

29. Turlings, T.C.J., Tumlinson, J.H., Lewis, W.J.: *Science* 250, 1251–1253 (1990)
30. Hopke, J., Donath, J., Blechert, S., Bolland, W.: *FEBS Letters* 352, 146–150 (1994)
31. Gundlach, H., Müller, M.J., Kutchan, T.M., Zenk, M.: *Proc. Natl. Acad. Sci. USA* 89, 2389–2393 (1992)
32. Schütz, S., Weißbecker, B., Klein, A., Hummel, H.E.: *Phytochemistry* (in press)
33. Schütz, S., Weißbecker, B., Hummel, H.E.: *Asp. Appl. Biol.* 45, 349–358 (1996)
34. Casagrande, R.A.: *Bull. Entomol. Soc. Am.* 31, 27–29 (1985)
35. Chappelka, A.H., Kraemer, M.E., Mebrahtu, T., Rangappa, M., Benepal, P.S.: *Envir. Exp. Bot.* 28, 53–60 (1988)
36. Schütz, S., Weißbecker, B., Koch, U.T., Hummel, H.E.: *Mitt. Dtsch. Ges. Allg. Angew. Ent.* 10, 231–236 (1995)
37. Levinson, H.Z., Levinson, A.R., Jen, T.-L.: *Naturwissenschaften* 66, 472–473 (1979)
38. Jermy, T.: *Ent. Exp. Appl.* 59, 75–78 (1991)
39. Baldwin, I.T., in: *Phytochemical Induction by Herbivores*, p. 47 (D.W. Tallamy, M. Raupp, eds.). New York: Wiley 1991
40. Meyer, A., Miersch, O., Buttner, C., Dathe, W.: *J. Plant Growth Regul.* 3, 1–8 (1984)

Naturwissenschaften 84, 217–218 (1997) © Springer-Verlag 1997

High Humidity in the Honey Bee (*Apis mellifera* L.) Brood Nest Limits Reproduction of the Parasitic Mite *Varroa jacobsoni* Oud.

B. Kraus, H.H.W. Velthuis

Universiteit Utrecht, Vakgroep Vergelijkende Fysiologie, Projectgroep Ethologie en Socio-oecologie, Centrumgebouw Noord, Padualaan 14, De Uithof, Postbus 80086, 3508 TB Utrecht, The Netherlands

Received: 26 August 1996 / Accepted in revised version: 19 February 1997

Factors influencing reproduction of the parasitic mite *Varroa jacobsoni* have become a central theme of honey bee pathology. In large parts of the world the mite has made it impossible for colonies of the honey bee *Apis mellifera* to survive if no measures of treatment are applied [1]. Originally a parasite of the Eastern honey bee *A. cerana*, the mite was detected in colonies of *A. mellifera* only less than 4 decades ago [2]. *A. cerana* colonies are not damaged by *V. jacobsoni* because several factors prevent the build-up of a large mite population [3]. The most important factor is that in colonies of *A. cerana* the parasite, which can reproduce only in capped brood cells, reproduces exclusively in drone brood cells while in colonies of *A. mellifera* it reproduces in worker brood cells as well [4]. In cold, tem-

perate, and Mediterranean climates the mite population grows exponentially until the colony collapses, due mainly to a high percentage of bees damaged by *V. jacobsoni* during their pupal development [5].

Since warmer climates enable honey bee colonies to produce a higher number of brood cycles per year than cold climates, the population growth of the parasite is higher in Mediterranean climates than in cold and temperate climates [6]. As a rule of thumb, the mite population grows the faster the warmer the climate is. Surprisingly, however, population growth of *V. jacobsoni* is reported to be low in tropical climates [7]. Temperature in brood cells has a significant impact on the proportion of female offspring that reach adulthood within the brood cell and emerge together with the young

bee [8], but even in tropical climates brood nest temperature does not exceed the temperature levels found in honey bee brood nests in colder climates [9]. Temperature within the brood nest can thus not explain low reproduction of *V. jacobsoni* in tropical climates. Tropical climates are often characterized by high humidity. We therefore examined the impact of high levels of relative humidity (RH) upon reproduction of the parasite in worker brood cells.

The experiments were conducted during May and June. Bee colonies were large sized with five to ten combs of open and sealed brood. Honey bee (*A. mellifera*) worker brood cells were infested with a single *V. jacobsoni* female within 5 h after capping. The mites were collected from adult honey bees. *V. jacobsoni* females mate within the brood cell with their brother or the male offspring of another mite reproducing within the same brood cell immediately after reaching the adult stage [10]. Therefore female mites are generally able to produce offspring after leaving the brood cell. The moment of capping was determined by marking almost capped brood cells on an overlaying transparent sheet and checking them at 1-h intervals until they were capped. The brood combs containing the infested cells were subsequently kept in an incubator at 34°C. The humidity within the incubator was kept either between 59% and 68% RH or between 79% and 85% RH. Previous studies found reproduction of *V. jacobsoni* to be higher at a humidity of 70% RH than at

40% RH [11]. Conditions for the test groups kept at 59–68% RH was thus close to optimum.

We found within a range of 31°–35°C no clear impact of temperature upon the percentage of reproducing mites [12]. Some 240–250 h after capping the brood cells were opened and the presence of mite offspring was scored. In three test series with a total of 174 brood cells kept at 59–68% RH on average 53% of the mites produced offspring (first series: 52%, $n = 33$; second series: 50%, $n = 18$; third series: 54%, $n = 123$). In three test series with a total of 127 brood cells kept at 79–85% RH on average only 2% (first series: 6%, $n = 17$; second series: 0%, $n = 83$; third series: 4%, $n = 27$) of the mites produced offspring. The difference in percentage of reproducing mites was highly significant (2×2 contingency table, $P < 0.0001$). *V. jacobsoni* females obviously react very sensitively to high RH and almost never reproduce at levels above 80% RH.

Temperature within the honey bee brood nest ranges from 31° to 36°C [13]. RH decreases with increasing temperature. Since ambient temperature in cold and temperate climates is generally clearly below brood nest temperature, RH within the brood nest is comparably low even when ambient RH is high. RH in the brood nest of *A. mellifera* colonies is usually about 40% [14], and most likely levels above 70% hardly occur in temperate and cold climates even under extreme conditions [15]. In Mediterranean climates during summer temperatures close to brood nest temperature are frequent, but RH is usually low. Only in tropical climates are both temperature and RH frequently high. The question is whether and how honey bees can reduce RH under high ambient temperature conditions. Honey bees can increase temperature within the brood nest by generating heat with their wing muscles or decrease temperature by simultaneously evaporating water and creating currents of air [16] while evaporation without air circulation enables them to increase RH within the brood nest. If, for example, during nectar flow

RH increases within the colony, the bees raise the temperature within the colony and produce currents of air to transport humid air outside the hive entrance. High ambient temperatures combined with high RH do not allow honey bees to control conditions significantly and the bees partially evacuate the nest, clustering at the nest entrance [17]. Under tropical conditions RH values within the brood nest are therefore most likely frequently equal to ambient RH. The results from our laboratory study provide thus information concerning conditions for reproduction of *V. jacobsoni* in honey bee colonies in tropical climates.

The present data provide a simple explanation for the fact that often in tropical climates population growth of *V. jacobsoni* is unexpectedly low. The significant impact of differences in relative humidity of only 9–25% upon reproduction and therewith on population growth of a parasite demonstrates another probable effect of environmental factors upon parasite virulence.

1. Ritter, W., in: Present Status of Varroa-tosis in Europe and Progress in the Varroa mite Control, p.25 (R. Cavalloro, ed.). Luxembourg: Office for Official Publications of the European Communities 1989; Ritter, W., in: Africanized Honey Bees and Bee Mites, p.349 (G. R. Needham, R.E. Page, M. Delfinado-Baker, C.E. Bowman, eds.). Chichester: Horwood 1988
2. Delfinado, M.D.: Apicultural Res. 2, 113 (1963); De Jong, D., Morse, R.A., Eickwort, G.C.: Ann. Rev. Entomol 27, 229 (1982)
3. Peng, Y.S.C., Fang, Y., Xu, S., Ge, L., Nasr, M.E.: J. Invertebrate Pathol. 49, 54 (1987); Rath, W., Drescher, W.: Apidologie 21, 311 (1990); Moritz, R.F.A.: J. Heredity 76, 267 (1985)
4. Koeniger N., Koeniger, G., Wijayagunasekara, N.H.P.: Apidologie 12, 37 (1981)
5. Schneider, P., Drescher, W.: Apidologie 18, 1001 (1987); Schatton-Gadelmeyer, K., Engels, W.: Entomol. Generalis 14, 93 (1988)
6. Frilli, F. in: Present Status of Varroa-tosis in Europe and Progress in the Varroa mite Control, p.37 (R. Cavalloro, ed.). Luxembourg: Office for Official Publications of the European Communities 1989; Korpela, S., Aarhus, A., Fries, I., Hansen, H.: J. Apicultural Res. 31, 157

(1992); Marcangeli, J.A., Eguaras, M.J., Fernandez, N.A.: Apidologie 23, 57 (1992); Kraus, B., Page, R.E.: Apidologie 26, 149 (1995)

7. De Jong, D., Gonçalves, L.S., Morse, R.A.: Bee World 65, 117 (1984); Ritter, W., De Jong, D.: Zeitschr. Angew. Entomol. 98, 55 (1984); Moretto G., Gonçalves L.S., De Jong, D., Bichuette M.Z.: Apidologie 22, 197 (1991)
8. Le Conte, Y., Arnold, G., Desenfant, P.: Environ. Entomol. 19, 1780 (1990); Kraus, B., Velthuis H.H.W. (in preparation)
9. Rosenkranz, P.: Entomologia Generalis 14, 123 (1988)
10. De Ruijter, A.: Apidologie 18, 321 (1987)
11. Le Conte, Y., Arnold, G., Desenfant, P.: Environ. Entomol. 19, 1780 (1990); Kraus, B., Velthuis H.H.W. (in preparation)
12. Kraus, B., Velthuis, H.H.W. (in preparation)
13. Gates, B.N.: Bulletin of the U.S. Department of Agriculture 96, 1 (1914); Büdel, A., in: Biene und Bienenzucht, p.115 (A. Büdel, E. Herold, eds.). Munich: Ehrenwirth 1960; Hess W.R.: Zeitschr. Vergleich. Physiol. 4: 465 (1926); Vanssell G.H.: J. Econom. Entomol. 23, 418 (1930); Himmer A.: Biol. Rev. 7, 224 (1932); Dunham W.E.: Glean. Bee Cult. 61, 527 (1933); Wohl-gemuth R.: Zeitschr. Vergleich. Physiol. 40, 119 (1957); Kronenberg F., Heller H.C.: J. Comp. Physiol. B 148, 65 (1982); Fahrenholz L., Lamprecht I., Schricker B.: J. Comp. Physiol. 159, 551 (1989); Levin, C.G., Collinson, C.H.: J. Apicultural Res. 29, 35 (1990); Rosenkranz, P., Engels, W.: Brazil. J. Genet. 17, 383 (1994); Kraus, B., Velthuis, H.H.W. (in preparation)
14. Büdel, A.: Zeitschr. Vergleich. Physiol. 31, 249 (1960); Wohl-gemuth, R.: Zeitschr. Vergleich. Physiol. 40, 119 (1957)
15. Wohl-gemuth, R.: Zeitschr. Vergleich. Physiol. 40, 119 (1957)
16. Hazelhoff, E.H.: Physiol. Comp. Oecol. 3, 343 (1954); Lindauer, M.: Zeitschr. Vergleich. Physiol. 36, 391 (1954); Wohl-gemuth, R.: Zeitschr. Vergleich. Physiol. 40, 119 (1957); Heinrich, B., Seeley, T., in: Insect Thermoregulation, p.206 (B. Heinrich, ed.). New York: Wiley 1981
17. Dunham W.E.: J. Econom. Entomol. 24: 606 (1931); Heinrich, B., Seeley, T., in: Insect Thermoregulation, p.206 (B. Heinrich, ed.). New York: Wiley 1981