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Original article

Infestation levels of *Apis mellifera scutellata* swarms by socially parasitic Cape honeybee workers (*Apis mellifera capensis*)*

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Abstract – A single clonal lineage of socially parasitic Cape honeybee workers, *Apis mellifera capensis*, has caused dramatic losses in managed populations of *A. m. scutellata*, raising concerns that wild populations might also be affected. We surveyed *A. m. scutellata* swarms at 27 localities in beekeeping areas (N = 87) and in nature reserves (N = 79). While eleven swarms were infested in beekeeping areas, we found no infestations in nature reserves. Eight swarms had no symptoms except workers with black tergites. However, DNA data revealed that these workers are not parasitic, showing that diagnoses based on tergite colour alone yield false positive results. Nevertheless, it is practical because we had no false negative diagnoses either. Nature reserves may be important refuges to protect wild *A. m. scutellata* populations against imported honeybees.

***Apis mellifera scutellata* / *Apis mellifera capensis* / honeybee / social parasitism / wild population**

1. INTRODUCTION

Beekeeping is a beneficial activity for the beekeepers who profit from the honeybee products, for the conservation of honeybees, *Apis mellifera* L., and perhaps most important for the pollination services to economically important plants and natural floras. However, with increasing exchange of honeybee colonies within and among continents there is also a negative aspect of beekeeping. The main risk is the spread of novel diseases and pests (e.g. Neumann and Elzen, 2004, Moritz et al., 2005), particularly into areas with indigenous honeybee populations. Indeed, honeybee diseases and pests imported by man have repeatedly caused substantial damage to local wild and feral populations (Rennie et al., 1921; Loper, 1995; Watanabe, 1994; Kraus and Page, 1995). Because host and pathogen have not co-evolved (Thompson, 1994), defensive mechanisms are thought to be less efficient or even lacking in the new environment (Neumann and Elzen, 2004).

The "dwindling colony syndrome" (Allsopp, 1993; Hepburn and Allsopp, 1994) caused by socially parasitic workers of the Cape honeybee, *Apis mellifera capensis* Escholtz, is a recent example of the spread of a pest due to anthropogenic movement of colonies (Moritz et al., 2005). In 1990, South African beekeepers moved large numbers of *A. m. capensis* colonies from the Cape region into the endemic range of

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the neighbouring subspecies *Apis mellifera scutellata* Lepeletier (Allsopp and Crewe, 1993; Neumann and Moritz, 2002). Since then, socially parasitic workers have caused considerable harm to *A. m. scutellata* based apiculture (Allsopp and Crewe, 1993; Hepburn and Allsopp, 1994; Swart et al., 2001; Swart, 2003). Commercial beekeepers with large numbers of colonies have been severely affected and have in some cases reported the complete loss of all managed colonies (Greeff, 1997). This has occurred repeatedly in every season for the last decade (A. Schehle, personal communication). The biological mechanisms underlying this form of social parasitism is believed to be well understood (Neumann and Hepburn, 2002; Neumann and Moritz, 2002) and is mediated through the queen-like pheromone secretions of the Cape honeybee workers (Ruttner et al., 1976; Hemmling et al., 1979; Wossler and Crewe, 1999a, b; Martin and Jones, 2004; Simon et al., 2005). Resistance mechanisms against socially parasitic workers seem to be less efficient in *A. m. scutellata* than in *A. m. capensis* (Allsopp and Crewe, 1993; Martin et al., 2002; Neumann et al., 2003, Härtel et al., 2006). Indeed, infested *A. m. scutellata* colonies die on average within nine weeks after infestation (Neumann and Hepburn, 2002). Recent genetic studies have shown that a single clonal lineage, derived from one individual worker by uninterrupted generations of thelytokous parthenogenesis caused the mass extinctions of managed *A. m. scutellata* colonies (Baudry et al., 2004). This clonal lineage covers vast regions in northern South Africa (Baudry et al., 2004).

The dramatic impact of socially parasitic Cape honeybee workers on apiculture raised the question whether natural populations in nature reserves were also affected. Since beekeeping is prohibited in nature reserves, swarms caught in these areas represent a sample of the endemic wild *A. m. scutellata* population. Epidemic extinctions of colonies in nature reserves would be particularly devastating, because honeybees are prominent pollinators of the flora in these protected areas (Barth, 1985; Allen-Wardell et al., 1998; Braack and Kryger, 2003). Moreover, ongoing activities to establish sustainable beekeeping for rural development (Bee Foundation, personal communication A. Schehle) are dependent on the availability of non-infested *A. m. scutellata* swarms. Even a low infestation level of trapped swarms would not only raise difficulties for developing beekeeping in rural communities, but also for large scale commercial beekeeping, because of the epidemic potential of socially parasitic workers in apiaries.

A recent model (Moritz, 2002) of the population dynamics of the host-parasite interaction predicted that the impact of the socially parasitic workers in wild *A. m. scutellata* populations would be reduced compared to managed populations in apiaries. However, the infestation levels of *A. m. scutellata* swarms by socially parasitic Cape honeybee workers have never been rigorously compared in wild and managed populations. We here present a comparison of infestation levels in wild swarms caught in nature reserves and in regions with beekeeping activities to assess the impact of beekeeping on the prevalence of the dwindling colony syndrome.

2. MATERIALS AND METHODS

2.1. Evaluation of *A. m. scutellata* swarms

A. m. scutellata swarms were caught in standard trap boxes (Swart et al., 2001) at 27 localities (Fig. 1; Tab. I) in beekeeping areas (N = 87) and in nature reserves (N = 79) representing samples of different *A. m. scutellata* populations with respect to apicultural impact. Our survey of the trapped swarms was the first beekeeping manipulation after settling. The screening of the trapped swarms was performed using the following criteria for *A. m. capensis* worker social parasitism, which inevitably occurs in all *A. m. scutellata* host colonies in the course of infestation (reviewed by Allsopp, 1993; Neumann and Hepburn, 2002; Neumann and Moritz, 2002):

(1) Queen status: The host queen is lost in the course of infestation (Neumann and Hepburn, 2002; Moritz et al., 2003).

(2) Tergite colour of workers: The tergites of *A. m. capensis* workers are black and those of *A. m. scutellata* host workers mostly yellow (Hepburn and Crewe, 1991; Radloff et al., 2002).

(3) Multiple eggs in worker cells: At later stages of infestations multiple eggs per worker cell are present (Neumann and Hepburn, 2002) with a bias towards the periphery of the frame (Allsopp, 1993).

(4) Brood pattern: In contrast to queens, parasitic workers produce a scattered brood pattern with

Table I. Sampling localities and infestation levels of trapped *A. m. scutellata* swarms with socially parasitic Cape honeybee workers in nature reserves and in areas with beekeeping activity are shown (N = number of swarms investigated; infestation levels: 0 = not infested, 1 = potentially infested, 2 = infested).

Location	Infestation levels		
	0	1	2
Nature reserves			
1. Tswalu	2		
2. Suikerbosrand	12		
3. Warmbaths	2		
4. Ezemvelo	8		
5. Olifants, Kruger Park	4		
6. Satara, Kruger Park	2		
7. Skukuza, Kruger Park	19		
8. Nwanetsi, Kruger Park	5		
9. Pretoriuskop, Kruger Park	7		
10. Malelane, Kruger Park	2		
11. Pafuri, Kruger Park	3		
12. Nyandu, Kruger Park	2		
13. Lower Sabie, Kruger Park	7		
14. Letaba, Kruger Park	2		
15. Punda Maria, Kruger Park	2		
sum	79	0	0
Beekeeping areas			
16. Douglas	6		
17. Graskop	9	1	2
18. Hartebeespoort	1		
19. Jacobsdaal	1		
20. Johannesburg	5		
21. Delmas	9		
22. Pretoria I	11		
23. Pretoria II	5		1
24. Settlers I	15	5	
25. Settlers II	4		7
26. Standerton I	1	1	1
27. Standerton II	1	1	0
sum	68	8	11

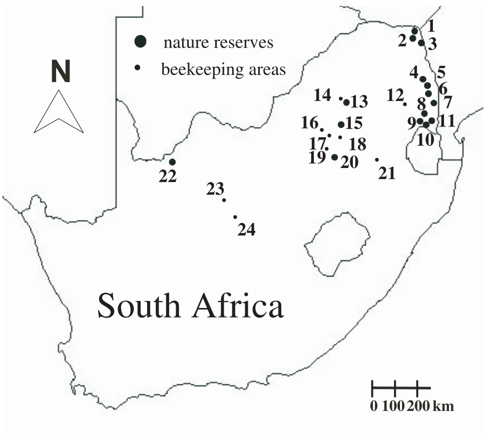

Figure 1. Map of South Africa, showing the sampling sites of *A. m. scutellata* swarms in nature reserves and beekeeping areas. (1 = Pafuri, 2 = Punda Maria, 3 = Nyandu, 4 = Letaba, 5 = Olifants, 6 = Satara, 7 = Nwanetsi, 8 = Skukuza, 9 = Pretoriuskop, 10 = Malelane, 11 = Lower Sabie, 12 = Graskop, 13 = Warmbaths, 14 = Settlers, 15 = Ezemvelo, 16 = Hartebeespoort, 17 = Pretoria, 18 = Delmas, 19 = Johannesburg, 20 = Suikerbosrand, 21 = Standerton, 22 = Tswalu, 23 = Douglas, 24 = Jacobsdaal).

different stages of development in neighbouring cells (Neumann and Hepburn, 2002). Moreover, preferential feeding of parasitic larvae by the host workers results in larger offspring and raised worker cell cappings (Beekman et al., 2000; Calis et al., 2002; Allsopp et al., 2003).

(5) Freshly emerged black workers after queen loss: While laying workers of *A. m. scutellata* produce drones (Hepburn and Radloff, 1998), the offspring of the socially parasitic workers are female and show a black tergite colour (Neumann and Hepburn, 2002; Baudry et al., 2004).

The expression of these symptoms was classified into three infestation levels (Tab. I):

0 = not infested: no criteria of infestation.

1 = potentially infested: only workers with black tergites were found in the colony, but no further criteria. Tergite colour has been used by beekeepers as a symptom of *A. m. capensis* social parasitism, even though the rare occurrence of dark *A. m. scutellata* workers (Johannsmeier, 1983; Martin et al., 2002) casts doubt on its reliability. Therefore, workers with yellow and black tergites were sampled from these potentially infested colonies and genotyped to verify the association of the black tergite workers with the ubiquitous clonal lineage (Baudry et al., 2004). This enables us to quantify unambiguously the frequency of infested *A. m. scutellata* swarms.

2 = infested: all of the above mentioned criteria are present.

Table II. DNA microsatellite analysis of potentially infested *A. m. scutellata* swarms. The inferred multi-locus genotypes of the resident *A. m. scutellata* queens and of non-native workers with black tergites are compared with that of the ubiquitous parasitic clonal lineage (Baudry et al., 2004; allele size in bp; Clone = ubiquitous parasitic *A. m. capensis* clone, Fw = foreign worker genotype; nd = not determined).

		Locus	A113	A14	A28	A35	A88	B124
		Clone	208/220	223/253	132/132	94/94	151/151	220/234
Location	Colony							
Settlers I	1	Queen	216/222	219/221	124/137	94/102	148/151	214/218
	1	Fw 1	206/218	219/225	127/132	94/94	nd/nd	218/220
	2	Queen	200/212	224/224	124/130	94/96	140/146	222/238
	2	Fw 1	nd/nd	217/223	128/132	93/98	144/144	216/246
	3	Queen	nd/nd	223/228	132/137	94/104	139/143	218/222
	4	Queen	nd/nd	nd/nd	127/137	94/94	139/148	218/220
	5	Queen	nd/nd	217/227	132/132	92/98	139/148	222/222
Standerton I	1	Queen	210/216	217/218	124/132	98/98	139/141	216/220
	1	Fw 1	206/222	209/211	138/138	87/92	137/152	218/220
	1	Fw 2	nd/nd	nd/nd	127/132	97/97	139/141	nd/nd
Standerton II	1	Queen	206/210	nd/nd	124/137	98/98	150/150	222/232
Graskop	1	Queen	220/220	215/227	132/135	93/94	131/148	218/222
	1	Fw 1	212/220	215/223	120/127	95/103	131/146	218/222

2.2. Microsatellite genotyping

DNA was extracted (Walsh et al., 1991) from the worker samples in the potentially infested colonies and genotyped at six polymorphic microsatellite loci (A14, A28, A35, A88, A113, B124; Solignac et al., 2003). Fragment sizes were scored using an ABI 310 automatic sequencer with the chemicals and protocols of the supplier (Applied Biosystems).

Queen and sire genotypes were inferred from worker genotypes using the Genotyper 2.0 software and Mendelian rules. Individuals lacking putative alleles of the resident queens, at least at one of the tested loci, were considered as foreign (Neumann et al., 1999; Moritz and Neumann, 2004). All genotypes were compared with the genotype of the ubiquitous parasitic clonal lineage that infests large areas in northern South Africa (Baudry et al., 2004; Tab. II). Based on the population allele frequencies, the probability of a random combination of the clone alleles at all tested loci for worker is $< 1.95 \times 10^{-8}$.

3. RESULTS

3.1. Infestation of *A. m. scutellata* swarms

A high proportion of *A. m. scutellata* swarms (N = 147; 88.6%) showed no signs of infestation (level 0; Tab. I). We did not find a single infested colony in nature reserves. However, in areas with beekeeping activity, 12.6% of the trapped swarms (11 out of 87) were infested (level 2 in Graskop, Pretoria, Settlers and Standerton; Tab. I), showing a significantly higher infestation level than in nature reserves (two tailed Fisher's exact test, $P < 0.001$; Tab. I). Eight swarms (9.2%) caught in areas with beekeeping activity were potentially infested and black tergite workers were present, but no further infestation criteria (see above) were found. The proportion of swarms with black tergite workers was significantly higher in beekeeping areas compared to nature reserves, where we exclusively observed yellow tergite workers (two tailed Fisher's exact test, $P < 0.01$).

3.2. Origin of black tergite workers from potentially infested swarms

A total of 72 workers were genotyped (37 with yellow tergites and 35 with black tergites) from the eight potentially infested colonies. Thirty workers with black tergites (86%) were unambiguously the offspring of the resident queens because they shared the putative queen genotype at all loci. The remaining five workers were identified as non-nestmate individuals. However, none of the genotypes of black tergite individuals matched that of the ubiquitous clonal lineage (Baudry et al., 2004; Tab. II). Furthermore, the black tergite workers found in the same colony or at the same location do not show the genetic signature of a clone, which is always the case for *A. m. capensis* laying worker offspring (Moritz and Haberl, 1994; Baudry et al., 2004).

4. DISCUSSION

Our data give empirical support to theoretical predictions (Moritz, 2002) that infestation levels of *A. m. scutellata* host populations are lower in nature reserves. In fact, we found no evidence for any infestation in the nature reserves. In contrast, swarms were significantly more infested in regions, where professional beekeepers reported severe losses. Also the frequency of black tergite workers was significantly higher in these colonies. However, as the genotyping showed, not all black tergite workers were social parasites.

Although genetic markers sometimes provide insufficient resolution for the assignment of individuals to different subspecies (Malausa et al., 2005), in the case of the clonal parasitic *A. m. capensis* worker lineage, this is completely unambiguous. Several previous genetic studies of infested *A. m. scutellata* colonies in northern South Africa, showed that every socially parasitic Cape honeybee worker belongs to the same single clonal lineage (Kryger, 2001a, b; Baudry et al., 2004). Since the black tergite workers in all eight swarms, which were initially classified as "potentially infested" had completely different genotypes, these colonies were clearly not parasitized.

While all trapped swarms in nature reserves had exclusively yellow tergite workers, a significant higher number of black tergite workers were found in beekeeping regions. Workers with black tergites have been repeatedly reported in *A. m. scutellata* populations at low frequencies (< 1%, Johannsmeier, 1983; Martin et al., 2002), probably the result of repeated introductions of dark coloured subspecies by beekeepers (Lundie, 1954; Johannsmeier, 1983; Allsopp and Crewe, 1993). These introductions are only permitted outside of nature reserves and may explain the different distribution of non-parasitic black tergite workers.

The trapped swarms may be either of wild origin or originate from apiaries. Thus, the ratio of swarms from the wild honeybee population and the one maintained by apiculturists will depend on local conditions and may vary at the various trapping sites. Moreover, manipulated colonies and wild ones in areas with beekeeping activity are members of the same population (Hepburn et al., 2004), because beekeepers trap swarms locally and let them escape (Spiewok et al., 2006). The exact timing between settling of the swarms and their screening for signs of infestation is not known. Therefore, we cannot discriminate in areas with beekeeping activity whether infestations naturally occurred after settlement via drifting, dispersing or swarm mergers (Neumann et al., 2001a, b; Neumann and Hepburn, 2002) or prior to settlement at an apiary. However, in nature reserves we expect the swarms to have exclusively originated from the wild population because of the absence of beekeeping activities.

The data show that infestation levels of *A. m. scutellata* swarms in nature reserves are lower than in areas with beekeeping activity. Indeed, infestation levels of swarms in regions with ongoing beekeeping activities (12.6%) are significantly higher than in nature reserves (0%), where apicultural activities are prohibited. This may seem surprising in light of the devastating impact of the "dwindling colony syndrome" in apiaries (Allsopp, 1993; Hepburn and Allsopp, 1994). One reason for the lesser infestation levels in nature reserves may be related to the lower *A. m. scutellata* host colony density in natural populations compared to dense aggregations in apiaries (Moritz, 2002). Under low host density conditions the transmission efficiency must be high to compensate for the scarcity of *A. m. scutellata* colonies. A high transmission potential has not been observed in socially parasitic workers, which seem to leave their colonies less often than other workers (Martin et al., 2002).

The infested swarms were not evenly spread over the localities (Fig. 1). Seven out of 11 infested swarms originated from one location (Settlers) and were trapped during a period of intense sun flower pollination. Likewise, the two infested swarms in another location (Graskop) were trapped during an Eucalyptus nectar flow, which regularly attracts migratory beekeepers as one of the most rewarding nectar flows for South African apiculture (Johannsmeier, 2001). This further supports the notion that large scale beekeeping operations facilitate the spread of socially parasitic workers (Neumann and Hepburn, 2002).

Our findings of infested swarms have considerable implications for both the establishment of rural beekeeping and the replacement of eradicated apiaries of large scale beekeeping enterprises. Clearly, the false negative diagnosis (colony is infested but classified as uninfested) is to be avoided at any cost, because a single infested swarm can destroy an entire apiary. Yet here tergite colour gave very safe results since none of the colonies with exclusively yellow tergite workers were infested. Tergite colour did however yield 4.8% (8 out of 166 swarms) false positive diagnoses (colony is not infested but classified as infested) because not all black tergite workers were parasitic. Elimination of all colonies with black tergite workers may thus not be an optimal solution, because healthy colonies could be destroyed in the process. However, this cost is traded off by saving the apiary. In the long run, the elimination of colonies with black tergite workers should result in a strong selection towards yellow tergite types. As a consequence, the black tergite type should reduce in frequency making the diagnosis more sensitive and less error prone. Clearly, selection for yellow tergite type colonies is a simple and more important sustainable procedure because the non-infested wild populations in the nature reserves will support the selection efforts by the beekeepers. Thus, though tergite colour is not a reliable criterion to avoid false positive diagnosis it is very powerful to avoid false negative diagnosis in *A. m. scutellata* swarms. Because South African beekeepers replenish their stock by trapped wild swarms they have an easy but "dirty" tool to avoid the introduction of infested swarms onto their apiaries.

In conclusion, our data show that nature reserves are not only important sites for the protection of pristine habitats and charismatic large mammals but also for the conservation of wild *A. m. scutellata* populations in northern South Africa. The absence of beekeeping also prevented the infestation of colonies with parasitic workers, whereas the infestation rate of swarms trapped in regions with beekeeping activity was sufficiently high to contribute to the persistence of the "dwindling colony syndrome". The management of extensive commercial beekeeping with large scale apiaries and dense colony assemblies will need to be considerably modified to cope with socially parasitic workers in the long run. Apicultural management will need to include enhanced diagnostic efforts, the change of apiary layouts and hive handling to particularly reduce the horizontal transmission of the socially parasitic Cape honeybee lineage.

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Résumé – Niveaux d'infestation des essaims d'*Apis mellifera scutellata* par les ouvrières de l'Abeille du Cap, parasites sociaux. Les ouvrières de l'Abeille du Cap (*Apis mellifera capensis*) sont des parasites sociaux de l'abeille *A. m. scutellata*. Depuis 1990 elles provoquent des pertes élevées parmi les colonies de cette dernière dans le nord de l'Afrique du Sud. L'action des ouvrières de l'Abeille du Cap sur les colonies sauvages d'*A. m. scutellata* n'a pas été quantifiée jusqu'à présent. On a recherché les symptômes de parasitisme dans 166 essaims d'*A. m. scutellata* provenant de 27 localités situées en zones d'apiculture ou dans des réserves naturelles (Tab. I, Fig. 1). Pour déterminer avec précision le nombre de colonies infestées, on a caractérisé à l'aide de six microsatellites d'ADN le génotype d'ouvrières (N = 72) possédant des tergites noirs (symptôme d'infestation) et jaunes prises dans des colonies (N = 8) potentiellement infestées (Tab. II). Le génotype des ouvrières aux tergites noirs se rapportait dans 86 % des cas au génotype présumé de la reine et en aucun cas on n'a pu établir de concordance avec le génotype du clone d'ouvrières parasites (Tab. II). Par conséquent ces essaims n'étaient absolument pas infestés. Les essaims prélevés dans les réserves naturelles, où il n'y a pas d'apiculture, ne sont pas infestés et ne comportent que des ouvrières aux tergites jaunes. Bien que la majorité des colonies avec tergites noirs soit infestée, la couleur des tergites ne doit néanmoins pas servir sur le terrain de critère fiable afin d'éviter des diagnostics faussement positifs. Il est recommandé aux entreprises apicoles de vérifier dans les essaims récemment récoltés la présence d'ouvrières à tergites noirs et d'éliminer ces colonies. C'est la seule façon efficace de réduire le nombre de diagnostics faussement négatifs. La présence d'essaims infestés pose un problème pour la pratique apicole, puisqu'un essaim infesté peut infester rapidement tout un rucher. La présence d'essaims infestés (12,6 %) indique que ceux-ci contribuent de façon importante au maintien du « syndrome de colonie dépérissante ». Les populations protégées ne présentent aucune infestation, indiquant que les réserves naturelles sont d'importants refuges pour l'Abeille africaine *A. m. scutellata.*

***Apis mellifera scutellata* / *Apis mellifera capensis* / parasitisme social / population sauvage**

Zusammenfassung – Befallsraten von *Apis mellifera scutellata* Schwärmen mit sozialparasitischen Kaphonigbienenarbeiterinnen (*A. m. capensis* Esch.). Seit 1990 führen sozialparasitische Kaphonigbienenarbeiterinnen, *Apis mellifera capensis,* im nördlichen Südafrika zu erheblichen Verlusten von *A. m. scutellata* Wirtschaftsvölkern. Der Einfluss sozialparasitischer *A. m. capensis* Arbeiterinnen auf Bienenvölker in wilden *A. m. scutellata* Populationen ist jedoch bislang nicht quantifiziert worden. Es wurden 166 gefangene *A. m. scutellata* Schwärme in 27 Standorten mit unterschiedlicher Imkertätigkeit auf Befallssymptome untersucht (Tab. I; Abb. 1). Um die genaue Anzahl infizierter Völker bestimmen zu können wurden Arbeiterinnen (N = 72) mit schwarzen (Infektionssymptom) und gelben Tergiten aus potentiell infizierten Völkern (N = 8) mit sechs DNA Mikrosatelliten Loci genotypisiert (Tab. II). Die Genotypen der Arbeiterinnen mit schwarzen Tergiten konnten zu 86 % auf den putativen Königinnengenotyp zurückgeführt werden. Eine Übereinstimmung mit dem Genotyp des parasitischen Arbeiterinnenklons, der weite Teile von Südafrika befallen hat, konnte in keinem Fall festgestellt werden (Tab. II). Folglich waren diese Schwärme eindeutig nicht infiziert. In Naturschutzgebieten gefangene Schwärme, ohne Imkerei, sind nicht infiziert und beinhalten ausschließlich gelb gefärbte Arbeiterinnen. Da die Mehrheit der Völker mit schwarzen Tergiten infiziert ist, muss nichtsdestotrotz im Feld die Färbung der Tergiten als zuverlässiges Kriterium dienen, um falsch negative Diagnosen zu vermeiden. Imkereibetrieben wird empfohlen, frisch gefangene Schwärme sofort auf Arbeiterinnen mit schwarzen Tergiten zu überprüfen und diese Völker zu eliminieren. Nur so kann die Zahl falsch negativer Diagnosen nachhaltig reduziert werden. Das Vorkommen von infizierten Schwärmen ist problematisch für die imkerliche Praxis, da ein befallener Schwarm in kurzer Zeit einen ganzen Bienenstand infizieren kann. Das Vorkommen (12.6 %) infizierter Schwärme deutet darauf hin, dass diese substantiell zum wiederholten Auftreten des „dwindling colony syndromes" beitragen. Geschützte Populationen zeigen keinerlei Infektionen, was darauf hindeutet, dass Naturschutzgebiete wichtige Refugien für die Afrikanische Honigbiene *A. m. scutellata* sind.

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

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