

**A hypothesis on the functions of juvenile hormone of host
in sexual maturation and oviposition of *Varroa jacobsoni*
(Acari: Mesostigmata: Varroidae)**

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Resumen: El ácaro *Varroa jacobsoni* Oudemans es una plaga de la apicultura asiática y europea, que actualmente se ha extendido al Africa y América del Sur. Este es un artículo teórico sobre la posible regulación del ciclo de vida del ácaro por la hormona juvenil (JH) de la abeja, *Apis mellifera*. El modelo propone que *V. jacobsoni* carece de hormona juvenil propia y la toma de la hemolinfa de la abeja, adquiriendo dos niveles hormonales ("X" y "Y") del adulto. La fertilización requiere un nivel mayor ("Z"). El ácaro con nivel "Y" se separa del adulto y, tal vez atraída por feromonas de la cría o la alta concentración del CO₂ de la larva, penetra en su celda, se alimenta y alcanza el nivel "Z". Se produce un huevo de hembra, el nivel hormonal baja a "Y" y se produce un huevo de macho partenogénico. Las hembras de *V. jacobsoni* que no alcanzan el nivel "Z" sólo producen huevos de macho. La reproducción exitosa de *V. jacobsoni* en larva de zángano de *Apis cerana*, y larva de zángano u obrera de *A. mellifera*, probablemente se asocia con un alto nivel de hormona juvenil durante cierta fase larval y un período de apertura de celda de más de 240 h. Finalmente, después de completarse la oviposición el nivel de JH de la hembra del ácaro probablemente desciende a la condición de la "diapausa" reproductiva invernal ("X").

The ectoparasitic mite *Varroa jacobsoni* Oudemans has become a scourge of commercial apiculture. It has rapidly extended its range from Asia westward in Europe and recently reached northern Africa. In America, it is now found from Brazil to Argentina, and may extend northward and reach North America as a parasite of africanized bees. The mite feeds on the hemolymph of adult and larval honey bees (*A. cerana*, *Apis mellifera*) and completes its life history within the cells of larval and pupal stages of the bee.

W. Engels (pers. com., Sept. 1984) has stated that the juvenile hormone (J.H.) of the bee plays no role in the behavior of *V. jacobsoni*. However, there is much evidence that the opposite is true (see Pound & Oliver 1979; De Ruijter, 1983; Hänel, 1983; Ruttner & Marx, 1984). Here I present a model of the possible role of the bee J.H. or a precursor of

this hormone, as governor of the sexual maturation, oviposition and maturation of spermatids in the female mites. This relationship appears reasonable, since it is advantageous for the parasite to synchronize its activities with those of the host, and because the host's hemolymph passes directly to the mite.

Female *V. jacobsoni* sucks hemolymph from all stages of the bee, except larvae 1-4 days of age, which have a low titre of JH (Smirnov, 1978). Proteins of the bee have been detected in the hemolymph and even in the oocytes of the mite which reabsorbs them without significant degradation (Tewarson, 1983). It seems probable, then, that the mite lacks the glands that produce JH, and takes the hormone or a precursor from the host.

Apparently, the eggs of *V. jacobsoni* become mature and fertilized one at a time, and it is possible that a low hormone titre of the

Note: After writing this paper, I learned of a manuscript by Hänel & Koeniger (Possible regulation of the reproduction of the honey bee mite *Varroa jacobsoni* (Mesostigmata, Acari) by a host's hormone: juvenile hormone (III). J. Insect Physiol., in press). There they report experimental evidence supporting that J.H. plays a role in the reproduction of the mite.

bee larva influences the high frequency of occurrence of a single male, second in the sequence: one female, one male, and three female eggs, in worker brood cells (see below), (Infantidis, 1983)

When parasitic on *A. mellifera*, the mite prefers drone over worker cells, and I have found that, under laboratory conditions, it oviposited in queen cells and the males developed to maturity. If the host is *A. cerana*, the mite develops only in drone larvae (Koeniger *et al.* 1981), perhaps because this species has a worker's larvae postcapping period of 216 to 240 h, or because it has a lower titre of J.H. The preference of these mites for 5-8 days old larvae of *A. mellifera* could be related to their high level of J.H., with the corresponding high production of CO₂ acting as a clue and as attractant to the parasite.

According to the level of J.H. present in the adult and the state of sexual maturation, *V. jacobsoni* has five developmental phases which fit with those described by Ramírez and Otis 1986.

I. Arrested phase: Emergence from the cell, mites become phoretic on adult drone or worker bees. Winter reproductive females feed on hemolymph of drone or worker bee and probably receive the first J.H. The female has 5 to 20 functional oocytes (Fig. 1).

During the winter the mites feed very little (let "X" be the J.H. level early reproductive *V. jacobsoni* females). In the tropics, the first levels of J.H. ("X" and "Y" = previtellogenic) are reached after a short period, and year around which could explain why the European races (post-capping period: more than 240 h) almost disappear when introduced in tropical areas where *V. jacobsoni* occurs (Ramírez & Otis, 1986).

II. Previtellogenic active phase: Female with J.H. level Y. enters food of a brood cell and becomes inactive. Capping occurs and the larva gorges food. In drone cells, gorging occurs some 60 h before capping, thus liberation of the mite takes place earlier than in worker cells. J.H. level in the mite is equal to "Y" (higher than "X"). See fig. 1. Five to 7 (occasionally 20) oocytes attain maturity and a me-

dium size, later 1 or 2 oocytes reach twice the size (previtellogenic oocytes).

III. First vitellogenic active phase and oviposition of first two eggs: The female probably feeds for the first time in the larval and prepupal stages, reaching level of J.H. ("Z"). One of the vitellogenic oocytes attains 10-20 more volume. The first spermatocytes mature and fertilization of an egg occurs. The first egg is laid 60 h after capping of the worker cell (Infantidis, 1983). At this time or shortly before, the second eggs grows and becomes mature, the J.H. probably reduces its level to "Y", which 30 h later determines oviposition of a parthenogenetic male egg. If the female does not reach "Z" again (e.g. she fails to feed again), she will then lay one or a few male eggs more (Fig. 1).

IV. Second vitellogenic active phase and oviposition of last two eggs: Female feeds on prepupa and reaches level "Z", maturation of a third eggs occurs. Some spermatocytes mature and fertilization occurs. A second female egg is laid 120-124 h after capping, and J.H. decreases to "Y". Feeding and acquisition of "Z" and oviposition occur two more times, 148-154 and 190-192 h after capping (Fig. 1).

V. Maturation and mating: Once *V. jacobsoni* reaches maturity in the capped brood cell, copulation occurs and females become infective, with probably a low or zero level of J.H. Other case of adaptation of a parasite to its host is that of the European rabbit flea, the breeding cycle of which is regulated by the reproductive hormones of the rabbit (Rothschild, 1977).

CONCLUSION

The reproductive cycle of the *Varroa jacobsoni* female is divided into five phases according to its productive biology and the level of juvenile hormone present in each:

Varroa jacobsoni seems to lack the glands that produce juvenile hormone (JH) or its

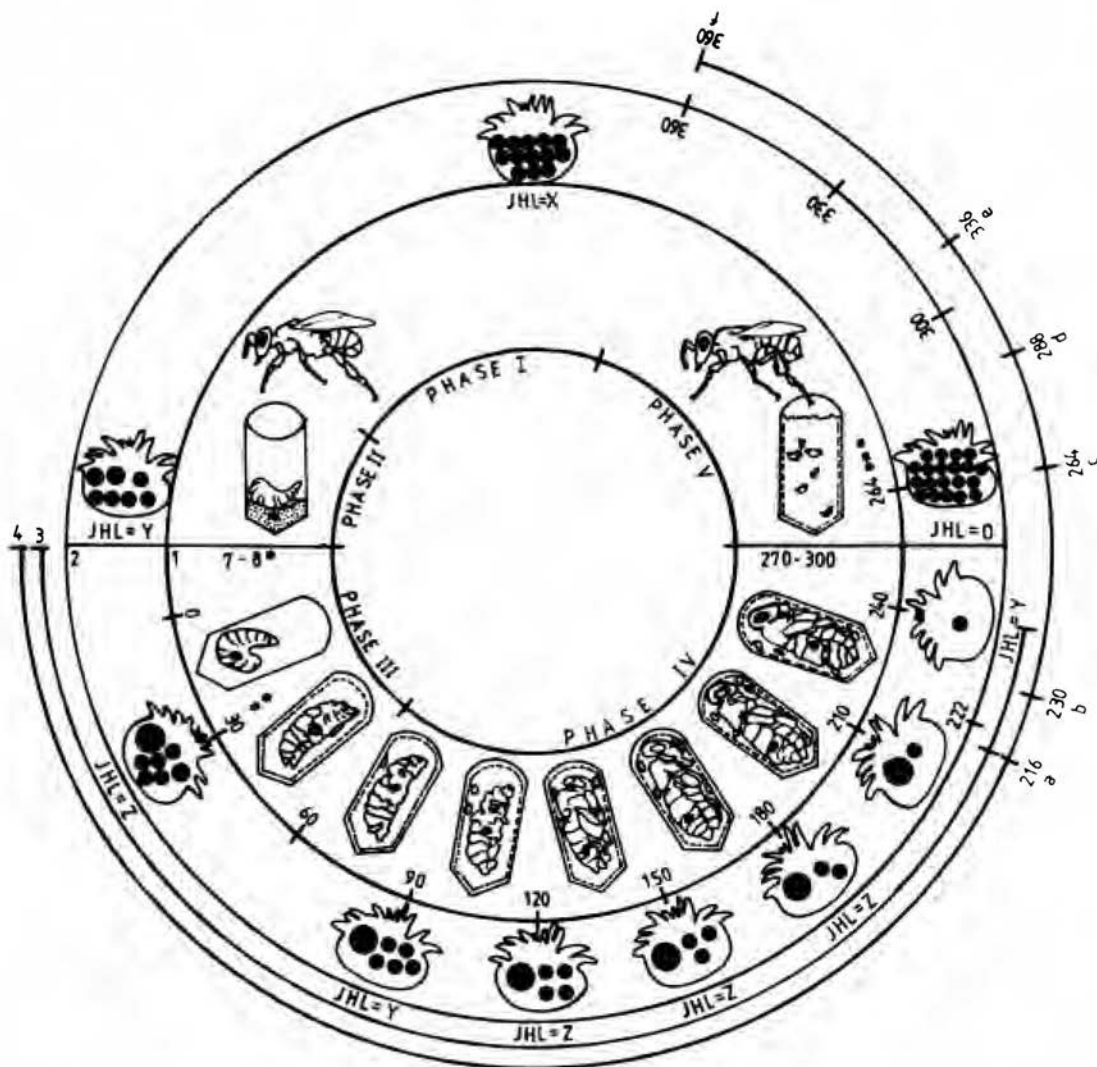


Fig. 1: Life cycle of *Varroa jacobsoni* in boney bees, levels of juvenile hormone (JH) and eclosion of adult mites.

- 1) Oviposition
- 2) Eclosion from egg
- 3) Dark-pigmented eye: 216; worker; 240, drone
- 4) Uncapping: a) queen; b-d) *A. m. scutellata*; c) *A. m. cecropia*; d) European drone.

* Days

** Hours after capping

*** Infective stage (Infantidris, 1983)

precursor which obtain, from the hemolymph of the honey bee. It acquires two levels of H.J. (J.H.L. = X and J.H.L. = Y) while ectoparasitic on the adult bee (drone or worker), which play an important role in the privitellogenesis and in maturation of the spermatocytes. Once previtellogenic *V.*

jacobsoni reaches J.H.L. = Y, it drops from the adult bee and searches for a brood cell with a bee larva of the right age and J.H. level. The mite is probably attracted by the brood pheromones or the CO₂ produced by the bee larva. As the mite feeds on the bee larva, it acquires a third level of J.H. (JH=

Z) which allows maturation of oocytes and spermatocytes, with the subsequent oviposition of a female egg.

Normal oviposition of a male egg (second egg) by parthenogenesis is governed by a low level of JH, ($JHL=Y$). *V. jacobsoni* females which do not reach the $JHL=Z$ after the second oviposition will lay only male eggs. The successful reproduction of the mite in the larval drone of *Apis cerana* and in larvae of the drones or workers of *A. mellifera* is probably associated with a high level of JH in the host and with a postcapping period of more than 240 hours. The amount of JH obtained by a mature mite in a worker or drone larva of *A. mellifera* fulfills its JHL requirements for laying female and male eggs. After completing the entire cycle of oviposition in a bee cell, the JHL in *V. jacobsoni* females probably drops to the level of the winter reproductive diapause, that is $JHL=X$. One of the factors that makes the worker larvae of *A. cerana* resistant to *V. jacobsoni* could be a lower level of JH compared to that of European races of *A. mellifera*, or its shorter postcapping period.

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