Apidologie (1992) 23, 503-508
© Elsevier/INRA/DIB/AGIB

Original article

Distribution of *Acarapis woodi* Rennie in the tracheae of honey bees

I Fries *, RA Morse

Entomology Department, Cornell University, Ithaca, NY 14853, USA

(Received 24 June 1991; accepted 12 June 1992)

Summary — Colonies infested by *Acarapis woodi* were analysed for the percentage of bilateral and unilateral infestations in the main tracheal trunks of infested bees. A χ^2 analysis demonstrated that the infestations were not randomly distributed in bee tracheae ($p < 0.001$, $n = 1\,512$), but that more bilateral infestations occurred than expected. Calculations from literature data confirmed this observation. The possible reasons for the skewed distribution have been discussed.

***Acarapis woodi* / distribution / trachea / *Apis mellifera* / sensitivity–resistance**

INTRODUCTION

Although many details of the life history of tracheal mites (*Acarapis woodi* Rennie) are understood, little is known about the movements of mites between or within bees. The tracheal mite enters the first thoracic spiracles of young adult honey bees (*Apis mellifera* L) and reproduces within the tracheal system. Adult mites or immature stages of *A woodi* are usually found in the large tracheal trunk connected to the first spiracle, but occasionally the infestation is also found in the air sacs of the head (Örösi-Pal, 1935; Giavarini and Giordani, unpublished observations). Movement of mites between hosts occur as mated adult females migrate out of the spiracle, attach to a thoracic hair of the former host and then to the hair of another bee in close contact (Hirschfelder, 1952). Cage experiments indicate a random distribution of mites between bees of the same age as well as between trachea within bees (Gary and Page, 1987). Movement of mites between spiracles within a single bee has not been described.

Young bees up to 4 days old are much more susceptible to tracheal mite infestations than older bees (Gary *et al,* 1989). Genetic differences in mite resistance among bees have been reported (Adam, 1962; Alexeenko and Vovk, 1971; Page and Gary, 1990) but very little is known

* Present address: Bee Division, Swedish University of Agricultural Sciences, Box 7024, 75007 Uppsala, Sweden

about why some bees are resistant to infestion as female mites migrate to find new hosts. Stiffening of the vestibular guard hairs at the thoracic spiracle in older bees has been thought to increase resistance in older bees (Sachs, 1952); however, other factors must be responsible since removal of these hairs does not change the host preference of the mite (Lee, 1963). It has been suggested that differences in cuticular hydrocarbons in different age groups may be involved in host preference, since extracts from younger bees are preferred (Smith *et al*, 1989).

To further the understanding of tracheal mite movements between bees, this paper examines the distribution of *A woodi* infestations among honey bee tracheae under natural conditions.

MATERIALS AND METHODS

Samples of 25–30 bees were collected from the inner hive covers of 34 colonies in the fall and 23 colonies in the spring. A total of 1 512 bees were examined for the presence of *A woodi* in the main tracheal trunks using the slicing technique described by Milne (1948). Records were kept of whether infested bees had a unilateral or a bilateral infestation.

With a known proportion of infested tracheae, the expected values of non-infested, unilaterally infested, and bilaterally infested bees can be calculated under the hypothesis of random distribution of mites among tracheae. The expression $(1-\Pi)^2 + 2\Pi(1-\Pi) + \Pi^2 = 1$ where Π = proportion of infested tracheae, gives the expected proportions of non-infested + unilaterally infested + bilaterally infested bees (Colton, 1974). A χ^2 analysis was used to compare observed and expected values of non-infested, unilaterally infested, and bilaterally infested bees.

RESULTS

The average infestation rate of tracheae in the collected samples was 0.290. Under the hypothesis of random distribution of mites, a χ^2 analysis of the observed and expected number of unilateral and bilateral infestations in individual bees shows that the infestations were not randomly distributed among the tracheae of the bees (χ^2 = 188.7, n = 1512, df = 2, $p < 0.001$). There were more bilaterally infested (n = 237)

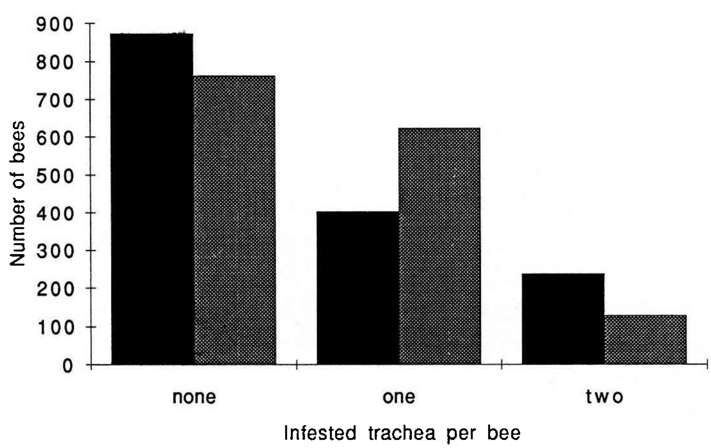

Fig 1. Distribution of observed and expected number of bees non-infested (none), unilaterally infested (1), and bilaterally infested (2) by *Acarapis woodi*. ■ observed; ▩ expected.

and non-infested bees (n = 872) than expected, while less unilaterally infested bees (n = 403) than expected were found. The expected numbers were 127, 762 and 623 respectively. The distribution of observed and expected type of infestation is illustrated in figure 1. The distribution pattern was similar irrespective of sampling in spring or fall.

DISCUSSION AND CONCLUSION

The calculations on mite distribution show that the infestation is not randomly distributed among tracheae. Bilateral infestations and non-infested bees are more common than expected if tracheae are randomly infested. Calculations from literature data where frequencies of unilateral and bilateral infestations are given (Bailey, 1959, 1965; Giavarini and Giordani, unpublished observations) show the same skewed distribution as presented here. This finding is contrary to results published by Gary and Page (1987), who found a random distribution of mites among tracheae of 1-week-old bees in cage experiments.

The non-random distribution described could be the result of several factors:

– infested bess might have more contact with other infested bees, thus creating subgroups of infested and uninfested bees. Transference of mites would then be more likely among already infested bees, thus creating the observed skewed distribution. This hypothesis does not seem very likely. In colonies with brood, bees > 4 days old rarely become infested (Gary *et al,* 1989), and sampling for infested bees in the brood area where the young most susceptible bees are found actually yields lower infestation levels than samples from the supers (Calderone, 1990);

– perhaps female mites from highly infested trancheae migrate periodically in large numbers, thus creating a fluctuation in number of migrating mites. Since the males do not migrate, the sudden change from the normal sex ratio of 3–4 females for every male (Delfinado-Baker, 1988) to predominantly males that occurs in highly infested tracheae (Henderson and Morse, 1990), suggests this type of migrating behaviour. Another explanation for the change in sex ratio that has been suggested is that of arrhenotoky (Royce et al, 1988), with old mites laying unfertilized eggs that produce males as their supply of viable sperms run out. Migration of a large number of females from highly infested tracheae would result in a variation in infestation pressure on the most susceptible young bees, and would also yield a skewed distribution with more non-infested and bilaterally infested bees than expected. This could contribute to the observed deviation from random distribution of infested tracheae;

– a higher probability of migration of female mites between trachea of an individual bee, rather than migration between bees, would yield the same type of skewed distribution as observed in this study. When migrating mites move between bees, they crawl out on the hair of the host and attach to a new host with which the bee makes contact (Hirschfelder, 1952). However, the mite does not have to find a new trachea instantaneously. Tracheal mites can feed outside the trachea and survive for days close to the bee's body where they can move about (Örosi-Pal, 1935, Sachs, 1951), possibly from one part of the bee's body to the other. The non-random distribution of mites among tracheae found in 1-week old bees in cage experiments (Gary and Page, 1987) suggests that the skewed distribution described in this study might develop as the infestation develops. The hypothesis of a higher probability for movement of mites within rather than between bees seems most likely.

If different subgroups in the colony vary in their susceptibility to tracheal mite infestations, a skewed distribution of infested bees would also occur. A honey bee colony consists of different subgroups, or patrilines, that might differ in tracheal mite resistance. Indeed, differences in several behavioural characteristics among different patrilines in honey bee colonies have been observed (Frumhoff and Baker, 1988; Robinson and Page, 1988). Racial differences in mite susceptibility have also been reported (Adam, 1962; Alexeenko and Vovk, 1971; Gary and Page, 1987), even with special reference to the drone's influence on susceptibility (Adam, 1987), making this hypothesis also a likely explanation for the observed results.

More research is required to undestand the epidemiology of tracheal mites.

ACKNOWLEDGMENTS

The comments and suggestions on the manuscript by S Camazine and T Seeley are highly appreciated.

Résumé — Répartition d'*Acarapis woodi* entre les trachées des abeilles. Bien que de nombreux détails du cycle évolutif de l'acarien des trachées *(Acarapis woodi)* soient compris, on connait peu de choses concernant les mouvements des acariens à l'intérieur des abeilles et entre elles. Afin de mieux comprendre ces mouvements, nous avons étudié la répartition des infestations d'*A woodi* entre les trachées des abeilles. Des échantillons de 25 à 30 abeilles ont été prélevés sur les couvre-cadres de 34 colonies à l'automne et de 23 colonies au printemps. Au total 1 512 abeilles ont été examinées. On a recherché la présence d'*A woodi* dans les principaux troncs trachéens à l'aide de la technique de coupes décrite par Milne (1948). On a comptabilisé les abeilles qui étaient infestées d'un seul côté et celles qui l'étaient des 2 côtés. Une analyse du χ^2 montre que les infestations ne sont pas réparties au hasard entre les trachées des abeilles (p < 0,001, n = 1 512) mais que les infestations bilatérales sont plus nombreuses que prévu. Les calculs à partir des données de la littérature confirment ce résultat.

La répartition non aléatoire décrite peut résulter de divers facteurs :

– les abeilles infestées peuvent avoir plus de contacts avec d'autres abeilles infestées, créant ainsi des sous-groupes d'abeilles infestées et d'abeilles indemnes;

– la migration d'un grand nombre de femelles à trachées fortement infestées causerait une variation dans la pression d'infestation sur les jeunes abeilles les plus sensibles et donnerait une répartition biaisée avec plus d'abeilles indemnes et plus d'abeilles infestées des 2 côtés que prévu;

– une probabilité plus élevée de la migration des acariens femelles entre les trachées d'une abeille, plutôt que la migration entre abeilles, donnerait une répartition biaisée semblable à celle observée ici;

– si la sensibilité aux infestations de différents sous-groupes de la colonie varie, il en résulte également une répartition biaisée des abeilles infestées.

Les hypothèses 3 et 4 semblent les plus probables.

***Acarapis woodi* / répartition / trachée / *Apis mellifera* / acariose / sensibilité–résistance**

Zusammenfassung — Die Verteilung von *Acarapis woodi* auf die Tracheen

der Honigbienen. Obwohl man heute sehr viel über die Lebensgeschichte der Tracheenmilbe *(Acarapis woodi)* weiß, so ist doch nur wenig über die Bewegungen der Milbe zwischen den Bienen oder in der Biene selbst bekannt. Um die Bewegungen der Tracheenmilbe zwischen den Bienen oder möglicherweise in der Einzelbiene besser zu verstehen, wurde in dieser Arbeit die Verteilung des Befalls mit *A woodi* auf die Tracheen der Arbeitsbiene untersucht. Es wurden Proben von 25–30 Bienen vom inneren Beutendeckel von 34 Völkern im Herbst und 23 Völkern im Frühjahr gesammelt. Insgesamt wurden 1512 Bienen mittels der Schnittechnik von Milne (1948) auf die Anwesenheit von *A woodi* in den Haupttracheenstämmen untersucht. Es wurde protokolliert, ob ein einseitiger oder doppelseitiger Befall vorlag.

Eine Chi-Quadratanalyse zeigte, daß der Befall nicht zufällig auf die Tracheen der Bienen verteilt ist ($p < 0.001$, $n = 1\,512$), sondern daß ein doppelseitiger Befall häufiger als zu erwarten vorkommt. Berechnungen mit Daten aus der Literatur bestätigen dieses Ergebnis. Die beschriebene Nicht-Zufallsverteilung könnte das Ergebnis mehrerer Faktoren sein:

– Befallene Bienen könnten mehr Kontakt mit anderen befallenen Bienen haben, so daß im Volk Untergruppen von befallenen und nicht befallenen Bienen entstehen.

– Die Wanderung einer großen Zahl von Milbenweibchen aus stark befallenen Tracheen würde zu erhöhtem Befallsdruck auf höher empfängliche Jungbienen führen, wodurch auch eine schiefe Verteilung mit einer über der Erwartung liegenden Zahl an nicht befallenen und doppelseitig befallenen Bienen entstünde.

– Eine höhere Wahrscheinlichkeit der Wanderung von weiblichen Milben zwischen den Tracheen ein und derselben Biene, statt der Wanderung zwischen Bienen, würde zu derselben schiefen Verteilung führen wie sie in dieser Untersuchung gefunden wurde.

– Wenn innerhalb des Volkes Untergruppen mit unterschiedlicher Milbenempfänglichkeit bestehen, käme es ebenfalls zu einer schiefen Verteilung der befallenen Bienen.

Die Hypothesen einer größeren Häufigkeit von Bewegungen der Milben auf einer Biene statt zwischen Bienen, und des Bestehens von Untergruppen mit höherer Befallsempfänglichkeit für Milben erscheinen am wahrscheinlichsten.

***Acarapis woodi* / Tracheenbefall / *Apis mellifera* / Empfänglichkeit der Bienen**

REFERENCES

Adam B (1962) Eigene Erfahrungen mit der Milbenseuche. *Bienenvater* 83, 35-38, 79-81

Adam B (1987) The tracheal mite – breeding for resistance. *Am Bee J* 127, 290-291

Alexeenko FM, Vovk RM (1971) Age and race resistance of bees to acarine disease and new means for its control. *In: 23rd Apimondia Beekeep Congr Moscow.* Apimondia Publ House, Bucharest, 481-483

Bailey L (1959) The effect of infestation with *Acarapis woodi* (Rennie) on the mortality of honey bees. *J Invertebr Pathol* 1, 15-24

Bailey L (1965) Susceptibility of the honey bee, *Apis mellifera* Linnaeus, infested with *Acarapis woodi* (Rennie) to infection by airbone parasites. *J Invertebr Pathol* 7, 141-143

Calderone NW (1990) The distribution and sampling of *Acarapis woodi* in honey bee colonies. *Am Bee J* 130, 187

Colton T (1974) *Statistics in Medicine.* Little, Brown and Co, Boston, MA

Delfinado-Baker M (1988) The tracheal mite of honey bees; a crisis in beekeeping. *In: Africanized Bees and Bee Mites* (Needham GR, Page RE, Jr, eds) Ellis Horwood, Chichester, 493-497

Frumhoff PC, Baker J (1988) A genetic component to division of labour within honey bee colonies. *Nature (Lond)* 333, 358-361

Gary NE, Page RE (1987) Phenotypic variation in susceptibility of honey bees, *Apis mellifera*, to infestations by tracheal mites, *Acarapis woodi*. *Exp Appl Acarol* 3, 291-305

Gary NE, Page RE Jr, Lorenzen K (1989) Effect of age of worker honey bee *(Apis mellifera)* on tracheal mite *(Acarapis woodi)* infestation. *Exp Appl Acarol* 7, 153-160

Henderson C, Morse RA (1990) Tracheal mites. *In: Honey Bee Pests, Predators, and Diseases* (Morse RA, Nowogrodzki R, eds) Cornell Univ Press, Ithaca, 219-234

Hirschfelder H (1952) Das Verhalten der Trachenmilbe *Acarapis woodi* R beim Verlassen und Aufsuchen der Wirtsbienen. *Z Bieneforsch* 1, 141-147

Lee DC (1963) The susceptibility of honey bees of different ages ot infestation by *Acarapis woodi* (Rennie). *J Insect Pathol* 5, 11-15

Milne PS (1948) Acarine disease of bees. *J Minist Agric Fish* 54, 473-477

Örosi-Pal Z (1935) Bau, Entwicklung und Lebensweise des Bienenparasiten *Acarapis woodi* (Acarina). *Z Parasitenkde* 7, 233-267

Page RE, Gary NE (1990) Genotypic variation in susceptibility of honey bees *(Apis mellifera)* to infestations by tracheal mites *(Acarapis woodi)*. *Exp Appl Acarol* 8, 275-283

Robinson GE, Page RE Jr (1988) Genetic determination of guarding and undertaking in honey-bee colonies. *Nature (Lond)* 333, 356-358

Royce LA, Krantz GW, Ibay LA, Burgett DM (1988) Some observations on the biology and behaviour of *Acarapis woodi* and *Acarapis dorsalis* in Oregon. *In: Africanized Bees and Bee Mites* (Needham GR, Page RE, Jr, eds) Ellis Horwood, Chichester, 493-505

Sachs H (1952) Über das Verhalten und die Orientierung der Tracheenmilben *Acarapis woodi* (Rennie, 1921) auf Bienen. *Z Bienenforsch* 1, 148-170

Smith AW, Phelan PL, Needham GR, Page RE Jr (1989) Chemical ecology of the honey bee tracheal mite. *Am Bee J* 129, 822