

# Population dynamics of the Cape bee phenomenon: The impact of parasitic laying worker clones in apiaries and natural populations

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**Abstract** – A population ecological host- parasite model is used to evaluate the potential impact of clonal parasitic laying workers of the Cape honeybee, *Apis mellifera capensis* on populations of *Apis mellifera scutellata* host colonies in apiaries and in the wild. The model includes three basic life history parameters: reproductive rate of the host colonies, transmission efficiency of the parasite and the death rate of parasitised colonies. The population dynamics of host and parasites are computed for 100 generations after an initial infestation with parasitic workers. The model reveals that infestations are likely to be fatal for apiary populations irrespective of beekeeping activities compensating for colony losses due to parasitisation. Wild *A. m. scutellata* populations are however less likely to be affected by parasitic laying workers and stable equilibria between host and parasite occur over a wide range of the parameter space. Although it is unlikely that the parasitic clone represents a threat to the conservation of biodiversity, even low frequencies of parasitic *A. m. capensis* workers in wild honeybee population can cause a permanent threat to beekeeping activities.

**Cape honeybee / *Apis mellifera capensis* / parasitic worker / population model / biodiversity / apiculture**

## 1. INTRODUCTION

The Cape honeybee (*Apis mellifera capensis* Escholtz) is known as a subspecies of *Apis mellifera* L. with an extremely high reproductive potential for laying workers (Onions, 1912, 1914). Laying

workers produce female offspring parthenogenetically (Anderson, 1963) and can establish themselves as pseudoqueens in queenless colonies (Velthuis et al., 1990; Hepburn, 1994; Hepburn and Radloff, 1999, 2002). The latter trait enables these workers to parasitise other colonies, which

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is the biological basis for the so called “*Capensis* calamity” (Allsopp, 1992). This calamity was characterized by the loss of thousands of honeybee colonies of the neighbouring subspecies *Apis mellifera scutellata* Lepeletier in South African beekeeping operations throughout the last decade (Allsopp, 1992; Allsopp & Crewe, 1993). It was a major disaster to the honeybee industry in the northern provinces of the Republic of South Africa (Hepburn and Allsopp, 1994). Moreover the *Capensis* calamity may cause a serious problem for wild, endemic honeybee populations and threaten biodiversity if they cause extinction of wild populations. The basic reproductive cycle of parasitic laying workers appears to be well understood (Neumann and Hepburn, 2002). Parasitic laying workers of the Cape honeybee (*Apis mellifera capensis*) spread into colonies of *A. m. scutellata* after massive transports of *A. m. capensis* colonies by migratory beekeepers from the Cape into the northern provinces of South Africa. Parasitic *A. m. capensis* workers enter the host colonies, establish themselves as pseudoqueens, cause the loss of the host colony’s queen, and parthenogenetically produce female worker offspring. The worker produced eggs can escape policing (Pirk et al., 2002) and are preferentially fed by the host’s workers (Calis et al., 2002). With increasing frequency of parasitic workers the colonies lose efficiency, dwindle and eventually die or abscond (Martin et al., 2002).

Several models have dealt with the spread of the thelytoky trait of parasitic workers in honeybee populations (Greeff, 1996a, 1996b, 1997; Moritz, 1986, 1989; Moritz et al., 1998). The theoretical work suggested that thelytoky of laying workers should be advantageous under a variety of ecological constraints. In particular long queenless periods in the life history should favour thelytoky, because workers can replace the queen. Moritz (1989) argued that the risk of losing a queen might be an important factor favouring thelytoky. How-

ever, other factors can also cause long queenless phases in the colony. For example the ability of *A. m. capensis* pseudoqueens to suppress queen rearing (Wossler, 2002) may be an intrinsic factor extending queenless periods and favouring thelytoky.

The past modelling was based on the assumption that both subspecies can interbreed and form panmictic populations. Indeed there is a natural hybrid zone between the two subspecies with clear indications of hybridisation (Hepburn and Crewe, 1991 a,b; Crewe et al., 1994; Moritz et al., 1998). The *Capensis* calamity seems however not to be affected by hybridisation. Given that the endemic honeybee population in South Africa’s northern provinces outnumbers introduced *A. m. capensis* colonies, one would expect a rapid solution to the problem by natural selection and dilution of the introduced alleles. If *A. m. scutellata* colonies infested by *A. m. capensis* workers die rapidly (dwindling colony syndrome), and the *A. m. capensis* genotype thus represents a selective disadvantage to the colony, it should have disappeared rather swiftly. Clearly this was not the case, and Kryger et al. (unpublished data) could convincingly show the underlying biological mechanism: parasitic *A. m. capensis* strains do not hybridise with their hosts, but are instead maintained as clonal lineages (Radloff et al., 2002). Apparently, *A. m. capensis* sexual reproductives are not produced in the parasitic laying worker strain causing the *Capensis* calamity. As a consequence there is a genetic separation of the parasite and the host population, and population genetic models are rendered inappropriate to deal with this problem. The genetically based theoretical models need to be replaced by host-parasite models. I therefore use a very simple host – parasite population model to illustrate the dynamics of an *A. m. capensis* infestation in a finite population of *A. m. scutellata* colonies and to compare situations found on apiaries of beekeepers with those under natural conditions. The goal will be to screen the

parameter space and see under which conditions the parasite will spread or decline. This is helpful in order to elucidate if the parasitic strain not only poses a risk for beekeeping but also for wild populations.

## 2. THE MODEL

Classic host-parasite population dynamics can be modelled with Nicholson-Bailey (1935) type models. These can easily be modified to match the “*capensis* calamity” case. Let us assume a finite population, in our case an apiary or a wild endemic population, of  $K$  colonies, consisting of  $h_0$  healthy uninfested colonies and  $i_0$  infested colonies. Let  $K$  also be the maximum number of colonies at the apiary or the carrying capacity of the habitat under natural conditions. Let us now follow the dynamics of this infestation in this population considering the following parameters:

### 2.1. Transmission rate

The transmission efficiency of the infestation,  $e$ , depends on the search and invasion efficiency of parasitic workers from already infested colonies. The transmission rate at a given time  $t$  after the initial infestation,  $m_t$ , is dependent on the density of healthy colonies ( $h_t/(h_t+i_t)$ ) at the apiary or in the population and  $e$ , the transmission efficiency.

$$m_t = e \left( \frac{h_t}{h_t + i_t} \right) \quad (1)$$

### 2.2. Growth rate of healthy colony

The growth rate,  $r$ , of a healthy colony reflects the number of successful swarms issued per colony. Under beekeeping conditions at the apiary, this reflects the creation of healthy colonies, e.g. through colony splits added to the apiary to compensate for losses. For example, a growth

rate of  $r = 0.2$  indicates that 20% of the healthy colonies are added to the apiary through a split procedure.

### 2.3. Dwindling syndrome

Infested colonies have not been observed to issue reproductive swarms and instead suffer the dwindling syndrome. The infestation of a host colony with parasitic workers eventually causes its death at a “dwindling” rate,  $d$ . This is the probability that an infested host colony dies or absconds and leaves the population or the apiary.

Taking these three very simply basic features of reproduction at the colonial level, we can apply classical host-parasite population ecological modelling (e.g. Nicholson and Bailey, 1935) to the problem. We can compute the number of healthy colonies at time  $t$  after the initial infestation

$$h_t = h_{t-1} + rh_{t-1} \left( 1 - \frac{h_{t-1} + i_{t-1}}{K} \right) - m_{t-1} i_{t-1} \quad (2)$$

where

$h_t$  = number of healthy colonies at time  $t$

$h_{t-1}$  = number of healthy colonies at time  $t-1$

$i_{t-1}$  = number of infested colonies at time  $t-1$

$r$  = growth (replacement) rate of healthy colony

$K$  = carrying capacity of the habitat; total number of colonies at the apiary

$m$  = transmission rate.

For the number of infested colonies at time  $t$  we obtain:

$$i_t = i_{t-1} + m_{t-1} i_{t-1} - di_{t-1} \quad (3)$$

where

$d$  = dwindling rate.

Thus in conclusion, we model a host-parasite system based on the growth rate of healthy colonies ( $r$ ), the mortality of infested colonies ( $d$ ), and transmission efficiencies of the infestation ( $e$ ). Equations (1) to (3) were analysed with a standard spreadsheet software (EXCEL Microsoft®) which also produced the graphic presentations used for the interpretation.

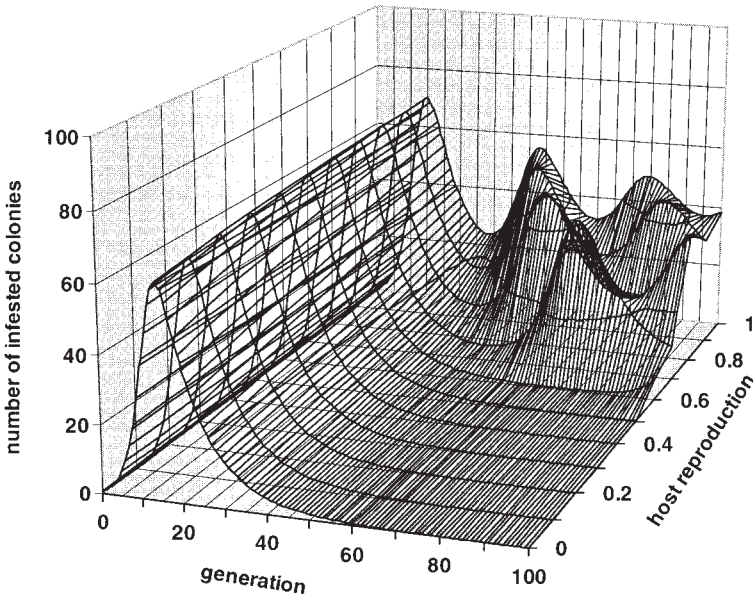
### 3. RESULTS

By screening the parameter space, one can quantify the impact of the spread of the disease and the dynamics of the host population. In order to illustrate these systematically, let us look at each parameter in turn, by keeping the other two constant. Let us then focus on the parameter space typical

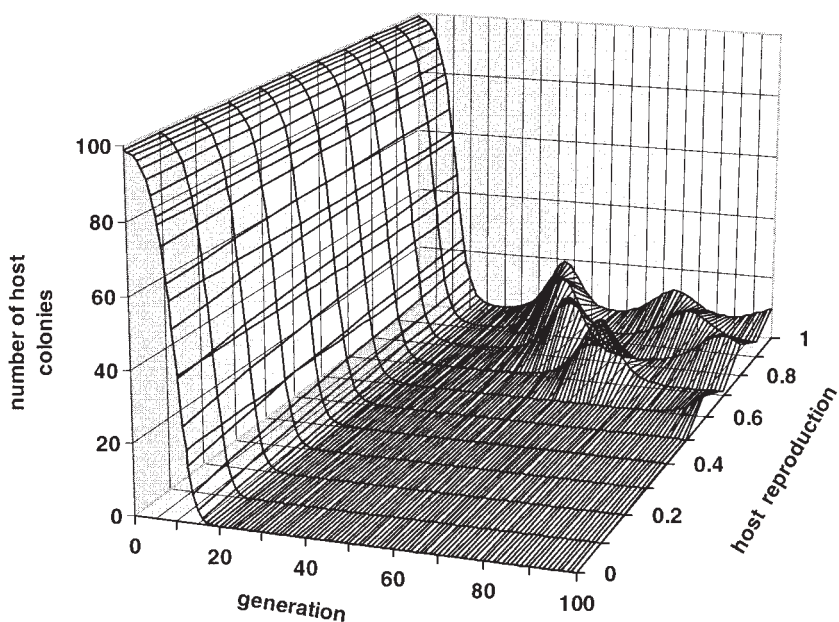
for the apiary and that typical for the natural habitat. The modelling is based on finite populations of 100 colonies, one of which is infested at generation 0. We look at the dynamics over a time period of  $t = 100$  generations. In general, the number of colonies  $K$  does not affect the resulting dynamics qualitatively.

#### 3.1. Host growth rate

Uninfested colonies should reproduce according to their natural growth rate, which is given by the rate of successful reproductive swarming. At the apiary, this figure relates to the number of healthy colonies produced by the beekeeper. Clearly the number of available host colonies determines the spread of the parasite. Figure 1 shows how the number of infested colonies



**Figure 1.** The dynamics of the number of colonies infested by parasitic workers. The transmission efficiency is set to  $e = 0.6$  and the dwindling rate to  $d = 0.1$ . The growth rate  $r$  is denoted as host reproduction and the range from  $r = 0$  to 1 is shown. Host and parasite are assumed to have equal generation intervals.



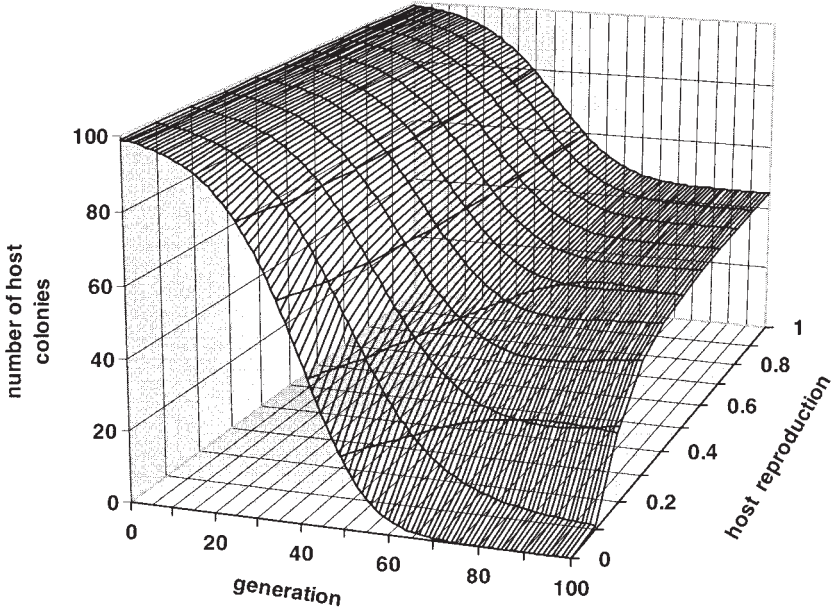
**Figure 2.** The dynamics of the number of *host* colonies. Same parameter settings as in Figure 1.

rapidly increases after an initial infestation with *A. m. capensis* laying workers. The transmission efficiency is set high, at  $e = 1$ , because beekeeping management facilitates the transmission of laying workers (e.g. through splitting colonies, proximity of colonies at the apiary, drifting of workers after migratory beekeeping). The dwindling rate is set rather low ( $d = 0.1$ ) to reveal the impact of the parasitic workers more clearly. We see that the initial increase of the infested colonies is almost unaffected by the host's growth rate. Throughout the tested parameter space of  $r$ , the peak number of infested colonies in generation 9 is close or equal to 80. Thus irrespective of the hosts's growth rate, the rate of parasitised colonies rises dramatically after a new infestation. Likewise the number of healthy colonies dramatically decreases (almost to zero) within this period of time (Fig. 2).

### 3.2. Transmission efficiency

In the apiary situation, this is clearly the end of the story. In the natural condition where we would allow for a longer time span, we see however, that oscillations are possible in spite of the high transmission efficiency and stable equilibria. With decreasing transmission efficiencies the equilibria are higher and the amplitude of the oscillations decrease, eventually getting into steady state equilibria as shown in Figure 3. In this setting the transmission efficiency is less than in Figure 1 with an arbitrarily chosen value of  $e = 0.2$ . This situation might reflect the natural population, where healthy colonies are nesting at distant locations, scattered over the habitat, and are not concentrated in apiaries. Because the new infestation is not anthropogenically facilitated, the probability of finding suitable host colonies (transmission





**Figure 3.** The dynamics of the number of host colonies under “natural population” conditions. Same parameter settings as in Figure 2, but the transmission efficiency is  $e = 0.2$  instead of  $e = 0.6$ .

efficiency  $e$ ) and the transmission rate is clearly reduced. If we ignore possible effects of secondary infestations, the dwindling rate should not be affected and is kept constant at  $d = 0.1$  to allow for comparisons. We see that the various steady state equilibria are not strongly affected by the growth rate  $r$ . Only with a growth rate of zero, do we see a marked effect of this parameter on the host population, which seems rather trivial. We can conclude from this first set of models, that we are to expect differences between the apiary and the natural population. However, the growth rate of the host

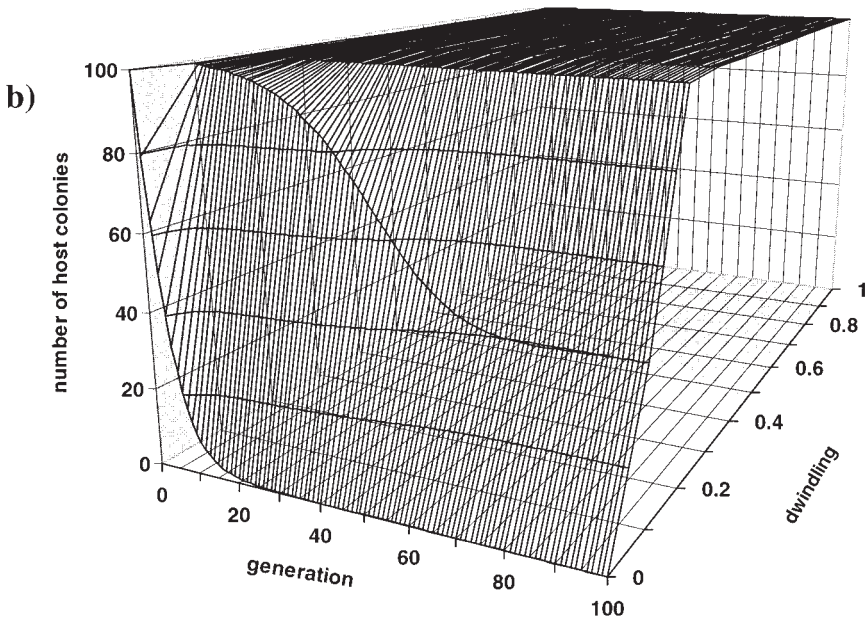
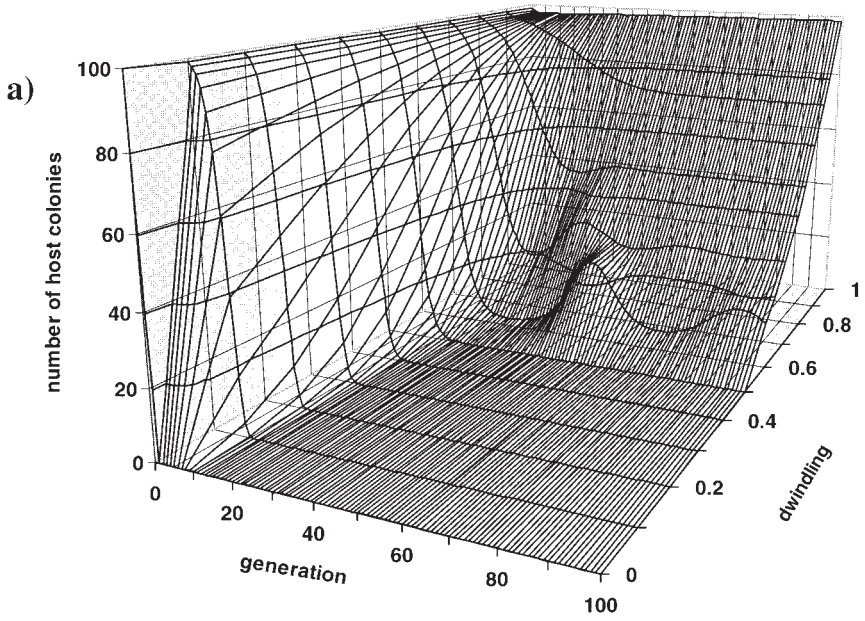
appears not to be a very strong parameter generating these differences.

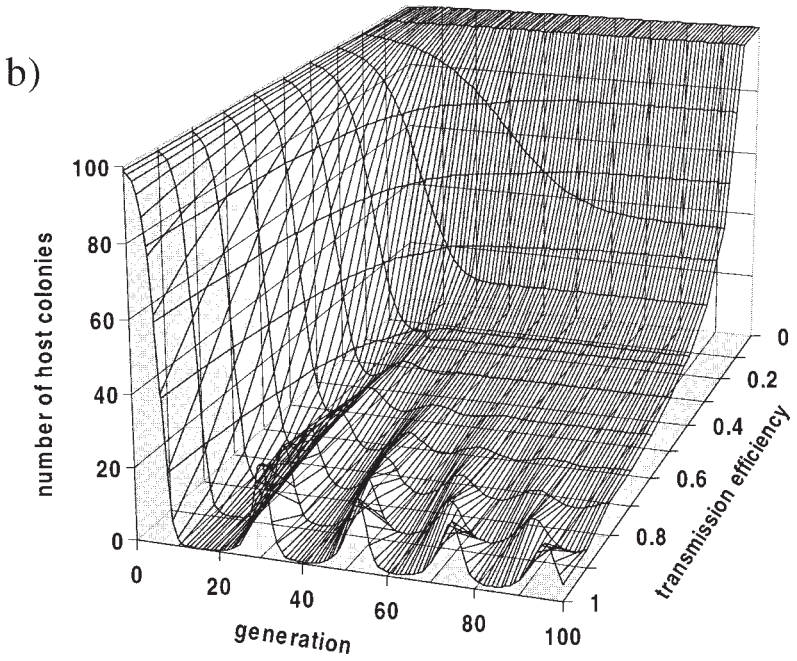
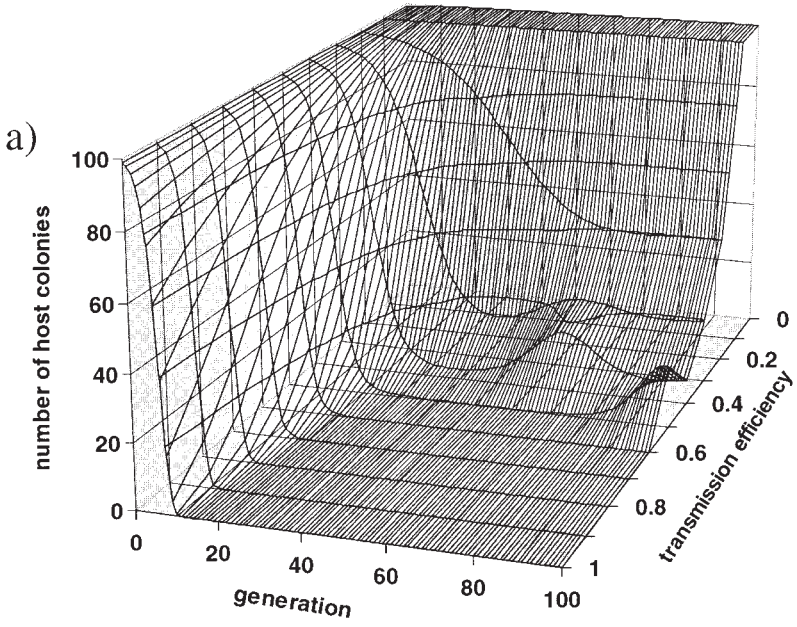
### 3.3. Dwindling

Dwindling was kept low and constant in Figures 1–3. The death rate can vary between  $d = 0$  (all survive) and  $d = 1$  (all die). Figure 4 shows an example setting for an arbitrarily chosen growth rate of  $r = 0.5$  and the apiary transmission efficiency of  $e = 1$ . It is no surprise to see the number of host colonies to be constant at its initial value if the transmission efficiency equals the

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**Figure 4.** (a) Apiary: the dynamics of the number of host colonies under the “apiary” condition with a high transmission efficiency  $e = 1$ . The growth rate is  $r = 0.5$  and the dwindling rate ranges over the full parameter space from  $d = 0$  to  $d = 1$ . (b) Field: the dynamics of the number of host colonies under the “field” condition with a low transmission efficiency  $e = 0.2$ . The growth rate is  $r = 0.5$  and the dwindling rate ranges over the full parameter space from  $d = 0$  to  $d = 1$ . Note that the number of host colonies remains constant in both cases apiary and field, if the death rate of parasitised colonies is higher than the transmission efficiency of the parasite ( $d \geq e$ ).







dwindling rate ( $d = e = 1$  in this case). With an increasing survival of parasitised colonies (decreasing  $d$ ), the numbers of host colonies decrease. They first establish steady state, and then (with  $d < 0.8$ ) the oscillating patterns typical for Nicholson-Bailey type models already observed in Figure 2. It is also clear that the impact of the parasitic colonies on the host population is most dramatic if  $d = 0$  and all infested colonies survive. If we look at the condition in the natural population with low transmission efficiencies ( $e = 0.2$  the “natural” case setting), we see that the impact of the parasites disappears over a wide parameter space. Obviously the parasite is bound to die out, whenever the transmission efficiency is less than the survival of the infested colony ( $e < d$ ).

### 3.4. The eager beekeeper

One might argue that increasing the growth rate (e.g. by replacing lost colonies with healthy ones) might be a realistic strategy to cope with the *capensis* problem. This setting is modelled in Figure 5 where in every generation the number of healthy colonies is tripled ( $r = 3$ ). The dwindling rate is kept at  $d = 0.1$ . We see that even for relatively low transmission efficiency, the effect is negligible. The difference to a low reproductive growth rate of  $r = 0.5$  (every second colony produces a successful swarm) is also rather unspectacular (Fig. 5b). The frequencies and the amplitudes of the oscillating equilibria are modulated but the mean values differ only slightly if at all. Most important, as already stressed before, the initial decline of host colonies is virtually unaffected by the growth rate.

## 4. DISCUSSION

Although the model is rather crude and ignores many aspects of the life history of both host and parasite, several general aspects become very clear. The *capensis* calamity, with thousands of colonies disappearing, is something we would not expect to occur in natural populations. Not surprisingly, the transmission rate is the most essential factor for the spread of parasitic laying workers. If colony density is low and host colonies are difficult to find, the parasitic clone cannot spread. If more colonies “dwindle” away before they can infest new colonies, the parasitic clone must go extinct. At the apiary the conditions are fundamentally different. Beekeeping activities concentrate both healthy and parasitised colonies at large scale at apiaries. Transmission efficiency at the apiary is extremely high (Neumann et al., 2001; Reece, 2002). Splitting techniques and exchange of frames and bees among colonies tremendously increases the transmission efficiency to values close to  $e = 1$ . In fact, the capacity of parasitic workers to spot host colonies does not need to be very high at all, because beekeeping operations facilitate the spread of parasitic workers. But this is not novel and has been recognised already by Hepburn and Allsopp (1994). So what do we learn from the model? The main message is, that the *capensis* phenomenon is unlikely to develop into a biodiversity problem for endemic wild honeybee populations. As long as the dwindling of infested colonies exceeds the transmission efficiency, problems should remain locally constrained. Only if the number of managed honeybee colonies exceeds the number of honeybee colonies



**Figure 5.** (a) The number of host colonies with a parameter setting under field conditions with a growth rate of  $r = 0.5$  (only every second colony issues a reproductive swarm). (b) The same setting under the “eager beekeeper” condition on an apiary with a double “growth”-rate of non-infested colonies ( $r = 2$ ).

in wild populations may problems occur. This may be a typical situation in many European countries with a high density of beekeepers, but may occur only locally in South Africa with large wild honeybee populations (Hepburn and Radloff, 1999). In most cases large colony aggregations are due to migratory beekeeping, where beekeepers move large apiaries following specific nectar flows. This results in an extremely patchy distribution of managed colonies over time and space with a limited impact on wild populations.

The modelling also shows that both steady and oscillating equilibria between host and parasite are possible over a wide range of the parameter space. It is this that should be of concern for the apiarist. Parasitic worker strains are unlikely to cause extinction of local wild honeybee populations. Wild populations however, are likely to maintain these parasitic strains for long periods of time. As soon as a single parasitic worker from the odd infested colony in the wild infests an apiary and successfully reproduces, it will spread immediately among the colonies, due to the loss of the transmission handicap in the natural situation. Thus in short, though biodiversity may not be at stake, the prospects for sustainable large scale extensive beekeeping are meagre as long as parasitic workers are around.

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**Résumé – La dynamique de population du phénomène de l'abeille du Cap : impact des clones d'ouvrières pondeuses parasites dans les ruchers et les populations naturelles.** Les ouvrières pondeuses de l'abeille du Cap (*Apis mellifera capensis* Escholtz) peuvent s'établir comme « pseu-

do-reines » dans des colonies d'abeilles domestiques étrangères et, en tant que parasites sociaux, monopoliser la reproduction de ces colonies. Cette capacité a été à l'origine du problème dénommé « la calamité capensis », qui a causé de grosses difficultés à l'apiculture dans les provinces du nord de la république d'Afrique du Sud. Des centaines de colonies se sont effondrées après que les abeilles du Cap ont été apportées de la région du Cap vers le nord du pays par l'intermédiaire de la transhumance des ruches. On pouvait craindre que, par ces transhumances, l'abeille du Cap ne conduise à la perte de colonies non seulement chez les apiculteurs mais aussi dans les populations sauvages d'abeilles. Un modèle écologique de population (simulation 3) montre comment des populations naturelles d'abeilles et des populations élevées par les apiculteurs sont affectées par des ouvrières parasites. Le modèle repose sur le taux de croissance de colonies saines ( $r$ ), le taux de mortalité de colonies infestées ( $d$ ), ainsi que sur l'efficacité de transmission du parasite ( $e$ ). Il suit la logique d'un modèle classique de Nicholson-Bailey (1935) pour les relations hôte-parasite. Le modèle montre clairement que le taux de croissance de la colonie hôte n'a que peu d'influence sur la dynamique de population de l'hôte et du parasite (Figs. 1 et 2). Lorsque l'efficacité de transmission est faible ( $e = 0,2$ ), un équilibre stable s'établit entre l'hôte et le parasite (Fig. 3). Lorsque l'efficacité de transmission est élevée (cas typique des situations rencontrées sur un rucher), on arrive à des réductions drastiques de la population hôte, mais des équilibres oscillants s'établissent néanmoins entre l'hôte et le parasite (Fig. 4a). Tant que l'efficacité de transmission est plus faible que le taux de mortalité des colonies infestées ( $e < d$ ), la population hôte n'est pas touchée (Fig. 4a). Un triplement du taux de croissance de la population hôte saine (par exemple par introduction de colonies achetées) n'a lui non plus aucune action sur l'effondrement du rucher (Figs. 5a et b).

Au total les modèles montrent que l'efficacité de transmission du parasite sur un rucher est le paramètre le plus important pour la propagation des abeilles parasites. La proximité des ruchers ainsi que les pratiques apicoles telles que la constitution de nuclei, la transhumance, l'échange des cadres favorisent la propagation du parasite. En conditions naturelles l'efficacité de transmission est très réduite puisque les colonies sont dispersées dans l'habitat, que leur densité est faible et qu'elles ne font l'objet d'aucune manipulation apicole. Il faut donc s'attendre à ce que le problème de l'abeille du Cap reste confiné aux ruchers des apiculteurs sans devenir une menace pour les abeilles endémiques. Mais les abeilles parasites constituent une menace latente pour l'apiculture du fait que les populations sauvages peuvent propager les ouvrières parasites.

***Apis mellifera capensis* / abeille du Cap / ouvrière parasite / modèle de population / biodiversité / apiculture / parasite social**

**Zusammenfassung – Populationsdynamik des Kapbienens-Phänomens: Der Einfluss von Klonen parasitisch lebender Arbeiterinnen auf Bienenständen und in natürlichen Populationen.** Legende Arbeiterinnen der Kaphonigbiene (*Apis mellifera capensis*) können sich als „Pseudoköniginnen“ in fremden Völkern der Honigbiene etablieren und als Sozialparasiten die Reproduktion dieser Völker monopolisieren. Diese Eigenschaft war die Grundlage für die sogenannte „Capensis Kalamität“, die zu großen Problemen in der Imkerei in den nördlichen Provinzen Südafrikas führte. Tausende Völker brachen zusammen, nachdem durch Bienentransporte Kaphonigbienen aus der Kapregion nach Norden verbracht worden waren. Es stand zu befürchten, dass die Verbreitung der Kaphonigbienen durch diese Bienentransporte nicht nur Völkerverluste bei Imkereien, sondern auch in der wilden Honigbienenpopulation zur Folge hatte. In

einem populations-ökologischen Modell (Gleichung 3) wird dargestellt, wie imkerlich gehaltene und natürliche Populationen der Honigbiene von parasitischen Arbeiterinnen betroffen sind. Das Modell basiert auf der Wachstumsrate gesunder Völker ( $r$ ), der Sterberate infizierter Völker ( $d$ ) sowie der Transmissionseffizienz des Parasiten ( $e$ ). Es folgt der Logik eines klassischen Nicholson-Bailey (1935) Modells für Parasit-Wirt-Beziehungen. Das Modell macht deutlich, dass die Wachstumsrate  $r$  des Wirts kaum Einfluss auf die Populationsdynamik von Wirt und Parasit nimmt (Abb. 1, Abb. 2). Bei geringer Transmissionseffizienz ( $e = 0,2$ ) stellen sich stabile Gleichgewichte zwischen Wirt und Parasit ein (Abb. 3). Bei hoher Transmissionsrate (typisch für die Situation auf dem Bienenstand) kommt es zu drastischen Verringerungen der Wirtspopulation, aber es stellen sich dennoch oszillierende Gleichgewichte zwischen Wirt und Parasit ein (Abb. 4a). Solange die Transmissionseffizienz geringer ist als die Überlebensrate der infizierten Völker ( $e < d$ ) bleibt die Wirtspopulation unberührt (Abb. 4b). Auch eine Verdreifachung der Wachstumsrate der gesunden Wirtspopulation (z.B. durch Zukauf von Völkern) hat keinen Einfluss auf den Zusammenbruch des Bienenstandes (Abb. 5a, 5b). Insgesamt zeigen die Modelle, dass die hohe Transmissionseffizienz des Parasiten auf dem Bienenstand der wichtigste Parameter für die Ausbreitung der parasitischen Arbeiterinnen darstellt. Die Nähe der Völker, sowie imkerliche Maßnahmen (z.B. Ablegerbildung, Wanderung, Austausch von Waben) fördern die Ausbreitung des Parasiten. Unter natürlichen Bedingungen ist die Transmissionseffizienz wesentlich reduziert, da die Völker verstreut im Habitat nisten, geringere Dichten haben und imkerliche Eingriffe unterbleiben. Es steht daher zu erwarten, dass das Capensis Problem auf Imkereien beschränkt bleibt und nicht zur einer Bedrohung für endemische Honigbienenpopulationen führt. Dadurch, dass die wilden Populationen

parasitische Arbeiterinnen jedoch in geringer Frequenz fortführen können, bleibt die Imkerei latent vom Capensisproblem bedroht.

**Kap-Honigbiene / parasitische Arbeiterin / Populationsmodell / Biodiversität / Imkerei / *Apis mellifera capensis***

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