Infertility of Varroa jacobsoni females after invasion into Apis mellifera worker brood as a tolerance factor against varroatosis

P Rosenkranz, W Engels

Apidologie (1994) 25, 402-411

Original article

Infertility of *Varroa jacobsoni* females after invasion into *Apis mellifera* worker brood as a tolerance factor against varroatosis

P Rosenkranz *, W Engels

Department of Developmental Biology, Zoological Institute, University of Tübingen, Auf der Morgenstelle 28, D-72076 Tübingen, Germany

(Received 13 May 1993; accepted 11 May 1994)

Summary — The fertility of *Varroa jacobsoni* females was studied in worker brood invaded by a single mite. Africanized and European colonies of *Apis mellifera* were used as sources to sample capped brood cells in a tropical area of Brazil and, in addition, Carnolian colonies were sampled in Germany. In the Africanized bees over 40% of the female mites in worker brood were infertile, whereas in European bees only 10–20% infertile *Varroa* females were found. These differences do not depend on broodnest or ambient temperatures. If a female mite was fertile, then the fecundity, measured as the mean number of eggs produced, was the same, irrespective of the host honey bee race. The low *Varroa* fertility in worker brood of the Africanized bees resembles the situation known from the original host species, *Apis cerana*. Since host-dependent infertility evidently has a strong influence on the population dynamics of this parasite, it should be properly considered in future selection and breeding efforts in order to produce European bee strains tolerant against varroatosis.

***Varroa jacobsoni* / infertility / tolerance against varroatosis / *Apis mellifera* / Africanized bee**

INTRODUCTION

In the original host species, the Eastern honey bee, *Apis cerana* Fabr, reproduction of the ectoparasitic mite, *Varroa jacobsoni* Oud, occurs almost exclusively in drone brood (Koeniger *et al,* 1981; De Jong, 1988; Tewarson *et al,* 1992; Rosenkranz *et al,* 1993a). The resulting mite population density in an *A cerana* colony always remains under the threshold of damage, indicating a balanced parasite–host relationship. In contrast to these conditions, in colonies of the western honey bee, *A mellifera* L, a species only recently infested by the *Varroa* mite, a high rate of propagation (Ifantidis, 1984) of the parasite is observed (reviews: De Jong *et al,* 1982; De Jong,

* Present address: Bayerische Landesanstalt für Bienenzucht, Burgbergstr 70, D-91054 Erlangen, Germany

1984, 1990; Ifantidis and Rosenkranz, 1988). Without control measures, the breakdown of a colony occurs inevitably within 3–4 years of the initial infestation (Rosenkranz and Engels, 1985).

Several factors have been assumed to cause the rapid increase of *Varroa* populations in colonies of *A mellifera*: lack of efficient grooming behavior (Peng *et al,* 1987); insufficient removal of parasitized worker brood (Rath and Drescher, 1990; Boecking and Drescher, 1991; Boecking, 1992); long duration of the postcapping brood phase (Moritz, 1985); high titer of juvenile hormone in the hemolymph of postcapping larval instars (Hänel and Koeniger, 1986); and differences in the mites' reproductivity (Ritter and De Jong, 1984; Ruttner *et al,* 1984; Camazine, 1986; Thrybom and Fries, 1991). Within the species *A mellifera*, only the Africanized honey bees in Brazil demonstrate a stable tolerance against varroatosis (Engels *et al,* 1986). The infertility of *Varroa* females infesting worker brood of this biotype is of particular interest, but has not yet been investigated in detail in comparison with European subspecies (Ritter and De Jong, 1984; Camazine, 1986; Rosenkranz *et al,* 1990). We determined the percentage of infertile mites sampled from colonies of Africanized and European honey bees at the same tropical study site in Brazil in comparison with data collected at Tübingen, Germany, under temperate climate conditions.

MATERIALS AND METHODS

Six colonies of Africanized honey bees (*A mellifera scutellata* hybrids) established from captured swarms were kpet in Langstroth hives in the apiary of the Department of Genetics, University of São Paulo, at Ribeirão Preto, Brazil. In addition, 2 Carniolan colonies with mated queens imported free of mites from Germany, and 3 hybrids between Italian and Africanized bees were used. The latter contained *A m ligustica* queens originating from the United States, which had mated presumably with Africanized drones in the apiary at Ribeirão Preto. All colonies had at least 5 brood frames. Carniolan colonies of the same strain kept in the apiary of the University of Tübingen were hived in Deutsch Normal magazine boxes. Worker brood was inspected 5 d after the cells had been capped and those invaded by only one *Varroa* female were checked for mite progeny. For the temporal pattern of ovipositions, brood cells were inspected until day 11 after capping. We did not observe high rates of removal of infested brood cells, and we found no indication of an influence of the presence of eggs or nymphs on this behavior of worker bees. The calculation of infertility percentages in Brazil is based on 361 brood cells from 3 Africanized colonies, 152 from 2 Carniolans and 147 from 2 Italian hybrids, and in Germany on 204 from several free-flying outdoor and 108 from 2 flight-room indoor Carniolan colonies. The brood cell temperature was measured in 2 Africanized colonies with Siemens M 841/S1 thermistors Ø 2 mm. The significance of mean values was checked in the χ^2, the Wilcoxon rank, or the Friedman test.

RESULTS

During the southern hemisphere summer, November through March, all the colonies in Brazil had ample brood throughout the season so that worker cell samples could be taken over the entire period. The average percentage of infertile *Varroa* females was 43.2% in the Africanized, 19.4% in the Carniolan, and 22.5% (including one sample with nearly 40%) in the Italian hybrid colonies. These differences between Africanized and European colonies in mite fertility are significant ($p < 0.01$, Wilcoxon rank test). At different times and between colonies there was a considerable variation in mite infertility, but there was no overlap of these values between the Africanized and the European groups (fig 1).

To test whether temperature affected mite fertility, some recently capped brood frames were placed from the center to the

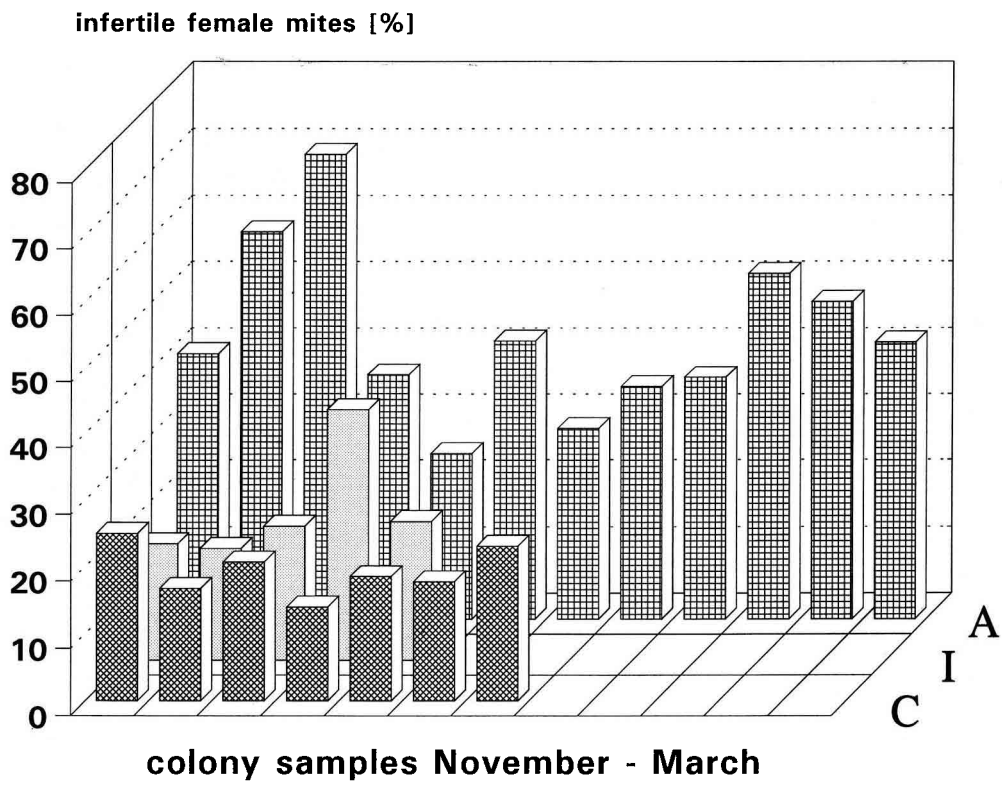

Fig 1. Percentage of infertile *V jacobsoni* females in worker brood of Africanized (A) and European (C = Carniolans, I = Italian hybrids) colonies of *A mellifera* studied in tropical Brazil. Each column represents the mean of 25–45 brood cells sampled in one particular colony and infested by only one mite.

side of the broodnest in 2 colonies of Africanized bees. The temperature in the brood cells was subsequently measured, and 5 d later the sealed cells were checked. The mean temperature was about 1°C lower at the side than at the central warm part of the brood nest. In both colonies the percentage of infertile mites was slightly higher in the center of the brood nest (fig 2). These differences, however, were not significant ($p > 0.05$, χ^2 test).

The time course and number of offspring produced by the mites were compared between Africanized and European colonies from 5 to 11 d after capping of worker brood cells (fig 3). There was no further increase in the total number of mite progeny after the 9th postcapping day. From this date the mean offspring number was 3.3–4.1 in Africanized colonies, and 3.9–4.1 in Carniolans with a range of 1 to 6. These differences were not significant ($p > 0.05$, Friedman test). Evidently the average fecundity of all the fertile *Varroa* females was the same irrespective of the race or biotype of the host bees.

At Tübingen, during the summer and early fall (May through September) the aver-

Fig 2. Dependence of infertility of *V jacobsoni* mites on the position of the worker brood cell within the hive. In 2 colonies of Africanized honey bees in Brazil more infertile mites were found in the center of the brood nest (hatched bars) where the mean local temperatre, as measured in 20 cells per sample over a week after capping, was 34.9°C compared to the periphery (white bars) with 34.0°C. Only cells invaded by a single mite were considered.

age percentage of infertile mites found in Carniolan worker brood was 9.0% which is significantly less than in Brazil ($p < 0.01$, Wilcoxon rank test). The seasonal variation was small (fig 4) with a range from 4.2–13.5%. Surprisingly, in an indoor flight room under summer conditions, January and February within 2–8 weeks after introduction of 2 colonies, on average 48.1% of infertile *Varroa* females were observed (fig 4). This largely increased percentage evidently indicates an influence of environmental and perhaps also of seasonal factors.

DISCUSSION

The data presented here confirm the earlier reports on a high percentage of infertile *Varroa* females in worker brood of Africanized honey bees (Ritter and De Jong, 1984; Camazine, 1986; Engels *et al*, 1986; Rosenkranz *et al*, 1990). A similar case was recently described for *A m intermissa* in Tunisia (Ritter *et al*, 1990). As shown by our experiments in a tropical area, the fertility of the mite is not much influenced by temperature conditions in the parasitized brood cell (Le Conte and Arnold, 1989; Le Conte *et*

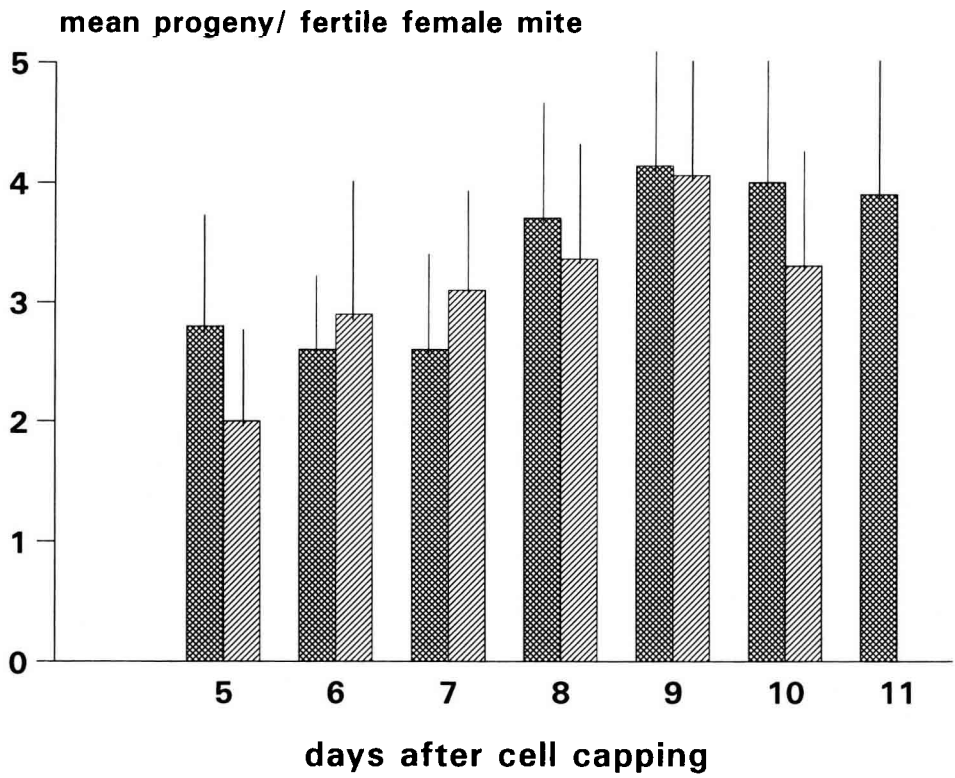

Fig 3. Overall offspring production by the fertile *V jacobsoni* females at different times after sealing of worker brood in Africanized (crossed bars) and Carniolans (hatched bars) colonies in Brazil. Rules = standard deviation. 9–27 cells invaded by only one mite per sample. A total of 111 such cells from Africanized and 149 from Carniolan colonies were considered.

al, 1990) or the environment (Rosenkranz, 1988). Peaks of increased temperatures within the hive (Villa *et al,* 1987) were never observed. Nevertheless, there is an effect of tropical climate on mite fertility (De Jong *et al,* 1984; Moretto *et al,* 1991). The increased *Varroa* infertility in Carniolan colonies of our Tübingen strain kept under tropical conditions in Brazil was observed previously (Rosenkranz *et al,* 1990) and is possibly caused in part (Engels *et al,* 1986) by genetically different mites (Issa, 1989). The data of the flight-room experiment also indicate environmental factors, such as a prolongated phoretic phase during winter, influencing mite fertility in a yet unknown way.

It is interesting to note that the fertility and the fecundity of an individual female mite are not controlled by the same factors. If oviposition is initiated at all, a normal number of eggs is always laid. This is true for mites reproducing in Africanized and in European colonies, respectively, and was also observed in colonies of *A m capensis*, an African subspecies in which high rates of infertile mites in worker brood were also recorded recently (Rosenkranz and Stürmer, 1992). Blum (1989) found the same in

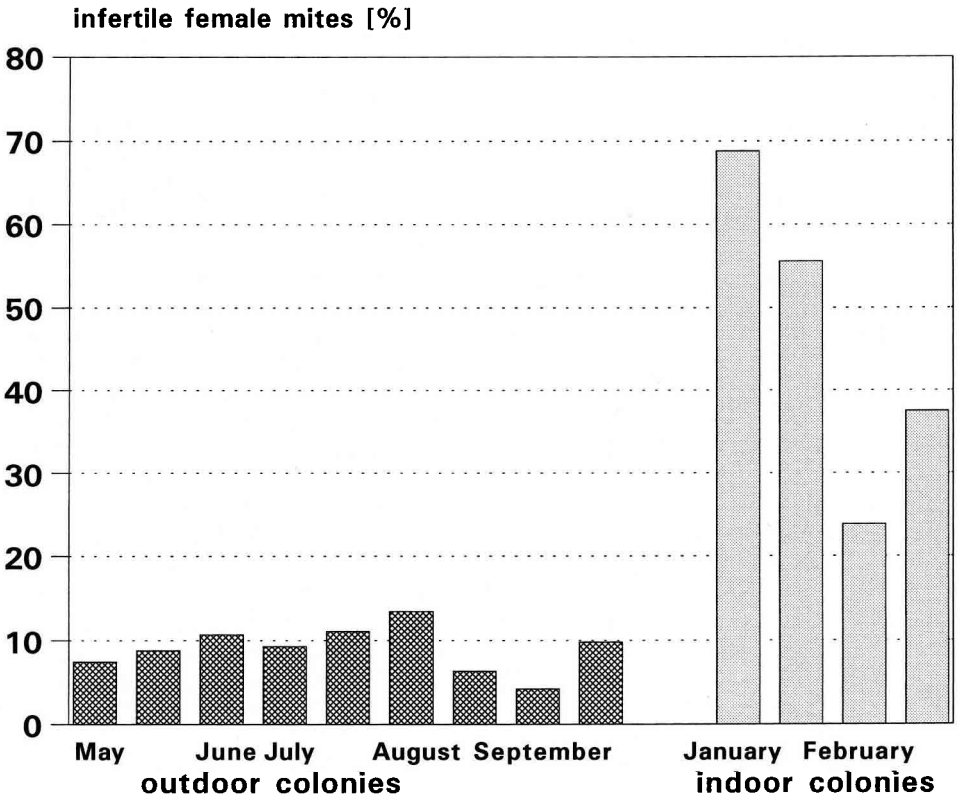

Fig 4. Infertility of *V jacobsoni* mites in worker brood of Carniolan colonies at Tübingen. Per sample 20–43 cells invaded by only one mite.

colonies with varying protein supply. Since the hypothesis of mite fertility control by host-derived juvenile hormone (Hänel and Koeniger, 1986) has been disproved (Rosenkranz *et al,* 1993a), the mode of action of host-dependent influences on reproduction of this parasite remains unknown.

The significance of different tolerance factors against varroatosis on the population dynamics of *V jacobsoni* is still a matter of discussion (Camazine, 1988; Engels, 1988; Kulincevic and Rinderer, 1988; Büchler, 1990; Boecking, 1992; Rosenkranz, 1992; Rosenkranz *et al,* 1993b). Concerning reproduction, the main question is to what degree a different fertility of the mites affects the *Varroa* population development within a colony. Under European conditions an annual increase by a factor estimated as 10 fold or more is assumed for untreated colonies (Rosenkranz, 1992). A computer model (Fries *et al,* 1994) corroborates the great effect of mite fertility. Recent data on reproduction of *V jacobsoni* in colonies of its original host, *A cerana,* also support this view because the percentage of infertile mites in worker brood is close to 100% (De Jong, 1988; Rath and Drescher, 1990; Tewarson *et al,* 1992; Rosenkranz *et al,*

1993a). Therefore, in future research and breeding programs aimed at establishing tolerant lines of *A mellifera*, consideration should be given to the factor 'host-dependent infertility of mites in worker brood'.

ACKNOWLEDGMENTS

This work was supported by a DAAD scholarship to P Rosenkranz and in cooperation with the Departments of Biology and Genetics, USP, at Ribeirão Preto, Brazil.

Résumé — Infertilité des femelles de *Varroa jacobsoni* Oud après invasion du couvain d'ouvrières (*Apis mellifera* L) comme facteur de résistance à la varroatose. Parmi les facteurs qui conditionnent la résistance des abeilles à la varroatose, la reproduction des acariens dans le couvain d'ouvrières joue un rôle décisif. Chez l'hôte d'origine, l'abeille orientale *Apis cerana* Fabr, les acariens se reproduisent presque exclusivement sur le couvain de mâles. Les dégâts aux colonies chez l'abeille domestique *Apis mellifera* sont dus au fort parasitisme du couvain d'ouvrières. Le seul cas bien établi jusqu'à présent de résistance à la varroatose a été décrit chez les abeilles africanisées au Brésil et ressemble à la situation présente chez *A cerana*, dans la mesure où les acariens ne se multiplient dans le couvain d'ouvrières que dans une proportion limitée. On dispose de quelques données mais pas d'étude détaillée. C'est pourquoi nous avons examiné, dans une localité tropicale au Brésil (Ribeirão Preto, São Paulo) sur des colonies d'abeilles africanisées en comparaison avec des colonies de race européenne (*carnica* et *ligustica*), combien de femelles d'acariens étaient infertiles après l'invasion des cellules de couvain d'ouvrières et si ce phénomène pouvait être lié à la température. En outre des expériences correspondantes ont été faites sur des colonies de *carnica* de la même lignée à Tübingen, localité au climat tempéré. Au Brésil, pendant les mois d'été, plus de 40% de femelles d'acariens trouvées dans des cellules d'ouvrières se sont montrées infertiles, tandis que, chez les races européennes, ce taux n'est que de 20%. Les chiffres ont varié un peu d'une colonie à l'autre au cours de la saison mais les moyennes sont pourtant restées significativement différentes pour les abeilles africanisées et les européennes (fig 1). Afin de tester quel rôle pouvait jouer la température, quelques rayons de couvain récemment operculé provenant du centre ont été suspendus sur les bords d'une hausse. Durant cinq jours les températures à l'intérieur des cellules operculées d'ouvrières ont été enregistrées et on a finalement vérifié si les femelles d'acariens trouvées dans ces cellules avaient pondu. Au centre du nid à couvain, où la température à l'intérieur des cellules est en général supérieure d'un degré à celles des rayons du pourtour, le pourcentage de femelles infertiles n'était néanmoins que faiblement supérieur (fig 2). Le succès reproducteur ne dépend donc pas essentiellement du même niveau de température, du reste fort étendu, chez les abeilles africanisées et les races européennes. En outre on a cherché à savoir combien d'œufs les femelles fertiles pondaient dans le couvain d'ouvrières des différentes colonies et ce, combien de temps après l'operculation. Là non plus, aucune différence. Dans les 11 j suivant l'operculation, on a dénombré 1-6 descendants dans chaque cellule parasitée. Chez les africanisées comme chez les colonies de *carnica* il y avait en moyenne 4 œufs ou nymphes (fig 3). À Tübingen en été et au début de l'automne, le pourcentage de femelles infertiles dans le couvain d'ouvrières de *carnica* est resté relativement constant autour de 10%. En janvier et février en revanche, chez 2 colonies maintenues en chambre de vol, il a atteint presque 50% (fig 4). On discute ces résultats en rapport avec les influences du milieu et les différences génétiques chez

les abeilles et les acariens. Un grand intérêt pratique revient au facteur «infertilité liée à l'hôte des acariens dans le couvain d'ouvrières» lors d'efforts futurs pour sélectionner une lignée d'*A mellifera* tolérante à la varroatose. Après que l'hypothèse de l'hormone juvénile s'est révélée inexacte, nous avons provisoirement besoin d'hypothèses en ce qui concerne les causes de l'infertilité des femelles de *V jacobsoni*.

Varroa jacobsoni* / infertilité / varroatose / résistance / abeille africanisée / *A m carnica

Zusammenfassung — Unfruchtbarkeit von Milbenweibchen *(Varroa jacobsoni)* nach Invasion von Arbeiterinnenbrut *(Apis mellifera)* als Toleranzfaktor gegenüber der Varroatose. Unter den Faktoren, die eine Varroatose-Toleranz von Honigbienen bedingen, spielt die Vermehrung der Milben in Arbeiterinnenbrut eine entscheidende Rolle. Bei der ursprünglichen Wirtsart, der östlichen Honigbiene *Apis cerana*, pflanzen sich die Milben fast ausschließlich in Drohnenbrut fort. Die Völkerschäden bei der westlichen Honigbiene *Apis mellifera* beruhen auf einer starken Parasitierung der Arbeiterinnenbrut. Der bislang einzige gut belegte Fall einer Varroatose-Toleranz bei *A mellifera*, die afrikanisierten Bienen in Brasilien, ähnelt den Verhältnissen bei *A cerana* insofern, als auch nur in begrenztem Ausmaß eine Vermehrung der Milben in Arbeiterinnenbrut stattfindet. Hierzu gab es wohl einige Angaben, aber noch keine detaillierte Untersuchung. Wir prüften daher an einem Tropenstandort in Brasilien (Ribeirão Preto, São Paulo) bei Völkern von afrikanisierten im Vergleich zu europäischen Rassen (*carnica* und *ligustica*), wieviele Milbenweibchen nach Invasion von Arbeiterinnen-Brutzellen unfruchtbar bleiben und ob dies temperaturbedingt sein kann. Außerdem wurden entsprechende Untersuchungen an *carnica*-Völkern der gleichen Linie in Tübingen, einem Standort mit gemäßigtem Klima, durchgeführt. In Brasilien erwiesen sich während der dortigen Sommermonate über 40% der Milbenweibchen, die einzeln in Arbeiterinnenzellen gefunden wurden, als unfruchtbar. Bei den europäischen Rassen waren es nur etwa 20%. Die Zahlen für einzelne Völker schwankten im Saisonverlauf ein wenig, die Mittelwerte für afrikanisierte und europäische Bienen waren jedoch stets signifikant unterschiedlich (Abb 1). Um zu prüfen, welche Rolle hierbei Temperatureinflüsse spielen, wurden in 2 afrikanisierten Völkern einige frischverdeckelte Brutwaben aus der Mitte an den Rand von Brutzargen umgehängt. 5 Tage lang wurden dann die Temperaturen innerhalb verdeckelter Arbeiterinnenzellen registriert und anschließend geprüft, ob in solchen Zellen vorgefundene *Varroa*-Weibchen Eier gelegt hatten. In der Brutnestmitte, wo es in den Zellen durchschnittlich 1°C wärmer war als in den Randwaben, lag der Prozentsatz unfruchtbarer Milben jedoch nur geringfügig höher (Abb 2). Der Fortpflanzungserfolg hängt also nicht wesentlich von dem im übrigen bei afrikanisierten und europäischen Bienenrassen weitgehend gleichen Temperaturniveau im Brutnest ab. Weiterhin wurde untersucht, wieviele Eier die fruchtbaren Milbenweibchen zu welchen Zeiten nach der Verdeckelung in Arbeiterinnenbrut der verschiedenen Völker legten. Auch hierbei ergaben sich keine Unterschiede. Binnen 11 Tagen nach Zellverdeckelung wurden in einzeln parasitierten Zellen 1–6 Nachkommen gezählt. Sowohl in afrikanisierten wie in *carnica*-Völkern waren es im Mittel 4 Eier bzw Nymphen (Abb 3). In Tübingen lag im Sommer und Frühherbst der Prozentsatz unfruchtbarer Milben in Arbeiterinnenbrut von *Carnica*-Völkern relativ konstant bei durchschnittlich 10%. Im Januar und Februar wurden im Flugraum dagegen bei 2 Völkern fast 50% unfruchtbare *Varroa*-Weibchen ermittelt (Abb 4). Die Ergebnisse werden im Hinblick auf Umwelteinflüsse und

genetisch bedingte Unterschiede bei Bienen und Milben diskutiert. Dem Faktor 'wirtsbedingte Unfruchtbarkeit der Milben in Arbneiterinnenbrut' kommt bei künftigen Bemühungen um eine Züchtung Varroatose-toleranter Linien von *A mellifera* unzweifelhaft eine große praktische Bedeutung zu. Nachdem die Juvenilhormon-Hypothese sich als unzutreffend erwiesen hat, sind wir hinsichtlich der Ursachen einer Unfruchtbarkeit bei *Varroa*-Weibchen einstweilen auf Vermutungen angewiesen.

Varroa jacobsoni* / Unfruchtbarkeit von Milben in Arbeiterinnenbrut / Toleranz gegenüber Varroatose / *Apis mellifera* / Afrikanisierte / *Carnica

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