying existing queen cells (Hepburn, 1992b; Hepburn et al., 1988). Similarly, the presence of queen-laid *A. m. scutellata* brood in usurped colonies may also initiate queen cell construction early on in the takeover, but the rapid reproductive development of the *A. m. capensis* invaders results in queen cell destruction later on.

6. *A. M. CAPENSIS* SOCIAL PARASITES IN *A. M. SCUTELLATA* TERRITORY

Approximately 25 years ago it was suggested that an *A. m. capensis* sanctuary be established to protect the Cape bee from the "aggressive" *A. m. scutellata* bee (Anderson, 1980; Ruttner, 1977). Today however, we have a complete reversal with *A. m. scutellata* under threat from *A. m. capensis*. This "*capensis*" problem or "colony dwindling syndrome" was reported in the savanna regions of South Africa, inhabited by *A. m. scutellata*, about 10 years ago. *A. m. capensis* workers move into *A. m. scutellata* colonies; develop queen-like signals and activate their ovaries, and at some critical pheromone threshold, the *A. m. scutellata* queen is lost. The dominant *A. m. capensis* workers then take over colony reproduction, and as the proportion of *A. m. capensis* workers increase in the colony so normal worker functions decrease and the colony "dwindles" and usually dies (Allsopp, 1992; Allsopp and Crewe, 1993; Hepburn and Allsopp, 1994; Martin et al., 2002b). These *A. m. capensis* social parasites invading *A. m. scutellata* colonies are all similar (not identical as suggested by Moritz and Haberl, 1994) in their genetic makeup (Kryger, 2001), and have been referred to as a pseudo-clone, arising from a thelytokous *A. m. capensis* worker (Radloff et al., 2002). Are these pseudo-clones unique? *A. m. scutellata* colonies have previously been lost to invasions by non-clonal Cape workers (Lundie, 1954; Guy, 1976; Johannsmeier, 1983). Many of the pseudo-clone's characteristics are common to *A. m. capensis* workers, but some appear to be unique or more advanced in the clone, making it a successful parasite. We are probably seeing the end product of rapid selection of the most "virulent" line of *A. m. capensis* that has outcompeted the less "virulent" lines of invaders. Some of the characteristics promoting the success of these social parasites and the expression of these traits in the dynamics of *A. m. scutellata* colony usurpation will be discussed in more detail below.

First, they are thelytokous and therefore produce female pseudo-clones of themselves passing on these so-called "dominance" genes (Moritz and Hillesheim, 1985; Hillesheim et al., 1989; Moritz et al., 1996; Hepburn and Radloff, 2002). As previously mentioned (Sect. 5.1), thelytoky has selected workers to produce queen pheromones and develop ovaries rapidly (Figs. 4, 5; Greeff, 1996, 1997), predisposing these pseudo-clones to vigorous worker reproduction.

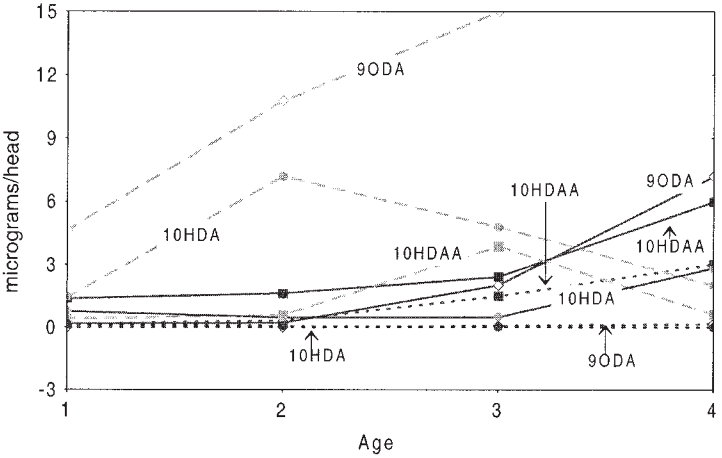

Figure 4. Changes in 9ODA, 10HDAA and 10HDA production in queenless *A. m. capensis* and *A. m. intermissa* workers, as well as an *A. m. intermissa* virgin queen, over a 4 day period. Queenless *A. m. capensis* workers show rapid pheromone development compared to queenless workers of other races, with queen signals developing the quickest. *A. m. capensis* signal ontogeny = solid line (red), *A. m. intermissa* = stippled line (blue), *A. m. intermissa* queens = dashed line (green). 9ODA = 9-keto-(E)-2-decenoic acid, 10HDAA = 10-hydroxy-decanoic acid, 10HDA = 10-hydroxy-(E)-2-decenoic acid (data from Crewe and Moritz, 1989; Simon et al., 2001).

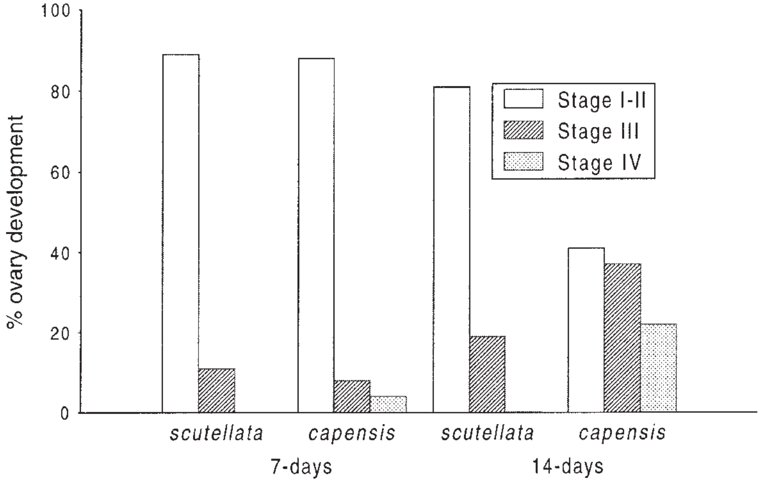

Figure 5. Percentage ovary development in *A. m. capensis* and *A. m. scutellata* workers at 7 and 14 days after dequeening. Queenless *A. m. capensis* workers develop their ovaries much more rapidly than their queenless neighbours and by 14 days, 22% of the *A. m. capensis* show active ovaries. Stages are: I-II = undeveloped, III = developing oocytes present, IV = eggs fully developed (data modified from Hepburn and Allsopp, 1994).

Second, the reproductive and chemical development of *A. m. capensis* workers is extremely rapid. The success of this usurpation of *A. m. scutellata* colonies hinges on the rapid production of queen-like pheromones and ovary development in the invaders (Figs. 1, 4, 5; Allsopp, 1992; Hepburn and Allsopp, 1994; Hepburn and Radloff, 1998), as discussed above (Sects. 3.2 and 5.3). Early in the usurpation of *A. m. scutellata* colonies, there's a very high level of aggression directed towards *A. m. capensis* individuals (Cooke, 1992) because their signals need time to develop. Only when they reach the end point of development do they produce sufficient 9ODA (Fig. 1; Crewe, 1984) to elicit pseudoqueen treatment from the resident *A. m. scutellata* workers. These invading pseudo-clones compete for pheromone dominance (Moritz et al., 2000), those leading the race in signal development will become the cohort of pseudoqueens, adopting the reproductive role within the colony.

Third, neither the *A. m. scutellata* queen nor brood reproductively regulates the *A. m. capensis* invaders (Allsopp and Crewe, 1993). To maintain colony coordination, it is necessary to disseminate queen and brood pheromones to all members, which is achieved by workers contacting the queen and then passing on the pheromone to other nestmates. *A. m. capensis* workers in queenless host colonies of other races are approached more frequently, than the resident bees, by subordinate workers and offered food (Velthuis et al., 1990). This trophallactic dominance is however not evident in queenright invaded *A. m. scutellata* colonies. It is likely that these invaders profit from an alternate approach of rather avoiding contact with "messenger workers", and in so doing increase their chances of escaping queen repression factors (Moritz et al., 2001). Additionally, *A. m. scutellata* queens do not emit so-called "super" signals (Fig. 2; Tab. I) necessary for the regulation of *A. m. capensis* workers who have high response thresholds to queen signals (Crewe, 1982, 1988; Magnuson, 1995). Thus, one approach is to introduce an *A. m. capensis* queen into an infected colony and see whether she would arrest pseudo-clone worker ovary development. This would then indicate whether the problem is low levels of queen pheromone from the *A. m. scutellata* queen or an increased response threshold by the pseudo-clones. Moreover, *A. m. capensis* queens may secrete certain compounds in a given ratio that is different for *A. m. scutellata* queens and/or secrete compounds (unidentified as yet) not produced by *A. m. scutellata* queens. Besides the potential to produce novel compounds, the relative proportions of the compounds are important in signal specificity (Crewe, 1988; Pankiw et al., 1996). The *A. m. scutellata* brood does not appear to affect pseudo-clone ovary development either. The reason could be that the response thresholds to brood pheromone are very high in these pseudo-clones. Moreover, these social parasites are most active on rich and abundant food sources and under these conditions, not only is brood pheromone suppression reduced, but adult workers also obtain pollen of high nutrition value which promotes ovary development (Williams and Free, 1975; Hepburn et al., 1988; Jay and Jay, 1993).

Four, they have increased propensity for dispersal, implying active host colony seeking. Neumann et al. (2001) demonstrated that *A. m. capensis* disperse significantly more often than *A. m. scutellata* or *A. m. capensis* × *A. m. scutellata* hybrids. This increased behaviour of active dispersal may represent a host finding mechanism. Besides active dispersal, drifting is a common phenomenon in apiaries (drifting can be as high as 69%) and another route for parasite dispersal (Pfeiffer and Crailsheim, 1998). The question is whether *A. m. scutellata* guards treat *A. m. capensis* pseudo-clones preferentially? Guy (1976) contended that *A. m. scutellata* guards did permit *A. m. capensis* workers in freely. More recently however, it was shown that *A. m. scutellata* guards do not treat *A. m. capensis* pseudo-clones preferentially (unpublished data; see also Reece, 2002). It has been suggested that guards should respond favourably to high levels of 9ODA (Ruttner, 1976; Crewe and Velthuis, 1980; Tribe, 1983) but foreign queens, as well as workers coated with queen mandibular gland secretions, are more readily attacked by guards (Gary, 1961; Pettis et al., 1998). Therefore, invading *A. m. capensis* with queen-like QMP would not be more acceptable to guards (unpublished data), and it may actually be an advantage to retain non-dominant worker-like signals until the host colony has successfully been invaded. Even with *A. m. scutellata* having low response thresholds to alarm behaviour, and regarded as aggressive (Crewe, 1976), sufficient numbers of pseudo-clones are getting through the *A. m. scutellata* defence.

Five, the resident *A. m. scutellata* workers do not remove the eggs laid by the *A. m. capensis* pseudo-clones. The Dufour's glands of the pseudoqueens produce a series of esters (see Sect. 2.3), the postulated egg-marking pheromone, that are analogous to those produced by *A. m. scutellata* queens (Sole, 2000). It is therefore likely that the pseudo-clones mimic queen egg-marking pheromone, and in so doing, escape detection by policing workers. An alternative explanation could be that the policing *A. m. scutellata* workers cannot cope with the sheer number of worker-laid eggs, and as a result, worker policing breaks down. Whatever the cause, a collapse in worker policing is evident in the increasing number of pseudo-clones within the host colony.

Six, the invaders' queen-like signals, together with the queen's signal, cause chemical mayhem in the colony (Ruttner, 1977) with the *A. m. scutellata* queen being lost when the combined signal of the *A. m. capensis* reaches a particular concentration threshold (Allsopp and Crewe, 1993). These colonies do not successfully requeen (personal observation). Potential emerging *A. m. scutellata* or *A. m. capensis* virgin queens do not survive, either due to the pheromone imbalance in the colony or as a result of being killed by the workers. *A. m. capensis* do not like *A. m. scutellata* virgins and it has been demonstrated that *A. m. capensis* workers readily kill them (Buys, 1984).

Seven, the *A. m. capensis* social parasites entering the host colony first, compete for dominance (Moritz et al., 2000), as reported above (see Sects. 3.2 and 5.3). Those developing their signals and ovaries first regulate further reproduction in the *A. m. scutellata* and emerging *A. m. capensis* (Ruttner et al., 1976; Crewe and Velthuis, 1980; Crewe, 1984, 1988; Plettner et al., 1993; Martin et al., 2002b). Host colonies at various stages of *A. m. capensis* takeover were collected, the number of *A. m. capensis* pseudo-clones counted, and their reproductive state evaluated. The number of egg layers rarely exceeded 20% of the pseudo-clone population within the hive; on average only 8% of the pseudo-clone population were reproductively active (Martin et al., 2002b).

Eight, *A.m. capensis* pseudo-clone larvae are royally fed by *A. m. scutellata* nurse bees (Calis et al., 2002), gaining a reproductive advantage in the host colonies as has been shown for *A. m. capensis* reared in *A. m. mellifera* colonies (Tab. III; Beekman et al., 2000). These larvae probably secrete more or more attractive pheromones than the neighbouring *A. m. scutellata* brood, resulting in the *A. m. capensis* being fed better, and more food, and in due course, more queen-like *A. m. capensis* workers emerge (see Sect. 4).

7. CONCLUSIONS AND PERSPECTIVES

The nature of the chemical signalling system of *A. m. capensis* accounts firstly for queens producing very high concentrations of queen substance necessary to regulate the reproductive behaviour of the resident *A. m. capensis* workers. Secondly, the unique reproductive traits of *A. m. capensis,* and the easiness and swiftness with which they switch from worker biosynthetic pathways of pheromone production to that of a queen, assists them in becoming pseudoqueens. They are able to deceive workers with their signals which ultimately supports their parasitic lifestyle. Even though the dynamics of colony usurpation by these social parasites is not well understood, it is obvious that the problem is largely one of communication. On one level, there is pheromone exploitation by *A. m. capensis* workers, and on the other, signal breakdown of the *A. m. scutellata* queens which is possibly the pivotal aspect of the problem facing *A. m. scutellata* colonies. Pheromonally competent queens would suppress the expression of queen-like characteristics in the invading workers, ultimately repressing thelytokous reproduction. Research needs to focus on the composite pheromones of *A. m. capensis* queens and compare these to *A. m. scutellata* queens. There is a great need for solid quantitative data. The ratios and absolute amounts of the various compounds secreted by the queen glands must be investigated and quantified. A better understanding of the unique pheromone system of *A. m capensis* queens and workers is essential, only then can we successfully implement a pheromone-administering plan.

ACKNOWLEDGEMENTS

Sincere thanks to Dr. Melodie McGeoch for providing useful comments on the manuscript. My research in this area has been supported by funds from the Communication Biology Research Group of the University of the Witwatersrand and by the National Research Foundation.

Résumé – Le mimétisme phéromonal des abeilles *Apis mellifera capensis* parasites sociales conduit à la reproduction anarchique dans les colonies hôtes d'*Apis mellifera scutellata.* Le contrôle de la reproduction des ouvrières d'abeilles domestiques (*Apis mellifera* L.) repose en grande partie sur les phéromones de la reine, à savoir les sécrétions des glandes mandibulaires, tergales, tarsales et de la glande de Dufour, et sur les phéromones du couvain. Les phéromones de la reine et du couvain signalent la présence et la fécondité de la reine et les ouvrières réagissent de façon à augmenter leur propre valeur sélective (« fitness »). Les ouvrières d'*A. m. capensis* ont trouvé un moyen d'exploiter ce système « honnête » de signalement : en Afrique du Sud les ouvrières d'*A. m. capensis,* qui sont toutes génétiquement semblables, envahissent les colonies d'*A. m. scutellata.* Ces colonies hôtes perdent leur reine, les ouvrières d'*A. m. capensis* se chargent de la reproduction de la colonie, les activités normales de la ruche cessent et il arrive que la colonie meure. Cet article traite du système phéromonal de l'hôte et des caractéristiques uniques des abeilles du Cap envahisseuses qui transforment ces dernières en parasites sociaux efficaces.

Les reines d'*A. m. capensis* sont compétentes pour régulariser les ouvrières d'*A. m. capensis* et supprimer le développement des ovaires et du signal. Ces reines produisent des « super signaux » nécessaires à l'établissement des relations reines-ouvrières (Figs. 1–3, Tab. I). Par contre la reine hôte *A. m. scutellata* ne contrôle pas le développement des pseudo-reines dans sa colonie. C'est probablement l'aspect essentiel du problème auquel les abeilles *A. m. scutellata* ont à faire face.

Les pseudo-reines *A. m. capensis* développent rapidement leurs ovaires et entrent en compétition les unes avec les autres. Le conflit conduit à l'exploitation des phéromones par les ouvrières d'*A. m. capensis* qui développent rapidement les sécrétions de type reine issues des glandes mandibulaires, sécrétions dominées par le 9-ODA (Fig. 2, Tab. I). Les pseudo-reines contrôlent la reproduction des autres ouvrières. Le succès de l'usurpation de la colonie par ces parasites sociaux repose sur la production rapide de signaux de type reine et sur le développement ovarien (Figs. 4–5). Ces signaux envoyés par *A. m. capensis* ainsi que ceux émis par la reine conduisent à un déséquilibre phéromonal de la colonie et à la perte de la reine. Les envahisseuses *A. m. capensis* pondent des œufs qui ne sont pas reconnus et éliminés dans les colonies hôtes, probablement parce qu'ils imitent les sécrétions de la glande de Dufour de la reine. Le nombre d'*A. m. capensis* augmente dans la colonie tandis que le nombre d'*A. m. scutellata* diminue et que la colonie peut finir par mourir. Les œufs d'*A. m. capensis* sont non seulement acceptés mais leurs larves reçoivent vraisemblablement plus de nourriture et de meilleure qualité. Les ouvrières qui naissent sont donc plus proches des reines (Tab. II). Les ouvrières d'*A. m. capensis* ont une grande propension à se disperser, ce qui constitue chez les parasites un mécanisme important pour trouver un hôte. Une meilleure compréhension de ce système phéromonal unique du parasite social et de son hôte est essentiel pour pouvoir appliquer une protection efficace des colonies par l'administration de phéromones.

***Apis mellifera* / reproduction des ouvrières / plasticité des castes / phéromone / parasite social**

Zusammenfassung – Pheromonale Mimikry sozialparasitischer *Apis mellifera capensis* führt zu reproduktiver Anarchie in den Wirtsvölkern von *A. m. scutellata*. Die Unterdrückung der Reproduktion von Bienenarbeiterinnen ist zu weitesten Teilen von den Königinnenpheromonen, den Sekretionen der Mandibel-, Tergal-, Tarsal- und Dufour's Drüsen, wie auch von Brutpheromonen bestimmt. Diese Königinnen- und Brutpheromone signalisieren die Anwesenheit und Fruchtbarkeit der Königin, auf die die Arbeiterinnen in einer ihre eigene Fitness optimierende Weise reagieren. Arbeiterinnen von *A. m. capensis* haben einen Weg gefunden dieses „ehrliche" Signalsystem auszubeuten, wodurch Arbeiterinnen von *A. m. capensis* in Südafrika, alle genetisch ähnlich, in Völker von *A. m. scutellata* eindringen. Diese Wirtsvölker verlieren ihre Königin und die Arbeiterinnen von *A. m. capensis* übernehmen die Reproduktion. Darüber hinaus schwindet die Aktivität der Völker und sie gehen zu Grunde. Dieses Manuskript konzentriert sich auf die Betrachtung des Hormonsystems des Wirtsvolkes und auf die besonderen Charakteristika der *A. m. capensis* Eindringlinge, durch die diese zu erfolgreichen Sozialparasiten werden.

Königinnen von *A. m. capensis* sind in der Lage die Arbeiterinnen von *A. m. capensis* zu kontrollieren und die Entwicklung der Ovarien und pheromonaler Signale zu unterdrücken. Diese Königinnen erzeugen die zur wirkungsvollen Etablierung von Königinnen-Arbeiterinnenbeziehung benötigten „Super" - Signale (Abb. 1–3; Tab. I, II). Die Königin des *A. m. scutellata* Wirtsvolkes dagegen kann die Entwicklung von Pseudoköniginnen nicht verhindern. Dies ist vermutlich die bedeutungsvollste Facette des Problems, dem *A. m. scutellata* Honigbienen gegenüberstehen. Die Pseudoköniginnen von *A. m. capensis* entwickeln rasch ihre Ovarien und treten miteinander in Wettbewerb um die reproduktive Dominanz. Dieser Konflikt führt zu pheromonaler Ausbeutung durch die *A. m. capensis* Arbeiterinnen, die rasch königinnenähnliche Mandibeldrüsensekrete mit der Hauptkomponente 9ODA entwickeln (Abb. 2; Tab. I), und als Pseudoköniginnen die Reproduktion der anderen Arbeiterinnen unterdrücken. Der Erfolg der Übernahme eines Wirtsvolkes durch die Sozialparasiten beruht damit auf möglichst schneller Produktion von königinnenähnlichen Pheromonen und Ovarienentwicklung (Abb. 4, 5). Diese Signale von *A. m. capensis* führen zusammen

mit den Königinnensignalen zu einer pheromonalen Ungleichgewichtigkeit in den Völkern mit der Folge, dass die Königin verloren geht. Die Eindringlinge von *A. m. capensis* legen Eier, die in den Wirtsvölkern nicht „policed“ werden (d.h. nicht von anderen Arbeiterinnen erkannt und entfernt werden), vermutlich indem sie das mutmaßliche Markierungspheremon der Königin nachahmen. Die Anzahl von *A. m. capensis* Arbeiterinnen in den Völkern nimmt daraufhin immer mehr zu, während gleichzeitig die Anzahl von *A. m. scutellata* Arbeiterinnen abnimmt und das Volk eingeht. Es werden nicht nur die Eier in den Wirtsvölkern angenommen, darüber hinaus werden die Larven vermutlich mit mehr und höherwertigem Futter versorgt. Die schlüpfenden Arbeiterinnen sind daraufhin königinnenartiger (Tab. III). Die *A. m. capensis* Arbeiterinnen haben eine hohe Neigung zur Ausbreitung, was im Leben eines Parasiten einen wichtigen Mechanismus zur Auffindung neuer Wirte darstellt. Ein besseres Verständnis des einzigartigen Pheromonsystems sowohl des Sozialparasiten als auch der Wirtsvölker ist vonnöten, um erfolgreichen Schutz der Völker durch Pheromongaben erreichen zu können.

***Apis mellifera* / Arbeiterinnenreproduktion / Kastenplastizität / Pheromone / Sozialparasiten**

REFERENCES

Allsopp M.H. (1988) Mandibular gland acids and laying workers in African honey bees, in: Needham G.R., Page R.E., Definado-Baker M., Bowman C.E. (Eds.), Africanized honey bees and bee mites, Ellis Horwood Limited, England, pp. 72–79.

Allsopp M.H. (1992) The *capensis* calamity, S. Afr. Bee J. 64, 52–55.

Allsopp M.H., Crewe R.M. (1993) The Cape honey bee as a Trojan horse rather than the Hordes of Genghis Khan, Am. Bee J. 133, 121–123.

Anderson R.H. (1963) The laying worker in the Cape honeybee, *Apis mellifera capensis*, J. Apic. Res. 2, 85–92.

Anderson R.H. (1980) Cape honey-bee sanctuaries, S. Afr. Bee J. 52, 5–9.

Anderson R.H. (1981) Queens and queen rearing, S. Afr. Bee J. 53, 3–12.

Arnold G., Le Conte Y., Trouiller J., Hervet H., Chappe B., Masson C. (1994) Inhibition of worker honeybee ovaries development by a mixture of fatty acid esters from larvae, C. R. Acad. Sci. Paris 317, 511–515.

Barron A.B., Oldroyd B.P. (2001) Social regulation of ovary activation in ‘anarchistic’ honey-bees (*Apis mellifera*), Behav. Ecol. Sociobiol. 49, 214–219.

Beekman M., Calis J.N.M., Boot W.J. (2000) Parasitic honeybees get royal treatment, Nature 404, 723.

Beetsma J. (1979) The process of queen-worker differentiation in the honeybee, Bee World 60, 24–39.

Billen J.P.J., Dumortier K.T.M., Velthuis H.H.W. (1986) Plasticity of honeybee castes: occurrence of tergal glands in workers, Naturwissenschaften 73, 332–333.

Blum M.S. (1974) Pheromonal bases of social manifestations in insects, in: Birch M.C. (Ed.), Pheromones, North-Holland Publishing Company, Amsterdam, pp. 194–199.

Boch R., Lensky Y. (1976) Pheromonal control of queen rearing in honeybee colonies, J. Apic. Res. 15, 59–62.

Butler C.G. (1954) The method and importance of the recognition by a colony of honey-bees (*A. mellifera* L.) of the presence of its queen, Trans. R. Entomol. Soc. London 105, 11–29.

Butler C.G. (1956) Some further observations on the nature of ‘queen substance’ and its role in the organization of a honey-bee (*Apis mellifera*) community, Proc. R. Entomol. Soc. London 31, 12–16.

Butler C.G. (1957) The control of ovary development in worker honeybees (*Apis mellifera*), Experientia 13, 256–257.

Butler C.G. (1959) Queen substance, Bee World 40, 269–275.

Butler C.G., Fairey E.M. (1963) The role of the queen in preventing oogenesis in worker honeybees, J. Apic. Res. 2, 14–18.

Butler C.G., Callow R.K., Johnston F.R.S., Johnston N.C. (1962) The isolation and synthesis of queen substance, 9-oxodec-trans-2-enoic acid, a honeybee pheromone, Proc. R. Entomol. Soc. London 155, 417–432.

Buys B. (1984) Cape worker-bees dislike African virgin queens, S. Afr. Bee J. 56, 63.

Calis J.N.M., Boot W.J., Allsopp M.H., Beekman M. (2002) Getting more than a fair share: nutrition of worker larvae related to social parasitism in the Cape honey bee *Apis mellifera capensis*, Apidologie 33, 193–202.

Cooke M.J. (1992) Turnabout is fair play – Cape bee invades African bee territory, Am. Bee J. 132, 519–521.

Crewe R.M. (1976) Aggressiveness of honeybees and their pheromone production, S. Afr. J. Sci. 72, 209–212.

Crewe R.M. (1981) Queens, false queens and *capensis*, S. Afr. Bee J. 53, 18–21.

Crewe R.M. (1982). Compositional variability: The key to the social signals produced by honeybee mandibular glands, in: Breed M.D, Michener C.D., Evans H.E. (Eds.), The Biology of Social Insects, Westview Press/Boulder, Colorado, pp. 318–322.

Crewe R.M. (1984) Differences in behaviour and morphology between *capensis* and *adansonii*, S. Afr. Bee J. 56, 16–21.

Crewe R.M. (1987) Lability of the mandibular gland signal of three races of African honey bees, in: Eder J., Rembold H. (Eds.), Chemistry and Biology of Social Insects, Verlag J. Peperny, Munich, pp. 433–434.

Crewe R.M. (1988) Natural history of honey-bee mandibular gland secretions: development of analytical techniques and the emergence of complexity, in: Needham G.R., Page R.E., Definado-Baker M., Bowman C.E. (Eds.), Africanized honey bees and bee mites, Ellis Horwood Limited, England, pp. 149–158.

Crewe R.M. (1993) Chemical and morphological differentiation of southern African honeybee races, Proc. 9th Entomol. Congr., S. Afr., p. 17.

Crewe R.M., Velthuis H.H.W. (1980) False queens: a consequence of mandibular gland signals in worker honeybees, Naturwissenschaften 67, 467–469.

Crewe R.M., Moritz R.F.A. (1989) Variation in the components of head extracts of workers and queens of *Apis mellifera intermissa* Buttel-Reepen, Z. Naturforsch. 44c, 590–596.

Crewe R.M., Wossler T., Allsopp M.H. (1990) Workers in queens clothing: why *capensis* workers become pseudoqueens, in: Anderson R.W., Buys B. (Eds.), Bees and beekeeping in Southern Africa, Apimondia, University Press, Stellenbosch, pp. 83–89.

De Groot A.P., Voogd S. (1954) On the ovary development in queenless worker bees (*Apis mellifera* L.), Experientia 10, 384–385.

De Grandi-Hoffman G., Martin J.H. (1993) Behaviour of egg-laying virgin and mated queen honey bees (*Apis mellifera* L.) and the composition of brood in their colonies, J. Apic. Res. 32, 19–26.

Delaplane K.S., Harbo J.R. (1987) Drone production by young versus old worker honeybees in queenless colonies, Apidologie 18, 115–120.

Espelie K.E., Butz V.M., Dietz A. (1990) Decyl decanoate: a major component of the tergite glands of honeybee queens (*Apis mellifera* L.), J. Apic. Res. 29, 15–19.

Ferguson A.W., Free J.B. (1980) Queen pheromone transfer within honeybee colonies, Physiol. Entomol. 5, 539–366.

Fletcher D.J.C. (1975) First observations of Cape bees in Natal, S. Afr. Bee J. 52, 5–9.

Free J.B. (1987) Pheromones of social bees, Chapman and Hall, London.

Free J.B., Ferguson A.W., Simkins J.R. (1985) Influence of virgin honeybees (*Apis mellifera*) on queen rearing and foraging, Physiol. Entomol. 10, 271–274.

Fuchs S., Moritz R.F. (1999) Evolution of extreme polyandry in the honeybee *Apis mellifera* L., Behav. Ecol. Sociobiol. 45, 269–275.

Gary N.E. (1961) Antagonistic reactions of worker honeybees to the mandibular contents of the queen (*Apis mellifera*), Bee World 42, 14–17.

Gary N.E., Morse R.A. (1962) Queen cell construction in the honeybee (*Apis mellifera* L.) colonies headed by queens without mandibular glands, Proc. R. Entomol. Soc. London 37, 76–78.

Greeff J.M. (1996) Effects of thelytokous worker reproduction on kin-selection and conflict in the Cape honeybee, *Apis mellifera capensis*, Philos. Trans. R. Soc. London B 351, 617–625.

Greeff J.M. (1997) The Cape honeybee and her way north: an evolutionary perspective, S. Afr. J. Sci. 93, 306–308.

Guy R.D. (1976) Whence the Cape bee? S. Afr. Bee J. 48, 7–8.

Harris J.W., Harbo J.R. (1991) Producing eggs from a single worker honey bee (Hymenoptera: Apidae), J. Econ. Entomol. 84, 818–824.

Hemmling C., Koeniger, K., Ruttner F. (1979) Quantitative Bestimmung der 9-oxodecensäure im Lebenszyklus der Kapbiene (*Apis mellifera capensis* Escholtz), Apidologie 10, 227–240.

Hepburn H.R. (1992a) Pheromonal and ovarial development covary in Cape worker honeybees, *Apis mellifera capensis*, Naturwissenschaften 79, 523–524.

Hepburn H.R. (1992b) The biology of queen production in the Cape honeybee, S. Afr. Bee J. 64, 132–138.

Hepburn H.R. (1994) Reproductive cycling and hierarchical competition in Cape honeybees, *Apis mellifera capensis* Esch, Apidologie 25, 38–48.

Hepburn H.R., Crewe R.M. (1991) Defining the Cape honeybee: reproductive traits of queenless workers, S. Afr. J. Sci. 86, 524–527.

Hepburn H.R., Allsopp M.H. (1994) Reproductive conflict between honeybees: usurpation of *Apis mellifera scutellata* colonies by *Apis mellifera capensis*, S. Afr. J. Sci. 90, 247–249.

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

Hepburn R., Radloff S.E. (2002) *Apis mellifera capensis*: an essay on the subspecific classification of honeybees, Apidologie 33, 105–127.

Hepburn H.R., Nefdt R.J.C., Whiffler L.A. (1988) Queen loss in Cape honeybees: the interactions of brood, laying workers (false queens?) and queen cells, S. Afr. J. Sci. 84, 778–780.

Hepburn H.R., Magnuson P., Herbert L., Whiffler L.A. (1991) The development of laying workers in field colonies of the Cape honey bee, J. Apic. Res. 30, 107–112.

Hillesheim E., Koeniger N., Moritz R.F.A. (1989) Colony performance in honeybees (*Apis mellifera capensis* Esch.) depends on the proportion of subordinate and dominant workers, Behav. Ecol. Sociobiol. 24, 291–296.

Jay S.C. (1968) Factors influencing ovary development of worker honeybees under natural conditions, Can. J. Zool. 46, 345–347.

Jay S.C. (1970) The effect of various combinations of immature queen and worker bees on the ovary development of worker honeybees in colonies with and without queens, Can. J. Zool. 48, 169–173.

Jay S.C. (1972) Ovary development of worker honeybees when separated from worker brood by various methods, Can. J. Zool. 50, 661–664.

Jay S.C., Jay D.H. (1993) The effect of kiwifruit (*Actinidia deliciosa* A Chev) and yellow flowered broom (*Cytisus scoparius* Link) pollen on the ovary development of worker honey bees (*Apis mellifera* L.), Apidologie 24, 557–563.

Johannsmeier M.F. (1983) Experience with the Cape bee in the Transvaal, S. Afr. Bee J. 55, 130–138.

Katzav-Gozansky T., Soroker V., Hefetz A., Cojocaru M., Erdmann D.H., Francke W. (1997) Plasticity of caste-specific Dufour's gland secretion in the honey bee (*Apis mellifera* L.), Naturwissenschaften 84, 238–241.

Katzav-Gozansky T., Soroker V., Hefetz A. (2000) Plasticity in caste-related exocrine secretion biosynthesis in the honey bee (*Apis mellifera*), J. Insect Physiol. 46, 993–998.

Keller L., Nonacs P. (1993) The role of queen pheromones in social insects: queen control or queen signal? Anim. Behav. 45, 787–794.

Korst P.J.A.M., Velthuis H.H.W. (1982) The nature of trophallaxis in honeybees, Insectes Soc. 29, 209–221.

Kryger P. (2001) An obligate social parasite in honey bees: the pseudo-clone of *Apis mellifera capensis*, Proc. 13th Entomol. Congr. S. Afr., p. 38.

Le Conte Y., Sreng L., Poitout S. (1995) Brood pheromone can modulate the feeding behaviour of *Apis mellifera* workers (Hymenoptera: Apidae), J. Econ. Entomol. 88, 798–804.

Lensky Y., Slabezki Y. (1981) The inhibiting effect of the queen bee (*Apis mellifera* L.) foot-print pheromone on the construction of swarming queen cups, J. Insect Physiol. 27, 313–323.

Leonardo A.M.C. (1985) Developmental cycle of the mandibular glands of *Apis mellifera* workers. 2. Effect of queenlessness, J. Apic. Res. 24, 76–79.

Lundie A.E. (1954) Laying worker bees produce worker bees, S. Afr. Bee J. 29, 10–11.

Magnuson P. (1995) The Cape honeybee problem – understanding honeybee biology offers possible solution, S. Afr. Bee J. 67, 134–136.

Martin S.J., Beekman M., Wossler T.C., Ratnieks F.L.W. (2002a) Parasitic Cape honeybee workers, *Apis mellifera capensis*, evade policing, Nature 415, 163–165.

Martin S., Wossler T., Kryger P. (2002b) Usurpation of African *Apis mellifera scutellata* colonies by parasitic *Apis mellifera capensis* workers, Apidologie 33, 215–232.

Mohammedi A., Paris A., Crauser Y., Le Conte Y. (1998) Effect of aliphatic esters on ovary development of queenless bees (*Apis mellifera* L.), Naturwissenschaften 85, 455–458.

Montague C.E., Oldroyd B.P. (1998) The evolution of worker sterility in honey bees: an investigation into behavioural mutant causing failure of worker policing, Evolution 52, 1408–1415.

Moritz R.F.A. (2002) Population dynamics of the Cape bee phenomenon: The impact of parasitic laying worker clones in apiaries and natural populations, Apidologie 33, 233–244.

Moritz R.F.A., Hillesheim E. (1985) Inheritance of dominance in honeybees (*Apis mellifera capensis* Esch.), Behav. Ecol. Sociobiol. 17, 87–89.

Moritz R.F.A., Crewe R.M. (1988) Reaction of honeybee workers (*Apis mellifera* L.) to fatty acids in queen signals, Apidologie 19, 333–342.

Moritz R.F.A, Crewe R.M. (1991) The volatile emission of honeybee queens (*Apis mellifera* L.), Apidologie 22, 205–212.

Moritz R.F.A., Haberl M. (1994) Lack of meiotic recombination in thelytokous parthenogenesis of laying workers of *Apis mellifera capensis* (the Cape honeybee), Heredity 73, 98–102.

Moritz R.F.A., Kryger, P., Allsopp M. (1996) Competition for royalty in bees, Nature 384, 31.

Moritz R.F.A., Kryger P., Allsopp M.H. (1999) Lack of worker policing in the Cape honeybee (*Apis mellifera capensis*), Behaviour 136, 1079–1092.

Moritz R.F.A., Simon U.E., Crewe R.M. (2000) Pheromonal contest between honeybee workers, Naturwissenschaften 87, 395–397.

Moritz R.F.A., Crewe R.M., Hepburn H.R. (2001) Attraction and repellence of workers by the honeybee queen (*Apis mellifera* L.), Ethology 107, 465–478.

Naumann K., Winston M.L., Slessor K.N., Prestwich G.D., Webster F.X. (1991) Production and transmission of honey bee queen (*Apis mellifera* L.) mandibular gland pheromone, Behav. Ecol. Sociobiol. 29, 321–332.

Naumann K., Winston M.L., Slessor K.N. (1993) Movement of honey bee (*Apis mellifera* L.) queen mandibular gland pheromone in populous and unpopulous colonies, J. Insect Behav. 6, 211–223.

Neumann P., Hepburn R. (2002) Behavioural basis for social parasitism of Cape honeybees (*Apis mellifera capensis*), Apidologie 33, 165–192.

Neumann P., Hepburn H.R., Radloff S.E. (2000) Modes of worker reproduction, reproductive dominance and brood cell construction in queenless honeybee (*Apis mellifera* L.) colonies, Apidologie 31, 479–486.

Neumann P., Radloff S.E., Moritz R.F.A., Hepburn H.R., Reece S.L. (2001) Social parasitism by honeybee workers (*Apis mellifera capensis* Escholtz): host finding and resistance of hybrid host colonies, Behav. Ecol. 12, 419–428.

Oldroyd B.P., Ratnieks F.L.W. (2000) Evolution of worker sterility in honey-bees (*Apis mellifera*): how anarchistic workers evade policing by laying eggs that have low removal rates, Behav. Ecol. Sociobiol. 47, 268–273.

Oldroyd B.P., Smolenski A.J., Cornuet J.M., Crozier R.H. (1994) Anarchy in the beehive, Nature 371, 749.

Oldroyd B.P., Halling L., Rinderer T.E. (1999) Development and behaviour of anarchistic honeybees, Proc. R. Soc. London B 266, 1875–1878.

Onions G.W. (1912) South African “fertile-worker bees”, Union S. Afr. Agric. J. 3, 720–728.

Onions G.W. (1914) South African “fertile” worker bees, Agric. J. Un. S. Afr. 7, 44–46.

Page R.E., Robinson G.E. (1994) Reproductive competition in queenless honey bee colonies (*Apis mellifera* L.), Behav. Ecol. Sociobiol. 35, 99–107.

Pain J. (1961) Absence du pouvoir d’inhibition de la phéromone I - Sur le développement ovarien des jeunes ouvrières d’abeilles, C. R. Acad. Sci. Paris 252, 2316–2317.

Pain J., Roger B. (1976) Variation de la teneur en acide céto-9 décène-2 oïque en fonction de l’age chez les reines vierges d’abeille (*Apis mellifica ligustica* S.), C. R. Acad. Sci. Paris 283, 797–799.

Pain J., Hügel M.F., Barbier M. (1960) Sur les constituants du mélange attractif des glandes mandibulaires des reines d’Abeilles (*Apis mellifica* L.) à différents stades de leur vie, C. R. Acad. Sci. Paris 251, 1046–1048.

Pain J., Barbier M., Roger B. (1967) Dosages individuels des acides céto-9 décène-2 oïque et hydroxy-10 décène-2 oïque dans les têtes des reines et des ouvrières d’abeilles, Ann. Abeille 10, 45–52.

Palmer K.A., Oldroyd B.P. (2000) Evolution of multiple mating in the genus *Apis*, Apidologie 31, 235–248.

Pankiw T., Winston M.L., Slessor K.N. (1994) Variation in worker response to honey bee (*Apis mellifera* L.) queen mandibular pheromone (Hymenoptera: Apidae), J. Insect Behav. 7, 1–15.

Pankiw T., Winston M.L., Plettner E., Slessor K.N., Pettis J.S., Taylor O.R. (1996) Mandibular gland components of European and Africanized honey bee queens (*Apis mellifera* L.), J. Chem. Ecol. 22, 605–615.

Pettis J.S., Winston M.L., Collins A.M. (1995) Suppression of queen rearing in European and Africanized honey bees *Apis mellifera* L. by synthetic queen mandibular gland pheromone, Insectes Soc. 42, 113–121.

Pettis J.S., Higo H.A., Pankiw T., Winston M.L. (1997) Queen rearing suppression in the honey bee – evidence for a fecundity signal, Insectes Soc. 44, 311–322.

Pettis J.S., Westcott L.C., Winston M.L. (1998) Balling behaviour in the honey bee in response to exogenous queen mandibular gland pheromone, J. Apic. Res. 37, 125–131.

Pfeiffer K.J., Crailsheim K. (1998) Drifting of honeybees, Insectes Soc. 45, 151–167.

Pirk C.W.W., Neumann P., Hepburn H.R. (2002) Egg laying and egg removal by workers are positively correlated in queenright Cape honeybee colonies (*Apis mellifera capensis*), Apidologie 33, 203–211.

Plettner E., Slessor K.N., Winston M.L., Robinson G.E., Page R.E. (1993) Mandibular gland components and ovarian development as measures of caste differentiation in the honey bee (*Apis mellifera* L.), Insect Physiol. 39, 235–240.

Plettner E., Sutherland G.R.J., Slessor K.N., Winston M.L. (1995) why not be a queen? Regioselectivity in mandibular secretions of honeybee castes, J. Chem. Ecol. 21, 1017–1029.

Plettner E., Slessor K.N., Winston M.L., Oliver J.E. (1996) Caste-selective pheromone biosynthesis in honeybees, Science 271, 1851–1853.

Plettner E., Otis G.W., Wimalaratne P.D.C., Winston M.L., Slessor K.N., Pankiw T., Punchiheewa P.W.K. (1997) Species- and caste-determined mandibular gland signals in honeybees (*Apis*), J. Chem. Ecol. 23, 363–377.

Prince R.C., Gunson D.E. (1992) Anarchie in the feminine monarchie: the case of the Cape bee, T.R.E.E. 7, 398–399.

Ratnieks F.L.W. (1995) Evidence for a queen-produced egg-marking pheromone and its use in worker policing in the honey bee, J. Apic. Res. 34, 31–37.

Ratnieks F.L.W., Visscher P.K. (1989) Worker policing in the honeybee, Nature 342, 796–797.

Reece S.L. (2002) A scientific note on the ovarial and pheromonal development of drifted and non-drifted Cape honeybee workers (*Apis mellifera capensis*), Apidologie 33, 213–214.

Robinson G.E. (1996) Chemical communication in honeybees, Science 271, 1824–1825.

Robinson G.E., Page R.E., Fondrk M.K. (1990) Intracolonial behavioral variation in worker oviposition, oophagy, and larval care in queenless honey bee colonies, Behav. Ecol. Sociobiol. 26, 315–323.

Ruttner F. (1976). African races of honeybees, Proc. XXV Apic. Congr. Apimondia, Grenoble, pp. 325–344.

Ruttner F. (1977) The problem of the Cape bee (*Apis mellifera capensis* Escholtz): parthenogenesis – size of population – evolution, Apidologie 8, 281–294.

Ruttner F., Hesse B. (1981) Rassenspezifische unterscheide in ovarentwicklung und eiablage von weisellosen arbeiterinnen der honigbiene *Apis mellifera* L., Apidologie 12, 159–183.

Ruttner F., Koeniger N., Veith H.J. (1976) Queen substance bei eierlegenden Arbeiterinnen der Honigbiene, *Apis mellifica* L., Naturwissenschaften 63, 434.

Saiovici M. (1983) 9-Oxodecenoic acid and dominance in honeybees, J. Apic. Res. 22, 27–32.

Sakagami S.F. (1958) The false-queen: fourth adjustive response in dequeened honeybee colonies, Behaviour 13, 280–296.

Sasaki M., Takuro I., Sato M. (1989) Humoral control of the queen pheromone (9ODA) biosynthesis in honeybees: Induction in queenless worker and in worker mandibular gland implanted into queen, Bull. Fac. Agric., Tamagawa Univ. 29, 11–21.

Seeley T.D. (1979) Queen substance dispersal by messenger workers in honey-bee colonies, Behav. Ecol. Sociobiol. 5, 391–415.

Seeley T.D. (1985) Honeybee ecology, Princeton Univ. Press, Princeton, NJ.

Seeley T.D. (1995) The wisdom of the hive, Harvard Univ. Press, Cambridge, MA.

Simon U.E., Moritz R.F.A., Crewe R.M. (2001) The ontogenetic pattern of mandibular gland components in queenless worker bees (*Apis mellifera capensis* Esch.), J. Insect Physiol. 47, 735–738.

Slessor K.N., Kaminski L.A., King G.G.S., Borden J.H., Winston M.L. (1988) Semiochemical basis of the retinue response to queen honey bees, Nature 332, 354–356.

Slessor K.N., Kaminski L.A., King G.G.S., Winston M.L. (1990) Semiochemicals of the honeybee queen mandibular glands, J. Chem. Ecol. 16, 851–860.

Sole C. (2000) Age specific Dufours gland secretion in *Apis mellifera scutellata* Lepeletier and the *Apis mellifera capensis* Escholtz pseudo-clone, Honours thesis, University of Pretoria, Pretoria, South Africa.

Tribe G.D. (1981) Cape honeybee behaviour, S. Afr. Bee J. 53, 10–12.

Tribe G.D. (1983) What is the Cape bee? S. Afr. Bee J. 55, 77–87.

van der Blom J. (1991) Social regulation of egg-laying by queenless honeybee workers (*Apis mellifera* L.), Behav. Ecol. Sociobiol. 29, 341–346.

van der Blom J., Verkade A.J. (1991) Does kin recognition in honey bees, *Apis mellifera* L., influence the workers' chances of becoming egg layers? Anim. Behav. 42, 867–870.

van der Blom J., Boot W.J., Velthuis H.H.W. (1994) Simultaneous queen rearing and egg laying by workers in Africanized honeybee colonies (*Apis mellifera* L.) in Costa Rica, Apidologie 25, 367–374.

Velthuis H.H.W. (1970a) Ovarian development in *Apis mellifera* worker bees, Entomol. Exp. Appl. 13, 343–357.

Velthuis H.H.W. (1970b) Queen substance from the abdomen of the honeybee queen, Z. Vgl. Physiol. 70, 210–222.

Velthuis H.H.W. (1972) Observations on the transmission of queen substances in the honeybee colony by the attendants of the queen, Behaviour 41, 105–129.

Velthuis H.H.W. (1976) Egg laying, aggression and dominance in bees, Proc. XV Int. Congr. Entomol., pp. 436–449.

Velthuis H.H.W. (1985) The honeybee queen and the social organization of her colony, in: Hölldobler B., Lindauer M. (Eds.), Experimental behavioural ecology and sociobiology, G. Fischer Verlag, New York, pp. 343–357.

Velthuis H.H.W. (1990) Chemical signals and dominance communication in the honeybee *Apis mellifera* [Hymenoptera: Apidae], Entomol. Gen. 15, 83–90.

Velthuis H.H.W., van der Kerk A. (1988) Age, environment, and genes in relation to the mandibular gland secretion of pure and hybrid *Apis mellifera capensis* worker bees, in: Needham G.R., Page R.E., Delfinado-Baker M., Bowman C.E. (Eds.), Africanized honey bees and bee mites, Ellis Horwood Limited, England, pp. 80–86.

Velthuis H.H.W., Verheijen F.J., Gottenbos A.J. (1965) Laying worker honey bee: similarities to the queen, Nature 207, 1314.

Velthuis H.H.W., Ruttner F., Crewe R.M. (1990) Differentiation in reproductive physiology and behaviour during the development of laying worker honey bees, in: Engels W. (Ed.), Social Insects, Springer, Berlin, pp. 231–243.

Vierling G., Renner M. (1977) Die Bedeutung des Sekretes der tergittaschendrüsen für die Attraktivität der Bienenkönigin gegenüber jungen Arbeiterinnen – The secretion of the tergit glands and the attractiveness of the honey bee queen, Behav. Ecol. Sociobiol. 2, 185–200.

Visscher P.K. (1989) A quantitative study of worker reproduction in honey bee colonies, Behav. Ecol. Sociobiol. 25, 247–254.

Visscher P.K. (1998) Colony integration and reproductive conflict in honey bees, Apidologie 29, 23–45.

Visscher P.K., Dukas R. (1995) Honey bees recognize development of nestmates' ovaries, Anim. Behav. 49, 542–544.

Wheeler D. (1996) The role of nourishment in oogenesis, Annu. Rev. Entomol. 41, 407–431.

Williams I.H., Free J.B. (1975) Effect of environmental conditions during the larval period on the tendency of worker honeybees to develop their ovaries, J. Entomol. A 49, 179–182.

Willis L.G., Winston M.L., Slessor K.N. (1990) Queen honey bee mandibular pheromone does not affect worker ovary development, Can. Entomol. 122, 1093–1099.

Winston M.L., Slessor K.N. (1992) The essence of royalty: honey bee queen pheromone, Am. Sci. 80, 374–385.

Winston M.L., Slessor K.N. (1998) Honey bee primer pheromones and colony organization: gaps in our knowledge, Apidologie 29, 81–95.

Winston M.L., Higo H.A., Colley S.J., Pankiw T., Slessor K.N. (1991) The role of queen mandibular pheromone and colony congestion in honey bee (*Apis mellifera* L.) reproductive swarming (Hymenoptera: Apidae), J. Insect Behav. 4, 649–660.

Wossler T.C., Crewe R.M. (1999a) Honeybee queen tergal gland secretions affects ovarian development in caged workers, Apidologie 30, 311–320.

Wossler T.C., Crewe R.M. (1999b) Mass spectral identification of the tergal gland secretions of female castes of two African honey bee races (*Apis mellifera*), J. Apic. Res. 38, 137–148.

Wossler T.C., Veale R.B., Crewe, R.M. (2000) How queen-like are the tergal glands in workers of *Apis mellifera capensis* and *Apis mellifera scutellata*?, Apidologie 31, 55–66.

To access this journal online:
www.edpsciences.org