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Original article

Usurpation of African *Apis mellifera scutellata* colonies by parasitic *Apis mellifera capensis* workers

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Abstract – Thelytokous *Apis mellifera capensis* workers recently brought into regions occupied by the arrkenotokous African bee *A. m. scutellata,* parasitise these colonies, causing colony death. These *capensis* workers are genetically almost identical and are referred to as a 'pseudo–clone'. We surveyed 120 *scutellata* colonies, 27 in detail, at various stages of usurpation by the pseudo-clone. The *scutellata* queen could co-exist with egg-laying pseudo-clones for 50+ days in one case but disappeared 1–15 days in three other cases. Despite the presence of emerged queen cells no new adult queens of either race were observed in usurped colonies. Only 11 ± 13% of the pseudo-clone population had fully active ovaries, suggesting ovarian development is inhibited in the majority of the pseudo-clones. Only 2.7 ± 1.7% of the foraging force were pseudo-clones. The data were modelled and showed the rapid (56–105 days) growth of the pseudo-clone population and colony death over a wide range of initial conditions.

***Apis mellifera capensis* / pseudo-clone / usurpation / reproduction / *Apis mellifera scutellata* / honeybee reproduction / South Africa**

1. INTRODUCTION

Honey bees (*Apis*) workers cannot mate but retain ovaries and lay unfertilised eggs. However, in a few rare cases unfertilised workers can produce female (diploid) offspring through the automictic fertilisation of the egg (Moritz and Haberl, 1994), a system normally referred to as thelytokous parthenogenesis. In other social Hymenoptera this system has only been reported in four species of ants (Cagniant, 1979; Itow et al., 1984; Tsuji and Yamauchi, 1995; Heinze and Hölldobler, 1995) and occasionally in queenless *Apis mellifera* L. colonies (Onions, 1914;

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Mackensen, 1943). In *A. mellifera* though (except for *Apis mellifera capensis* Escholtz) it is thought to be caused by rare meiotic faults. Thelytokous reproduction by workers was first described in the Cape honey bee *A. m. capensis*, in 1909 by Onions (1912) as a common and stable trait in this race, although it was many decades before his observations were widely accepted (Hepburn and Radloff, 2002).

The *capensis* honey bee is restricted to the fynbos biome in the Cape region of South Africa (Hepburn and Crewe, 1991; Hepburn and Guillarmod, 1991) a region of extraordinary floral richness and diversity. During the Pleistocene this region was an island (Guy, 1976) and it is possible that thelytoky arose then (Ruttner, 1977).

Although this region is no longer geographically isolated, there is a 200 km wide natural hybrid zone between the Cape (*A. m. capensis*) and African (*Apis mellifera scutellata* Lepeletier) honey bees, which inhabit most of sub-Saharan Africa (Hepburn and Crewe, 1991; Ruttner, 1988). This zone appears to be very stable, although the forces which maintain it are not well understood.

The artificial movement of *capensis* bees, which are predominantly black, into the savannah region has caused a dramatic effect on the surrounding native, primarily yellow, *scutellata* population (see Hepburn and Radloff, 2002 and Radloff et al., 2002 for alternative morphometric characters). The first recorded case of long distance movement of *capensis* colonies was in 1928 when five were moved to Pretoria (Lundie, 1954), a region of South Africa some 1000 km north of their natural range. During the following two years many ‘black’ *capensis* bees where found in nearby ‘yellow’ *scutellata* colonies, all of which eventually died because requeening to combat the increasing numbers of black bees failed. The second case occurred in 1977. Eight *capensis* colonies where moved to Pretoria and again workers moved into the 40 to 50 *scutellata* colonies in the same apiary, and caused queen loss and decline of the invaded colonies (Johannsmeier, 1983). Although all subsequent *scutellata* colonies, which contained black *capensis* bees, were destroyed, the problem persisted locally for another four years.

Despite the warnings of Johannsmeier (1983) in which he stated “It would be foolish for beekeepers to move Cape bees out of the western and southern cape regions for whatever reason”, in 1990 around 400 *capensis* colonies where moved to Rust-der-Winter, north of Pretoria (Allsopp, 1993). At Rust-der-Winter, the aloe (*Aloe greatheadii davyana*) a prodigious producer of nectar and pollen, attracts many migratory beekeepers who relocate thousands of *scutellata* colonies there for a few weeks each year (Allsopp and Crewe, 1993). In addition, during 1990 *scutellata* colonies were moved into the Cape region for three months to pollinate apples, before being moved back to other areas of South Africa (Allsopp and Crewe, 1993). Two years later there were widespread reports from many areas of South Africa of *capensis* infested colonies dying, with estimated losses of over 50 000 colonies (Allsopp and Crewe, 1993). Despite several attempts to eradicate infected colonies, the ‘*capensis* problem’ persists and now affects all provinces in South Africa and causes major annual losses (Allsopp, 1997).

Although the general picture of the usurpation of *scutellata* colonies by *capensis* workers has been previously described (Allsopp, 1992) few hard data exist and little is known about the actual dynamics of the problem (Allsopp, 1998; Moritz, 2002). Recent genetic data have revealed that *capensis* workers sampled from infested *scutellata* colonies from different areas from central/northern South Africa are genetically almost identical and have been termed a ‘pseudo-clone’, since they appear to be derived from the offspring of a single worker (Kryger, 2001).

The aim of this study is to provide a more detailed picture of the natural history and changing dynamics that occur during the usurpation of the *scutellata* colony by the pseudo-clone.

2. MATERIALS AND METHODS

The study was carried out in the Pretoria area of South Africa during November and December 2000. Eight *scutellata* colonies were moved to Pretoria from a region free of the *capensis* problem just prior to the study. A large number of *capensis* infested *scutellata* colonies which showed the typical symptoms of the *capensis* problem (scattered brood pattern, increasing number of black bees, loss of the *scutellata* queen, multiple eggs in cells, lack of pollen in the hive) were available locally. Identification of workers of the two subspecies was initially by colour. In this region colour is a reliable indicator of race, which was used in conjunction with ovariole counts, which differ greatly between *capensis* ($\bar{X} = 19$ ovarioles per ovary) and *scutellata* ($\bar{X} = 4$ ovarioles per ovary) workers (Crewe, 1984). In addition, five *capensis* workers were genetically analysed and found to be identical to those *capensis* workers analysed from across the northern regions of South Africa (Kryger, 2001). All dark bees encountered in the imported *scutellata* colonies were removed and their ovariole count determined. This confirmed that the number of black *scutellata* workers was well below 1% which is typical for bees in this region (Johannsmeier, 1983).

2.1. Fate of newly emerged pseudo-clones introduced into a queenright *A. m. scutellata* colony

Newly emerged adult pseudo-clones (n = 100) and *scutellata* workers (n = 70) were marked and then introduced into an unrelated queen-right *scutellata* colony (# 4). Unfortunately, at the time when the bees were introduced ten pseudo-clones (confirmed by high ovariole number) were already present. These were removed over the next two days. Thereafter no unmarked dark bees were seen during daily inspections carried out over the next nine days during which 30 marked bees of each race were removed for another study (see Martin et al., 2002). Forty days later the colony was killed, the sealed brood emerged in an incubator (see Sect. 2.2), and all remaining marked bees and any (unmarked) pseudo-clones removed and their ovariole number and activation determined.

2.2. Initial phase of usurpation

In addition to colony 4, five *scutellata* colonies (1, 2, 3, 6, 116) which had numerous worker sealed brood cells (≈ 2 000+), a large *scutellata* worker population (≈15 000+) and low (< 20%) proportion of *capensis* bees had their sealed brood removed and emerged in an incubator set at 33 °C. At the time of collection only colony 2 had a *scutellata* queen although the queens of colonies 3 and 4 were present three weeks earlier. Each day the number of newly emerged *scutellata* workers and pseudo-clones were recorded to quantify the number of *scutellata* queen and pseudo-clone laid eggs which were successfully reared.

2.3. Foraging

Two approaches were taken to determine the proportion of foraging pseudo-clone and *scutellata* workers. Firstly, two actively foraging colonies were manipulated to separate the foragers. To do this we turned the hive through 180° and placed it on the roof of another hive box containing frames of brood and honey whose entrance faced the same direction as the original hive. Foraging bees leaving the original (top) box returned to the new (lower) box.

After one hour both boxes were collected and the numbers of bees of each race in each box determined. Secondly, the entrances to eight other actively foraging colonies were sealed for 30 minutes and the number of pseudo-clones and *scutellata* returning foragers collected at the entrance were counted. The colonies were then killed to determine the proportions of adult workers belonging to the two races.

2.4. Whole colony study

120 *scutellata* colonies which had become naturally infested with pseudo-clones were placed in a remote location by a local beekeeper prior to being destroyed. From each colony we estimated the number of eggs, open and sealed brood, and the proportions of adult bees of each race. For large numbers (1000's) of cells containing brood, photographic standards of comb coverage (Martin, 1998) were used. For small numbers (100's) individual cells on each comb were counted. The number and condition of any recently-built queen cells and queens were also recorded. Only queen cells that were or had been sealed, as indicated by having a cocoon lining, were counted. Any sealed queen cells were collected and kept at 33 °C for several days to determine their viability. Based on these initial observations (Tab. I), 27 entire colonies which encompassed all the different phases of usurpation were collected by killing all the adults with chloroform. This allowed the precise number of *scutellata* and pseudo-clones and the percentage of those with fully activated ovaries to be determined. In addition, the apparent absence of adult queens could be confirmed. For these colonies the total number of adults was determined by weight and the proportion of adult pseudo-clones and *scutellata* workers was determined by counting the number of each race in a sub-sample of approximately 500 bees. To determine the number of bees with fully activated ovaries, approximately 100 bees of each race were dissected and classified into those with and without full sized eggs. Finally, all the adult bees were spread out on a large flat surface to search for any queen or queens.

2.5. Modelling the system

A honey bee simulation model (Martin, 2001) was used to investigate how different numbers of invading pseudo-clones and the length of any co-existence between egg-laying pseudo-clones and host queen affect the dynamics of usurpation. The general algorithms and construction methodology are given in Martin (2001), while the actual

Table I. Details of the 120 sampled *scutellata* colonies infested with the adult pseudo-clones.

Developmental stages present in each group of colonies	Number of colonies sampled	Number of colonies collected	% adult pseudo-clones range (mean + S.D.) of colonies sampled
Adults + eggs + open brood + sealed brood	24	18	1–50 ($\bar{X}$ = 19 ± 15)
Adults + eggs + sealed brood	18	6	22–75 ($\bar{X}$ = 50 ± 21)
Adults + eggs	5	2	80–92 ($\bar{X}$ = 89 ± 5)
Only adults	18	1	≈ 100
Dead and empty	55	0	
Totals	120	27	

parameters and assumptions used are given in Section 3.5.

3. RESULTS

3.1. Fate of newly emerged pseudo-clones introduced into a *scutellata* colony

Forty days after having been introduced, 35 of the 70 marked pseudo-clones remained. All had fully activated ovaries while only ten of the 67 unmarked pseudo-clones had fully activated ovaries. The unmarked pseudo-clones were the daughters of the originally invading pseudo-clones which were removed at the start of the experiment since the daughters of the introduced marked pseudo-clones were removed into an incubator before they emerged. In contrast, only ten of the 40 marked *scutellata* workers remained. None of these nor any of an additional 50 randomly chosen *scutellata* workers, showed any ovary development.

3.2. Initial phase of usurpation

In only two colonies (2, 4) did both *scutellata* and pseudo-clones emerge together over the study period of 10–15 days. During this period, the percentage of emerging pseudo-clones increased in both colonies from ≈10% to 100% (Fig. 1), indicating that both laying pseudo-clones and the *scutellata* queen can initially co-exist in the same colony. The first pseudo-clones emerged from the outside frames suggesting that pseudo-clone eggs are initially laid away from those of the queen's. Lundie (1954) also reported this.

From the pattern of emerging *scutellata* brood in colony 4, we estimated that the host queen died eight days prior to colony collection. Since the presence of ten pseudo-clones, one of which was seen emerging from a cell, had been observed 40 days earlier, the period of co-existence in this colony must have been at least 52 days i.e. pseudo-clones were emerging 32 days before colony collection and the pseudo-clone development time is 20 days. However, in colony 116 although all the emerging brood was still *scutellata*, there where ≈ 400 eggs in worker cells which must have been laid by the 75 pseudo-clones with fully activated ovaries (Tab. II). Since no pseudo-clones emerged during the study, egg-laying by the pseudo-clones must have only just started. Therefore, in this colony (which had lost its queen

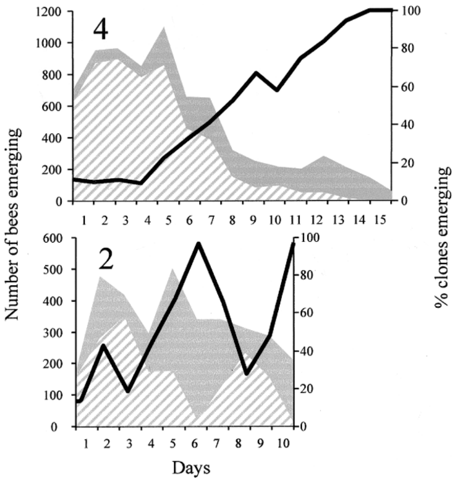

Figure 1. Change in numbers of emerging *A. m. scutellata* workers (hatched grey) and *A. m. capensis* pseudo-clones (grey) during the period when both the *scutellata* queen and pseudo-clones are both laying eggs in two study colonies (4 and 2). The percentage of emerging pseudo-clones is represented by the solid black line.

Table II. Details from the 27 collected colonies. Colonies are ordered according to the number of adult pseudo-clones present. '+' indicates present but number not estimated.

Hive no	# adult bees	# *scutellata* workers	# pseudo-clones	Eggs in worker cells	Open worker brood	Worker sealed brood	% pseudo-clones	% pseudo-clone with fully activated ovaries	# of pseudo-clone with fully activated ovaries
99	3808	3710	98	1500	100	1500	3	19	19
4	13831	13729	102	+	+	4076	1	44	45
116	14112	13986	127	400	220	4430	1	59	75
104	8751	8593	158	5490	190	250	2	16	25
40	2075	1881	194	200	180	1500	9	2	4
2	3856	3621	235	+	+	3795	6	<4	<9
103	5245	4668	576	6880	55	200	11	13	75
43	2953	2253	700	2250	130	1740	24	2	35
102	6689	5968	722	6680	260	2240	11	3	22
63	7578	6830	748	6500	900	2690	10	13	97
95	3140	2186	953	4520	0	170	30	3	29
67	5148	4066	1082	1150	330	4700	21	1	11
92	10614	9466	1147	+	+	+	11	6	69
96	4830	3625	1205	4230	150	400	25	4	48
93	5093	3657	1437	7600	280	1200	28	3	43
105	2328	595	1733	13230	0	1050	74	3	52
90	14985	12461	2523	7890	150	1500	17	<2	<50
34	12567	9747	2819	7740	0	3480	22	16	451
1	22691	19629	3062	+	0	1663	13	19	582
3	23128	19972	3156	+	+	9238	14	6	189
91	18450	15250	3200	1950	450	6700	17	6	192
5	3861	308	3554	200	0	0	92	2	71
35	8974	4753	4221	10740	0	300	47	21	886
94	25462	20746	4715	21130	350	2500	18	6	283
6	26157	21313	4844	19230	1500	13000	19	1	48
7	8000	424	7576	0	0	0	95	8	606
41	18172	9528	8645	11250	0	1750	48	20	1729

≈14 days earlier) there has probably been no, or a very short, period of co-existence between the *scutellata* queen and laying pseudo-clone/s.

In the remaining three colonies (1, 3, 6), all the emerging brood were pseudo-clones. Subsequent analysis (Tab. II) showed that all these colonies each contained in excess of 3000 pseudo-clones and the take-over of the colonies was well advanced when the sealed brood were removed for study.

3.3. Foraging study

The results from the two methods gave similar results despite the large differences in the number of foraging bees sampled (325–663 vs. 25–302). In nine of the ten colonies studied, the pseudo-clones constituted fewer of the foraging force (2.7% ± 1.7) than their representation in the colony (22% ± 10) which was consistent across a wide range of colony sizes (4830–25 462 adult bees) and colony composition (10–48% of adult bees were pseudo-clones). We do not know why one colony (34) had a much higher proportion (16%) of foraging pseudo-clones. However, this was still lower than the 22% of pseudo-clones present in this colony.

3.4. Whole colony study

3.4.1. Queen cell production

In the 120 colonies studied, 48 had recently constructed queen cells (133 in total), of which nine were sealed in five colonies, 64 appeared to have emerged (i.e. a hole in the tip) and 60 destroyed after sealing (i.e. a hole in the side of the cell). Of the nine sealed cells, six contained queens which had died at the larval-to-pupal moulting stage, one emerged with stunted wings and two emerged normally, one being *scutellata* (from a colony yet to produce pseudo-clones) and one pseudo-clone which was confirmed to be genetically identical to other pseudo-clone workers previously studied (Kryger, 2001). However, despite the presence of so many emerged queen cells no queens (live or dead) of either race were observed in any of the 120 colonies studied either during the initial checks or in any of the 27 colonies which were carefully studied. This shows that in some way successful requeening does not occur.

3.4.2. Development of pseudo-clone population within colonies after loss of the scutellata queen

The changing composition of a colony during usurpation is shown in Tables I and II. Initially, the colonies contain all developmental stages (eggs, open and sealed brood) and pseudo-clones eggs occur singly in worker cells (*scutellata* workers only lay in drone cells) although the pattern is not as regular as that of a queen. No sealed drone brood was found in any of the colonies studied. As the number of *scutellata* workers decline the number of larvae reared rapidly diminishes despite the increasing number of eggs, because insufficient food is being brought into the colony. This leads to irregular ‘pepper pot’ brood patterns and absence of pollen in the colony, and eventually to a period when there are no larvae in the colony. When this occurs the number of eggs in the colony greatly increases, with many eggs being laid in all cell types which, in extreme cases can result in up to 50 eggs per cell.

3.4.3. Number of pseudo-clone egg-layers

Dissection of adult bees from 27 colonies revealed that none of the 1350 *scutellata* bees had fully activated ovaries while a variable number of pseudo-clones did (Tab. II). The number of pseudo-clones with fully activated ovaries (11% ± 13, n = 27) in a colony appears to be negatively affected (i.e., through negative feedback) by the presence of other pseudo-clones with fully activated ovaries since the number with active ovaries remained below 100 even when the total number of pseudo-clones increased to 3000 (Fig. 2a). In addition, the presence of open brood may have a role in inhibiting ovarian development since only in its absence do large numbers of pseudo-clones with fully activated ovaries appear (Fig. 2b). However, even in the absence of open brood or when large populations (> 3000) of pseudo-clones exist, the number with fully activated ovaries rarely exceeded 20% of the population. However, this can still lead to very large numbers of eggs (20 000+) being present in a colony (Tab. II).

3.5. Modelling

The basic model structure of the usurpation process (Fig. 3) illustrates the main developmental pathways of the eggs laid by the *scutellata* queen and pseudo-clones and the major influences which affect survival from egg to adult. Based on this and other

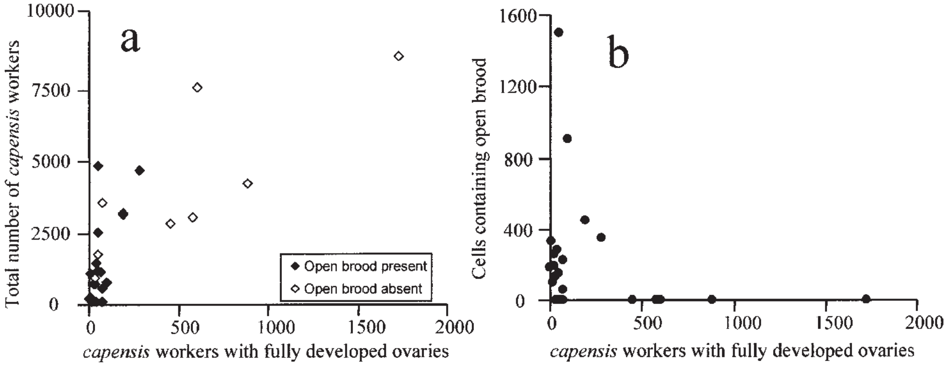

Figure 2. The relationship between the number of pseudo-clones (a), and cells containing open-brood (b) on the number of pseudo-clones with fully activated ovaries.

studies the following assumptions can be made:

(1) The average size of a *scutellata* colony was c. 27 500 adult workers. This can be generated in the model by a queen laying a maximum of 1250 eggs per day and a mean worker longevity of 25 days (see point 7). Smaller colony sizes (e.g. 20 000 workers) generate similar general predictions.

(2) The *scutellata* colony was invaded by 1, 10 or 100 pseudo-clones, which start

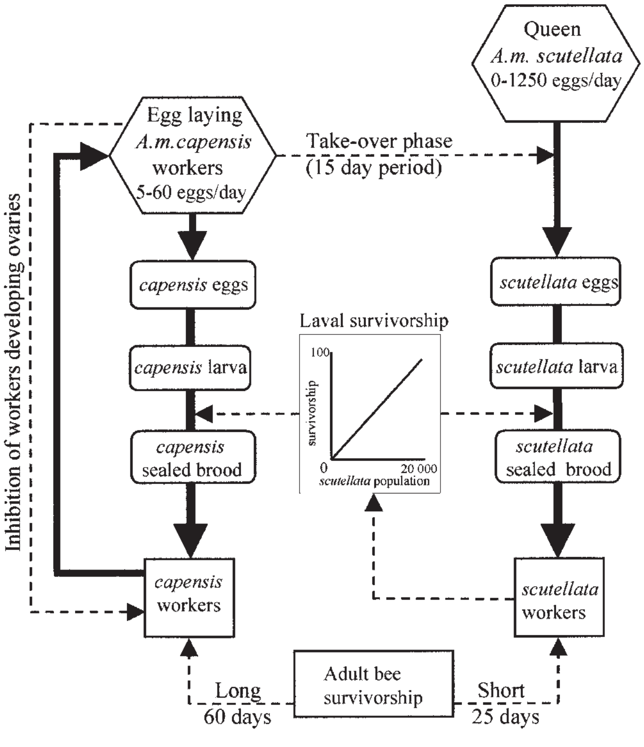

Figure 3. Basic model flow diagram for simulating the usurpation of an *A.m. scutellata* colony by *A. m. capensis* pseudo-clone workers. Solid lines indicate the flow of individuals between compartments and dotted lines indicate feedback influences.

egg-laying five days later (Martin et al., 2001). These eggs develop after 20 days into more adult pseudo-clones, which are also potential egg layers. Ovary development is unaffected by the presence of the *scutellata* queen but is affected by the presence of other pseudo-clones (see point 5).

(3) There is a 15 day period when the type of eggs laid and those subsequently reared changes from *scutellata* to pseudo-clone (see Fig. 1). This period either starts when the first pseudo-clone commences egg-laying (5 days after invasion), when the daughters of the invading pseudo-clone/s commences egg-laying (30 days after invasion) or 50 days after invasion.

(4) Each egg-laying pseudo-clone lays 20 eggs per day. However, this varied between five and 60 eggs per day when investigating population growth patterns.

(5) When open brood occurs, only the first 30 pseudo-clones become egg-layers. This varied between 5 to 60 when investigating population growth patterns. The number of egg layers (30) and daily egg-laying rates (20) used in all model runs represent intermediate values (Tab. III) over the wide range of actual values (Tab. II). When no open brood remains then 11% of the pseudo-clone population becomes egg layers.

(6) The survivorship of all open brood is linked to the number of *scutellata* adults, since they are the race which do almost all (97%) of the foraging (see Sect. 3.3). Therefore, as the *scutellata* worker population declines from 20 000 to 0 a corresponding linear decrease in the daily survivorship rate of the open brood from 92% to 0% is assumed. Both egg and sealed brood survival, although not directly affected by *scutellata* numbers, are indirectly affected by the open brood survival rates.

(7) The mean longevity of adult *scutellata* workers was assumed to be 25 days which is longer than reported for Africanised bees (12–18 days, Winston et al., 1981) but similar to that found in other races of *mellifera* during the summer. While the pseudo-clones lived much longer with mean longevity of 60 days, possibly due to their decreased work load, egg-laying workers are also known to have longer lifespans (Ruttner, 1988).

Using the above parameters and assumptions the following predictions can be made: once the invading pseudo-clone daughters start egg laying, the pseudo-clone population increases rapidly. The speed of increase is firstly dependant on the initial number of invading pseudo-clones (Fig. 4a), when low there is a 50 day lag

Table III. The number of days needed for a pseudo-clone population to reach 4000 individuals after an initial single pseudo-clone invades the host colony, as shown by simulation modelling.

		Daily egg laying rate of each pseudo-clone						
		5	10	20	30	40	50	60+
Maximum number of pseudo-clone egg layers in colony	5	*	*	102	81	71	66	62
	10	*	105	74	65	60	58	56
	20	108	76	62	57	55	54	53
	30	88	68	58	56	54	53	53
	40	80	64	57	55	53	53	53
	50	76	62	56	54	53	53	53
	60+	73	61	55	53	53	53	53

* Population unable to reach 4000.

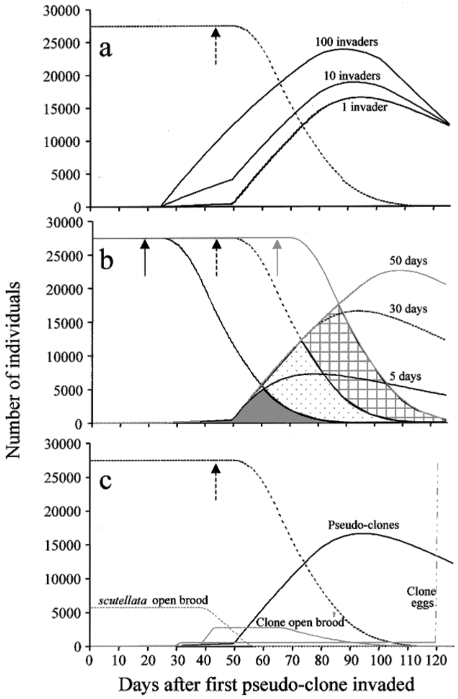

Figure 4. Model simulations for the usurpation of an *A. m. scutellata* colony under various conditions. Only the first 30 pseudo-clones become egg-layers and each lays 20 eggs per day. Arrows indicate the time of *scutellata* queen loss. (a) Effect of different numbers of invading pseudo-clones on the development of the population. (b) Subsequent effect on the pseudo-clone and *scutellata* populations caused by the decline in egg-laying ability of the *scutellata* queen arising from the presence of the pseudo-clones. Three different scenarios were modelled where the queens' egg-laying is affected as soon as the invading pseudo-clones starts to lay eggs (solid lines), by the egg-laying of the invading pseudo-clones daughters (dashed lines) or 50 days (grey lines) after the pseudo-clones invaded. The shaded areas indicate the differences in the relative periods when *scutellata* workers are present to rear pseudo-clone brood. (c) The usurpation of a *scutellata* colony invaded by a single pseudo-clone does not affect the *scutellata* queen until her daughters start to lay eggs as shown.

phase which is the time taken for the 3rd generation (i.e. the invaders granddaughters) to emerge. When large numbers invade, the lag phase is not present (Fig. 4a). The speed of population growth is also dependent on the egg laying rate of each pseudo-clone and number of egg laying pseudo-clones. Table III indicates the relationship between these two factors and their effects on population growth. This suggests that 53 to 108 days is required for a pseudo-clone population to increase to around 4000 adults. The model shows the rapid change over from *scutellata* to pseudo-clones once the *scutellata* queen's egg-laying is affected. The longer the period of co-existence between egg-laying pseudo-clones and the egg-laying *scutellata* queen the more pseudo-clones can be reared (Fig. 4b). This arises because, once queen egg-laying ceases, the number of *scutellata* workers declines while the number of pseudo-clone adults and their brood continues to increase. These changes during the entire usurpation process are shown in Figure 4c. Note the very rapid increase in pseudo-clone eggs once the open brood have disappeared despite only 11% of the pseudo-clone population laying eggs.

4. DISCUSSION

The sequence of events which leads to the usurpation of a *scutellata* colony by the pseudo-clone, with the important exception that pseudo-clone queens are not reared, are similar to those reported for previous usurpation events concerning *capensis* (Johannsmeier, 1983; Allsopp, 1992; Neumann and Hepburn, 2002) which are probably non-clonal workers. The following is a detailed account of the invasion and usurpation of *scutellata* colonies by the pseudo-clone and its relationship to *capensis* workers.

4.1. Invasion

Johannsmeier (1983) reported that *capensis* invasions mostly took place when colonies swarmed, superseded, were being manipulated, or had a large entrance. We observed that when opening an infested colony the pseudo-clones, unlike the *scutellata* bees, appeared reluctant to fly far and were often found crawling around on roofs of nearby beehives and on the beekeeper. This is probably a major route of transfer since few (< 3%) pseudo-clones forage. In addition, during transportation on trucks between pollination sites colonies are often packed close together with their entrances opened. This will assist the local dispersal of the pseudo-clones (Anton Schehle, personal communication).

Although dispersal within an apiary appears to be irregular but effective, the failure of the *capensis* bees to become widely established during previous limited introductions in 1927 and 1977 suggest that *capensis* workers may be unable to disperse long distances without human assistance (Johannsmeier, 1983). However, the movement of 400+ *capensis* colonies in 1990 created a problem which was always going to be very difficult to contain, even if dispersal was via local drifting, due to the human assisted dispersal of infested colonies during normal beekeeping activities. Neumann et al. (2001) found that *capensis* workers disperse (i.e. drift to colonies far from their maternal hive), significantly more than *scutellata* workers or hybrids and suggested that this represents a host finding mechanism. However Beekman et al. (2002) found that the pseudo-clones are recognised by *scutellata* guard bees as non-nest mates and prevented from entering the hive if they are challenged, indicating that the pseudo-clones have not developed any special mechanisms to circumvent the *scutellata* guards. So it remains unclear to what extent the pseudo-clones or *capensis* workers are adapted to seek out and invade new hosts.

4.2. Ovarian development phase

Ovarian development of workers is largely prevented in queen-right colonies of their own race by queen (Velthuis, 1970a; Robinson, 1999; Wossler, 2002) and brood (Perepelova, 1928; Jay, 1972; Wossler, 2002) pheromones or any queen cells (Hepburn et al., 1988). So 'same race' workers with fully activated ovaries, in *capensis* (Onions, 1914; Anderson, 1963; Hepburn et al., 1991; Hepburn, 1994), *scutellata* (Hepburn and Allsopp, 1994) and European *mellifera* colonies (Ratnieks, 1993) although present are always few (<< 1%) in number. Therefore, no ovary development was expected, or found, when *scutellata* workers were introduced into a queen-right *scutellata* colony. However, despite the presence of a *scutellata* queen and her brood, the introduced pseudo-clones all had fully activated ovaries after only six days (Martin et al., 2002).

In naturally usurped colonies only a small proportion of the pseudo-clone population (11% ± 13, n = 27 colonies) had fully activated ovaries and this never exceeded 21%. These figures are similar to *capensis* workers in a queenless *capensis* colony (5%, Hepburn et al., 1991; 11%, Hepburn, 1994; 12%, Hepburn and Allsopp, 1994) but lower than a *scutellata* colony invaded by *capensis* workers (21%, Hepburn and Allsopp, 1994) or *mellifera* workers in queenless *mellifera* colonies (24%, Miller and Ratnieks, 2001). It appears that pseudo-clones with fully activated ovaries are inhibiting the ovary development of other pseudo-clones (Fig. 2a), similar to what occurs in *capensis* workers (Anderson, 1963; Ruttner, 1977; Crewe and Velthuis, 1980), *mellifera* workers under laboratory conditions (Velthuis, 1970b) and bumblebee workers (*Bombus terrestris*) (Bloch and Hefetz, 1999). In addition, the presence or absence of open brood appears to play a role (Fig. 2b) although more data are required to ascertain its full influence. In addition, the frequency of pseudo-clones with fully activated ovaries did not increase greatly with longer periods of queenlessness which is consistent with studies on *capensis* (Hepburn et al., 1991) and *mellifera* (Ruttner and Hesse, 1979), which further supports the idea of mutual inhibition.

Mutual inhibition appears to be lacking when pseudo-clones are artificially introduced into a *scutellata* colony at the same time, since a large proportion, if not all, of them develop fully activated ovaries (Martin et al., 2002 and this study). This phenomena was clearly demonstrated by Wossler who introduced ≈700 marked *capensis* workers simultaneously into a *scutellata* colony. Eight days later 97% of the *capensis* workers dissected (n = 66) had fully activated ovaries while >1% of *scutellata* workers (n = 64) showed any ovarian development. A total of ≈18 900 eggs were present in this colony. This lack of inhibition, may it be pheromonal or behavioural, is initially absent since all the introduced bees are of the same age and have equal opportunity of developing reproductively. This situation is unlikely to occur in the field unless the pseudo-clones invade host colonies en-mass.

4.3. Loss of queen

We found both sudden queen loss and gradual change over from emerging *scutellata* to pseudo-clone bees (Fig. 1). The period of co-existence between egg-laying pseudo-clones and the queen may be as long as 50 days or may not occur at all if pseudo-clones start egg-laying in a queenless colony. However, a period of co-existence when both queen and pseudo-clone/s are laying concurrently, (Johannsmeier, 1983 and Fig. 1) appears to occur, although the queen disappears soon after she ceases to lay eggs. It remains unclear whether the *scutellata* queen is out-competed physically (killed) or chemically since *capensis* workers are capable of producing queen-like mandibular signals which may effect colony organisation or allow them to engage in chemical warfare with the queen (Moritz et al., 2000). It has already been shown that *capensis* larvae are preferentially reared by *mellifera* workers (Beekman et al., 2000; Calis et al., 2002) and it is likely that the pseudo-clones are also being preferentially treated by *scutellata* workers.

4.4. Re-queening of the colony

Despite mature queen cells being found in over 40% of the colonies studied, no queens of either race were found in any colony. It is not known at what time and by which race the queen cells were constructed. Normally, the production of a new queen starts within 10 hours after queen loss (Seeley, 1979) but in *capensis* queen rearing is often abandoned with the appearance of laying workers (Hepburn, 1994). However, we observed that laying pseudo-clones still posses a strong urge to lay eggs in queen cells with 50–100 eggs frequently laid in a single queen cell, even at a time when worker cells contained single eggs. The same thing was also recorded by Johannsmeier (1983) and Onions (1914). In dequeened *capensis* colonies the raising of and subsequent destruction of queens has been recorded (Onions, 1914; Hepburn, 1994) while *capensis* workers that invaded *scutellata* colonies usually made no attempt to rear new queens (Johannsmeier, 1983).

Of the nine sealed queen cells collected only one produced a viable pseudo-clone queen. However, the newly emerged queen must avoid being killed by the workers at emergence, which often occurs in *capensis* colonies (Onions, 1914). She has then to mate, and assert her dominance over the colony before the colony dwindles, which is highly unlikely. Even queenless *capensis* colonies seldom (0–20%) succeed in returning to a normal queen-right condition via worker derived queens (Onions, 1914; Anderson, 1963; Hepburn et al., 1988).

4.5. Pseudo-clone population expansion and collapse

There are several factors which affect the size of the pseudo-clone population a host colony can sustain. Field data show that 3 000 to 10 000 pseudo-clones can be reared in a *scutellata* colony (Tab. II) before the colony resources and number of host *scutellata* workers dwindle out (Fig. 4). Pseudo-clones are long-lived and capable of laying eggs for at least 40 days, which is also found in *capensis* workers kept in cages (Ruttner, 1988) with egg production lasting 4–56 days. It is only when colony resources dry up that the ovaries of the pseudo-clones regress. In the final stages very few egg-laying pseudo-clones are present. The pseudo-clones then appear to abscond or settle on nearby vegetation or hives where often they die in large numbers. This situation is very similar to that observed for queenless *capensis* colonies where the colonies either dwindle to the last bee or the last remaining bees desert the hive and form a little cluster on some hedge or bush where they perish (Onions, 1914). Lundie, (1954) also reports finding 'little piles of dead or dying black

Table IV. Comparison of traits displayed by a queen honey bee, normal *capensis* workers, pseudo-clones *capensis* workers and workers of other races. The f sign indicates that the information given from the *capensis* worker is relevant to the pseudo-clone.

	Queen	*Capensis* worker and pseudo-clone (ϕ)	*mellifera* worker
Ovariole number [1]	360	10–20 (ϕ)	3–5
Spermatheca size [2,3,7]	1.4 mm	0.3–0.6 mm (1/2 to 1/15 size of queen)	Small (1/15 size of queen)
Level of ovarian development in queen-right colony [4,7]	-	Slight	None
Latency time before capable of egg-laying [4]	-	4–10 days (ϕ)	20–30 days
Volume of mandibular gland [1]	Large	0.544 mm^3	0.275 mm^3
Age of worker larvae from which queens can be reared [5]		Old	Young
Amount of 9-ODA queen substance produced [6]	Large	1/2 of queen	Little-none
Occurrence of false queens [8]	-	Common	Rare
Cell type for egg-laying in queenless state *[2,9]		Worker (ϕ)	Drone
Comb type built in queenless state *[2]	-	Worker	Drone
Type of offspring produced *[2]		Workers (ϕ)	Drones

[1] Ruttner, 1988; [2] Onions, 1914; [3] Ruttner, 1977; [4] Hepburn and Radloff, 1988; [5] Pullinger, 1922; [6] Crewe 1988; [7] Anderson, 1963; [8] Allsopp, 1992; [9] this study.

*Linked with thelytokus reproduction.

bees' in the apiary. The longest period between the *capensis* bees being noticed in a *scutellata* colony and its death was four months (D. Swart and P. Kryger, unpublished data), which is similar to that predicted by the model simulations (8–15 weeks). Queenless *capensis* colonies appear to be able to survive longer (4 months, Anderson, 1963) than pseudo-clone colonies, possibly because the majority of non-clonal *capensis* workers are predisposed to foraging as well as normal hive activities which is not the case with the pseudo-clones.

5. CONCLUSION

We propose that *capensis* workers and pseudo-clones sit at the extreme end of the worker-queen spectrum being more queen-like than workers of any other race of *A. mellifera*. This is supported by the findings of many studies which are summarised in Table IV. This may help explain both their ability to develop their ovaries rapidly and lay eggs that are much more acceptable (queen-like) than worker-laid eggs of other honey bee races (Moritz, 1999; Martin et al., 2002). This coupled with their unique thelytokous trait allows them to usurp colonies of other honey bee races. Further research is needed to establish whether the pseudo-clone is a true social parasite or just a freak result of modern beekeeping practices which has circumvented natural barriers such as the *capensis-scutallata* hybrid zone.

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Résumé – Usurpation des colonies africaines d'*Apis mellifera scutellata* par les ouvrières parasites d'*Apis mellifera capensis*. La capacité des ouvrières non fécondées à produire une descendance femelle par parthénogenèse thélytoque est connue depuis longtemps chez les abeilles du Cap, *Apis mellifera capensis* Escholtz, race qui est confinée à l'extrémité méridionale de l'Afrique. En 1990 plus de 400 colonies *capensis* furent apportées dans des régions occupées par l'abeille africaine arrhénotoque *Apis mellifera scutellata* Lepeletier. Ceci a provoqué la mort de plus de 100 000 ruches exploitées, puisque les ouvrières *capensis* sont capables d'usurper avec succès les colonies *scutellata* provoquant ainsi le dépérissement et la mort de la colonie. Des études récentes ont montré que ces ouvrières *capensis* étaient presque identiques génétiquement et formaient un « pseudo-clone ». Afin de mieux comprendre ce processus nous avons suivi 120 colonies *scutellata* (Tab. I) usurpées par le pseudo-clone, dont 27 d'entre elles en détail (Tab. II). Dans un cas la reine *scutellata* résidente a coexisté pendant plus de 50 jours avec des pseudo-clones qui pondaient, mais a brusquement disparu après seulement 1–15 jours de coexistence dans d'autres cas (Fig. 1). Les pseudo-clones ne représentaient en moyenne que 22 ± 10 % de la population d'abeilles adultes d'une colonie, mais n'étaient présents dans la population de butineuses qu'à raison de 2,7 ± 1,7 %. Cela aboutissait à une quantité de plus en plus grande de couvain de pseudo-clone nourri par un nombre de plus en plus restreint d'ouvrières *scutellata*. Malgré la présence de cellules de reines ayant éclos, aucune nouvelle reine, vivante ou morte, d'aucune race n'a été observée dans aucune colonie étudiée. Il semble improbable que des reines, occasionnellement élevées à partir d'œufs pondus par un pseudo-clone, puissent reprendre le contrôle d'une colonie usurpée. Lorsque des abeilles fraîchement écloses de pseudo-clones et des ouvrières *capensis* normales ont été introduites artificiellement dans une colonie *scutellata* ayant une reine, elles ont toutes présenté des ovaires pleinement activés. Elles avaient toutes le même âge et donc la même chance de devenir reproductrices. Néanmoins dans les colonies de *scutellata* envahies, la proportion moyenne de pseudo-clones ayant des ovaires pleinement activés n'était que de 11 ± 13 % (n = 27) ; cela laisse à penser que le développement ovarien est inhibé chez la plupart des pseudo-clones par la présence de couvain non operculé et par d'autres pseudo-clones à ovaire pleinement activés (Fig. 2). La modélisation appliquée aux données obtenues par cette étude (Fig. 3) a montré que, dans une large gamme de conditions initiales, les abeilles *scutellata* étaient rapidement (56–105 jours) remplacées par des pseudo-clones et que la mort s'ensuivait (Tab. III et Fig. 4). Le fait que les ouvrières *capensis* et les ouvrières des pseudo-clones soient proches des reines et qu'elles possèdent ce caractère unique de parthénogenèse thélytoque leur permet d'usurper les colonies d'autres races d'abeilles.

Apis mellifera capensis **/ pseudo-clone / usurpation /** ***Apis mellifera scutellata*** **/reproduction / Afrique du Sud**

Zusammenfassung – Eroberung afrikanischer *Apis mellifera scutellata* Völker durch parasitische *Apis mellifera capensis* Arbeiterinnen. Die Fähigkeit von unbefruchteten Arbeiterinnen der Kaphonigbiene durch Thelytokie weibliche Nachkommen erzeugen zu können ist seit langer Zeit bekannt. Diese Bienen ist natürlicherweise auf die südliche Spitze von Afrika beschränkt, allerdings wurden 1990 mehr als 400 *A. m. capensis* Völker in das Verbreitungsgebiet der arrhenotoken afrikanischen Biene *A. m. scutellata* verbracht. Da die Kaparbeiterinnen in der Lage waren, erfolgreich die Völker von *A. m. scutellata* zu besetzen und hierdurch Schwund und Tod der Kolonien herbeiführten, führte dies zum Verlust von über 100 000 bewirtschafteten Bienenvölkern. Neue Studien haben gezeigt, dass diese Kaparbeiterinnen genetisch nahezu gleich sind und eine Art ‚Pseudoklon' bilden. Um ein besseres Verständnis des Prozesses zu erhalten, untersuchten wir 120 von dem Pseudoklon befallene Völker von *A. m. scutellata* (Tab. I), davon 27 detailliert (Tab. II). Die ursprüngliche Königin von *A. m. scutellata* wurde in einem Falle über 50 Tage gemeinsam mit eierlegenden Pseudoklons in dem Bienenvolk beobachtet, in anderen Fällen verschwand sie plötzlich innerhalb von 1–15 Tagen des Zusammenlebens (Abb. 1). Obwohl die Pseudoklons im Mittel nur 22 ± 10 % der adulten Bienenpopulation in den Völkern ausmachten, gehörten nur 2,7 ± 1,7 % der Sammlerinnen den Pseudoklons an. Hierdurch wird ein stets zunehmender Anteil von Brut des Pseudoklons von einem stets abnehmenden Anteil von *A. m. scutellata* Arbeiterinnen gefüttert. Obwohl geschlüpfte Königinnenzellen gefunden wurden, beobachteten wir in keinem der untersuchten Völker neue Königinnen, weder lebend noch tot. Es ist unwahrscheinlich, dass gelegentlich aus Eiern der Pseudoklons aufgezogene Königinnnen jemals die Kontrolle über befallene Völker übernehmen können. Nach Einbringung von frischgeschlüpften Arbeiterinnen der Pseudoklone und normaler Kaparbeiterinnen in weiselrichtige Völker von *A m. scutellata* wurden bei allen aktivierte Ovarien gefunden. Diese hatten alle das gleiche Alter und damit die gleiche Chance reproduktiv zu werden. In natürlich befallenen Völkern von *A. m. scutellata* lag der mittlere Anteil der Psedoklonarbeiterinnen mit voll aktivierten Ovarien bei nur 11 ± 13 % (n = 27). Dies legt nahe, dass die Ovarienentwicklung der meisten Pseudoklonarbeiterinnen durch die Anwesenheit offener Brut und anderer Pseudoklonarbeiterinnen mit bereits entwickelten Ovarien gehemmt wird (Abb. 2). Die aus dieser Studie erhaltenen Zahlen wurden in ein Rechenmodell eingegeben (Abb. 3), das über einen weiten Bereich von Anfangsbedingungen den raschen Wechsel von *A. m. scutellata* Bienen zu Pseudoklonbienen (56–105 Tage) und den darauffolgenden Tod der Völker zeigt. Die pseudoköniginnenartige Natur der Arbeiterinnen von *A. m. capensis* und der Pseudoklon-Arbeiterinnen (Tab. IV), zusammen mit der einzigartigen Fähigkeit zur Thelytokie ermöglicht es ihnen daher, die Völker anderer Rassen der Honigbienen zu erobern.

***Apis mellifera capensis* / Pseudoklone / Eroberung / Reproduktion / *Apis mellifera scutellata* / Honigbienen / Südafrika**

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