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Why do *Varroa* mites invade worker brood cells of the honey bee despite lower reproductive success?

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Abstract *Varroa jacobsoni* reproduces both in drone and worker brood cells of honey bees, but in drone cells reproductive success is higher than in worker cells. A simple model using clonal population growth as a fitness measure has been developed to study the circumstances under which specialization on drone brood would be a better strategy than reproduction in both types of cell. For European *Apis mellifera*, the model suggests that if mites have to wait less than 7 days on average before they can invade a drone cell, specialization on drone brood would be a better strategy. This is close to the estimated waiting time of 6 days. Hence, small differences in reproductive success in drone and worker cells and in the rate of mortality may determine whether specialization on drone brood will be promoted or not. In European *A. mellifera* colonies, *Varroa* mites invade both drone and worker cells, but specialization on drone brood cells seems to occur to some extent because drone cells are more frequently invaded than worker cells. In the parasite-host association of *V. jacobsoni* with African or Africanized *A. mellifera* or with *A. cerana*, the mites also invade both drone and worker cells, but the mites specialize on drone brood for reproduction since a large percentage of the mites in worker brood do not reproduce. Only in the parasite-host association of *Euvarroa sinhai*, a mite closely resembling *V. jacobsoni*, and *A. florea* is specialization complete, because these mites only invade drone brood.

Key words *Varroa jacobsoni* · *Apis mellifera* · Reproductive strategy · Optimization model

Introduction

Varroa jacobsoni is currently one of the most important pests of *Apis mellifera* colonies. It parasitizes adult bees, but reproduces only in capped honeybee brood. Therefore, mites have to invade either drone or worker brood cells before they are capped (Ifantidis and Rosenkranz 1988). After invading a brood cell, *Varroa* mites lay up to 6–7 eggs at 30-h intervals, the first egg being a (haploid) male egg and the following (diploid) female eggs (Ifantidis 1983; Rehm and Ritter 1989). However, the last eggs laid will usually not reach maturity, because the developmental time of the immature bee in the capped cell is too short to allow completion of mite development. Since the capped stage of drone cells is about 2 days longer than that of worker cells (Jay 1963), drone cells are in principle more rewarding in terms of mite reproduction than worker cells because more young mites can reach maturity. In west European *A. mellifera*, mites produce on average 2–3 viable female offspring in drone cells and 1–2 viable female offspring in worker cells (Schulz 1984; Fuchs and Langenbach 1989).

The question arises why *Varroa* mites do not restrict invasion to drone cells, thus maximizing their reproductive success. *Euvarroa sinhai*, a species closely related to *V. jacobsoni*, parasitizes *Apis florea* and apparently uses this reproductive strategy (Mossadegh and Birjandi 1986; Kapil and Aggarwal 1989). However, invading only drone brood cells may be less successful when mite density is such that invasion per drone cell is high. Since reproduction per mite is negatively correlated with the number of mites that have invaded the same cell (Fuchs and Langenbach 1989), reproductive success in worker cells may become just as high as that in drone cells when the density of mites in the colony increases. Using a mathematical model in which reproductive success was negatively influenced by mite density, Fuchs (1992) simulated the effect of

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the annual cycle of brood cell availability in typical European colonies on reproductive success. The simulations suggested that at an average infestation level of 300 or more mites per colony a *Varroa* mite should also invade worker cells to maximize reproduction. A second reason why exclusive invasion of drone cells may be a less successful strategy is the risk of spending a long time searching for a drone cell to invade, especially since drone brood cells may be scarce or even absent in the colony (Page and Metcalf 1984; Rowland and McLellan 1987). While mites remain on adult bees waiting for a drone cell they may die. Moreover, they might have used this period to produce offspring in worker cells.

In this paper we calculate the net rate of increase of a *Varroa* mite population assuming a strategy of invading exclusively drone brood cells. We then evaluate the circumstances under which invading both drone and worker brood cells will result in higher population growth. In *Varroa* mites sib-mating is the rule since mating takes place inside the capped brood cells and in most cases one mother mite is confined to a cell. Therefore daughters and granddaughters increase fitness of a mother mite equally and the mite clone that has the highest population growth will outnumber others.

Comparing different reproductive strategies is not a mere theoretical exercise to increase insight into the system. Different reproductive strategies do exist. A high percentage of *Varroa* mites that invade worker cells of Africanized honey bees in Southern America refrain from reproduction (e.g. Camazine 1986; Rosenkranz et al. 1990), and the same is reported for *Varroa* mites invading worker cells of *A. mellifera intermissa* (Ritter et al. 1990; Ritter 1993). In *A. cerana*, *Varroa* mites invade both worker and drone cells, but as a rule reproduce only in drone cells (Tewarson et al. 1992; Rosenkranz et al. 1993). Finally, *Euvarroa sinhai* invades and reproduces only in drone brood cells of *A. florea* (Mossadegh and Birjandi 1986; Kapil and Aggarwal 1989). This study aims to increase insight into the selective forces that may have shaped the various reproductive strategies used by honey bee mites.

The model

A model for the net rate of population increase

Consider a mite specializing on reproduction in drone brood cells only. At the beginning of her adult life she emerges from a brood cell and she stays for a certain time on adult bees searching for a new drone brood cell to invade. Subsequently she invades a drone brood cell and then reproduces, after which a new cycle starts. The expected number of offspring, $m(t)$, produced over

the total period from emergence via invasion to emergence (i.e. the sum of the time spent searching, T_s , plus the time spent in development, T_d ; $t = T_s + T_d$) is:

$$m(T_s + T_d) = f(T_s)N_d$$

where the time spent searching for a drone cell, T_s , is a stochastic variable with probability density function $f(T_s)$, T_d denotes the developmental time of capped drone brood, and N_d denotes the number of females emerging from the drone brood cell (N_d includes the mother if she survives, based on the assumption that the current reproductive effort is independent of the reproduction in the past). This parameter will also be determined by behaviour of the bees (brood care or brood removal). When $t < T_d$, the time is too short to produce offspring, and when $t > T_d$ offspring are produced if a mite finds a drone cell in the time that is left for searching, $T_s = t - T_d$:

$$\begin{aligned} m(t) &= 0 & (t < T_d) \\ m(t) &= f(t - T_d)N_d & (t > T_d) \end{aligned}$$

After emergence a mite remains "hitch-hiking" on adult bees and waits until she encounters a drone brood cell, which she then enters. If the mite has to wait δ time units on average, and if she encounters drone brood cells at a constant rate, $\alpha = 1/\delta$, the probability density function for the expected time until encounter is described by

$$f(t) = \alpha e^{-\alpha t}$$

The per capita rate of encounter α is the same as the per capita rate of invasion into drone cells which we determined recently (Boot et al. in press b), because a mite should always accept a suitable drone cell upon encounter. In colonies where the ratio between the number of brood cells capped per day and the number of bees in the colony is constant, mites do invade brood cells at a constant rate (Boot et al. 1994, in press b).

Hitch-hiking on a bee, a mite experiences a constant mortality rate of μ (Boot et al. in press a), which will be affected by grooming behaviour. This implies a survivorship function, $l(t)$, i.e. the probability of surviving up to age t after emergence from a brood cell, of

$$\begin{aligned} l(t) &= 1 & (t < T_d) \\ l(t) &= e^{-\mu(t - T_d)} & (t > T_d) \end{aligned}$$

Thus, a mite of age t has not experienced any risk of mortality during development and has been exposed to a constant mortality rate μ during searching, i.e. during $t - T_d$ time units. Note that mortality within the brood cell is incorporated in N_d .

The expected reproductive success of a mite per brood cycle is then given by

$$R_0 = \int_0^{\infty} l(t)m(t)dt$$

This could be used as a fitness measure. However, R_0 does not take into account the fact that the mite population may be growing, and that offspring produced at an early age contribute more to population growth. This is incorporated by weighing offspring produced at age t by a factor e^{-rt} , where r is the net rate of population increase:

$$\int_0^{\infty} e^{-rt} l(t) m(t) dt$$

By setting this expression equal to 1, Lotka's equation is obtained (Yodzis 1989), which can be used to calculate the net rate of population increase r . Substitution of $m(t)$ and $l(t)$ gives

$$\int_{T_d}^{\infty} e^{-rt} e^{-\mu(1-T_d)\alpha} e^{-\alpha(t-T_d)} N_d dt = 1$$

which can be solved, to yield

$$N_d e^{-rT_d} = 1 + (r + \mu)/\alpha \quad (1)$$

As a control, note that if the encounter rate with drone cells becomes very large (i.e. $\alpha \rightarrow \infty$), the searching time becomes very small and the above expression approaches

$$N_d e^{-rT_d} = 1$$

which has an explicit solution in r , the familiar

$$r = \ln(N_d)/T_d$$

When α is not infinite, Eq. (1) cannot be solved explicitly. Using a graphical method (Fig. 1), it can be shown that r will decrease when α decreases, which is intuitively obvious since growth rate decreases when it takes more time to find drone brood cells.

When to invade a worker brood cell

A mite hitch-hiking on a bee can also invade a worker brood cell and reproduce there. When drone brood cells are abundant, however, a mite will do best by ignoring

opportunities to invade worker brood cells, since the number of mites emerging from a worker brood cell, N_w , is less than the number emerging from a drone brood cell. The optimal strategy (invade only drone cells, or invade both types of cell) depends on the net rate of population increase r . Consider a mite on a bee encountering a worker brood cell. Should the mite invade, or should she remain on the bee? If she enters the worker brood cell, N_w mites emerge T_w time units later, where T_w is the developmental time of capped worker brood. If she remains on the bee, she may encounter a drone cell soon, but she may also have to wait for a long time. On average, a mite specializing on drone cells will have e^{rT_w} number of offspring after T_w time units, as follows from the expected rate of increase of mites specializing on drone cells (specified by Eq. 1). Therefore it is best to ignore worker bee cells if

$$N_w < e^{rT_w}$$

or equivalently,

$$\ln(N_w)/T_w < r \quad (2)$$

Estimates for input parameters are listed in Table 1. Reproductive success has been determined in many studies (see Fries et al. 1994 for a review). Here, five studies from Europe are listed in which the number of mites studied is relatively high in comparison to other studies on reproduction of *Varroa* mites. In our calculations, the number of viable daughters emerging from worker and drone cells is assumed to be 1.1 and 2.2 respectively. In addition, the mother's mortality during her stay in a brood cell is assumed to be 20%, which results in estimates for N_w and N_d of 1.9 and 3.0 respectively.

When the net rate of population increase is higher than the criterion for invading a worker cell, $r_{crit} = \ln(N_w)/T_w$ (Eq. 2), mites should not invade worker cells. With our set of parameters, this occurs when the average time that mites have to wait for a drone cell to invade, δ , is less than 7 days (Fig. 2a). When δ is longer, mites will do better invading both drone and worker brood cells.

The actual time mites would have to wait on average for a drone cell can be calculated as the inverse of the per capita rate of invasion into drone cells, σ (Boot et al. in press b). The per capita rate of invasion depends linearly on the ratio between the number of drone brood cells capped daily and the number of bees in the colony:

$$\sigma = 51.9 \times \text{number of drone cells capped daily} / \text{number of bees (day}^{-1}\text{)}$$

In a honey bee colony the ratio between the number of brood cells occupied and the number of bees present appears to be c. 1 on average (range 0.8–1.5), whereas c. 8% of the brood is drone brood (Table 1). If the ratio between the number of drone brood cells

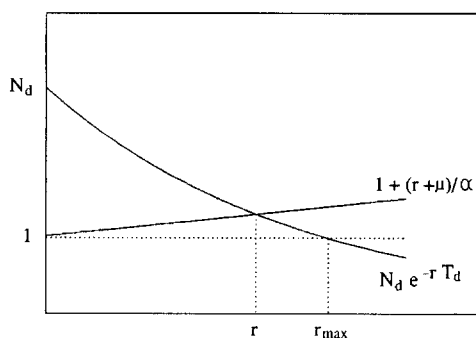


Fig. 1 Graphical method for finding the long-term rate of increase r , defined implicitly by Eq. 1. It can be seen that if the encounter rate with drone cells, α , decreases, the line becomes steeper and intersects the exponential function more to the left, implying a lower r .

Table 1 Estimates of input Parameters

Reproductive success of <i>Varroa</i> mites in worker brood cells:		
Number of viable daughters per mite (F_w)	Number of mites on which estimate is based	Reference
0.7	238	Ifantidis 1984
1.3	450	Schulz 1984
1.4	316	Fuchs and Langenbach 1989
1.1	1334	Martin 1994
1.1	1682	Boot et al. in press a
Reproductive success of <i>Varroa</i> mites in drone brood cells:		
Number of viable daughters per mite (F_w)	Number of mites on which estimate is based	Reference
1.7	155	Ifantidis 1984
2.6	660	Schulz 1984
2.2	279	Fuchs and Langenbach 1989
Mortality related to staying in a brood cell (μ_{cell}) is c. 20% during one brood cycle (Boot et al. in press a)		
Mortality related to staying on adult bees (μ_{bee}) is c. 0.6% per day (Boot et al. in press a)		
Developmental time of capped worker brood (T_w) is c. 12 days (Jay 1963)		
Developmental time of capped drone brood (T_d) is c. 14 days (Jay, 1963)		
Average brood/bee ratio in an <i>A. mellifera</i> colony over a season:		
Mean number of occupied brood cells per bee	Number of colonies on which estimate is based	Reference
0.8	16	McLellan 1978
0.9	3	Omholt 1986
1.1	30	Imdorf and Kilchenmann, 1987
0.8	2	Imdorf et al. 1987
1.5	3	Bühlmann 1992
Average drone/worker brood ratio in an <i>A. mellifera</i> colony over a season (Page and Metcalf 1984): 0.077 (Data from Allen 1965); 0.079 (Data from Page 1981)		

occupied and the number of bees is assumed to be 0.08, 0.08/24 drone cells will be capped daily per bee since total development time of drones is c. 24 days (Jay 1963), and $\sigma = 51.9(0.08/24) = 0.173 \text{ day}^{-1}$. Thus mites would have to wait on average $1/0.173 = 5.8$ days for a drone cell to invade, which seems to be short enough to favour specialization of mites on drone brood, but also quite close to the critical value of 7 days.

Effect of different parameters on the period that mites can afford to wait for a drone cell to invade

Effect of the number of mites emerging from a drone cell, N_d

When the number of mites emerging from a drone cell increases, mites can afford to wait longer for a drone cell before invading both types of brood cells will be a better strategy. If the criterion (Eq. 2) for invading both types of brood is met, then

$$r = \ln(N_w)/T_w$$

Substitution of r in Eq. 1 gives a linear relationship between N_d and the average period mites have to wait for a drone cell, δ (Fig. 2b). Whether mites should specialize on drone brood or not, is sensitive to changes

in N_d . When N_d is less than 2.1, both types of brood should always be invaded.

Effect of the mortality rate while on adult bees, μ

When μ increases, waiting for a drone cell to invade will incur a higher penalty. Invading both types of brood will be a better strategy at shorter average waiting times for a drone cell. Substitution of r by $\ln(N_w)/T_w$ in Eq. 1 gives an inverse relationship of μ with δ (Fig. 2c). Specialization on drone brood is most sensitive to changes in μ at low mortality rates. When $\mu = 0$ mites can afford to wait 7.8 days for a drone cell before invading both types of brood is a better strategy.

Effect of the number of mites emerging from worker cells, N_w

The criterion determining whether invading both types of brood cells is a better strategy or not increases logarithmically with increasing N_w . Invading both types of brood will be a better strategy at shorter average periods of waiting for a drone cell. Substitution of r by $\ln(N_w)/T_w$ gives the implicit relationship shown in Fig. 2d. As N_w approaches 1, the period mites can

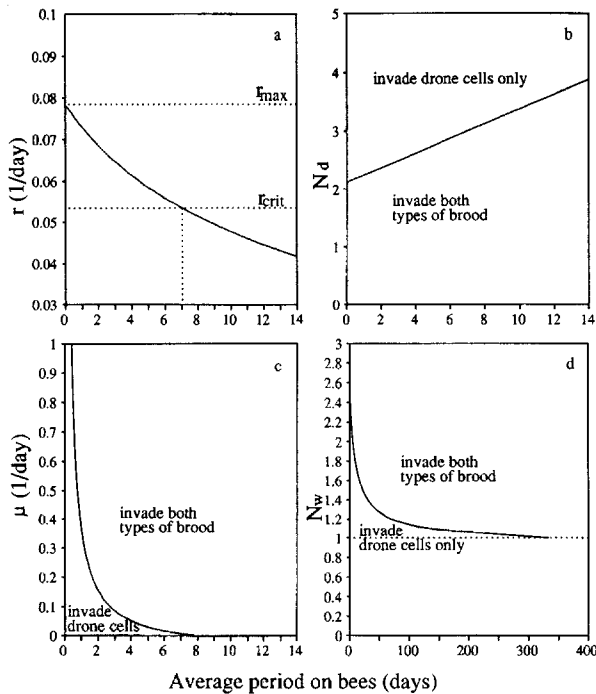


Fig. 2 a Relation between the net rate of population increase, r , and the average period mites have to stay on adult bees waiting for a drone cell to invade, δ ; $N_d = 3.0$, $N_w = 1.9$, $T_d = 14$ days, $T_w = 12$ days and $\mu = 0.006$ day⁻¹. b–d Sensitivity analysis of b the average number of mites emerging from a drone cell, N_d , c the relative mortality rate on adult bees, μ and d the average number of mites emerging from a worker brood cell, N_w on the period that mites can afford to wait for a drone cell

afford to wait for a drone cell before invading both types of brood will be a better strategy rapidly increases.

Discussion

The model shows that *Varroa* mites can afford to wait on average c. 7 days for a drone brood cell before invasion of both brood cell types would be a better strategy to adopt. This period of 7 days is close to the actual period mites have to wait for a drone cell, which was estimated to be c. 6 days on average. Whether mites do better by specialization on drone brood or not is therefore sensitive to small differences in the parameters (Fig. 2), and the result may well depend on local circumstances.

In the model the mite population is assumed to grow exponentially. Thus, mite density will increase in a colony and more mites will invade per cell. Since the number of viable daughters produced per mite is negatively correlated with the number of mites that have invaded the same cell (Fuchs and Langenbach 1989), N_d will slowly decrease with increasing mite density. On the short term, however, during which the mites should choose either to invade a worker cell or to wait for a drone cell, N_d may be assumed constant. When

mite density is high, the model may therefore be applied by adjusting the number of viable daughters per mite produced in a drone cell, F_d , where $N_d = F_d +$ the fraction of mother mites that survive in the cell. Fuchs (1992) simulated to what extent F_d is lowered at different densities: at an average density of 2, 6, 10, 16 and 20 mites per drone cell, F_d decreases 18, 41, 58, 69 and 76%, respectively.

In European *A. mellifera* colonies, specialization for drone brood cells seems to occur to some extent, because a drone cell is invaded 12 times more frequently than a worker cell (Boot et al. in press b). Since the mites should always accept a suitable drone brood cell when they encounter one, the rate of invasion of drone cells is a measure of the encounter rate. One cannot expect a suitable worker brood cell to be encountered as often as a suitable drone brood cell, because drone brood cells are attractive to mites for 2–3 times as long as worker brood cells, and will therefore be encountered 2–3 times more often. Moreover, the chance of encountering a cell may be proportional to its surface area, which is 1.7 times larger for a drone cell than a worker cell. By combining these effects on the encounter rate, a suitable drone brood cell is expected to be encountered 3.4–5.1 times more frequently than a suitable worker cell. However, since drone cells are invaded 12 times more frequently, this suggests that suitable worker cells are not accepted in c. 70% of the encounters.

In the host-parasite relationship between *A. florea* and *E. sinhai*, specialization on drone brood cells is complete. In principle, mites could reproduce in worker brood cells of *A. florea*, because the development time of capped worker brood is 11.2 days (Sandhu and Singh 1960). By transferring *E. sinhai* to *A. mellifera* brood, which *A. mellifera* bees keep at the same temperature as *A. florea* bees do (Dyer and Seeley 1991), Mossadegh (1990a, b) showed that 11.2 days should be long enough to produce viable daughters. Hence, *E. sinhai* has probably specialized on drone brood cells because waiting for drone cells is a better strategy to adopt than invading both types of cell.

In the host-parasite relationship between *A. cerana* and *V. jacobsoni* the mites do invade worker cells, but as a rule do not reproduce in these cells (Tewarson et al. 1992; Rosenkranz et al. 1993). In African or Africanized *A. mellifera* the same phenomenon occurs, albeit less conspicuously: a high percentage of the mites do not reproduce after invading worker cells (e.g. Camazine 1986; Ritter 1993). This is difficult to understand because the mites will be trapped for 11–12 days without any possibility of invading a drone cell. In this case, our model predicts invasion of worker cells only during periods of negative population growth and if invasion of worker cells implies a less negative growth than staying on adult bees. This might occur during periods when drone brood cells are absent or scarce

and mite mortality on adult bees is high. It has indeed been suggested that "grooming" behaviour by the bees causes high mortality of the mites on adult bees in colonies of *A. cerana* (Boecking et al. 1993), Africanized *A. mellifera* (Moretto et al. 1993) and *A. mellifera intermissa* (Boecking and Ritter 1993). In all of these hosts the phenomenon of a high percentage of mites that invade worker cells but do not reproduce has been reported. Another reason why mites might invade worker cells in which they do not reproduce is that by parasitizing a larva/pupa the mite enhances reproduction later. This implies that reproduction is negatively correlated with how long the mite stays on adult bees before reproducing. Al Ghzawi (1992) indeed found that after more than 26 days on adult bees, reproduction in worker brood cells rarely occurred. However, when mites stayed 1–20 days on bees, Boot et al. (in press a) found no correlation between the period spent on bees and reproduction.

Whether or not a mite reproduces after invasion into a worker cell, she will be trapped for 11–12 days. Therefore, refraining from reproduction, as occurs in *A. cerana* and African or Africanized honey bees, only makes sense if this results in a higher average number of emerging mites, N_w , than would be obtained by reproducing. This may be the case under the following circumstances. Firstly, mites that reproduce may have a higher chance of dying than mites that do not, because reproduction increases their physiological age. In addition, mortality may increase when the chance of an infested brood cell being removed by the bees is increased by reproduction of the mite (Boecking et al. 1993). Secondly, developmental time of capped worker brood is only 11 days in *A. cerana* (Kapil 1959; Tan et al. 1993) versus 12 days in European *A. mellifera* (Le Conte and Cornuet 1989; Harbo 1992). Hence, fewer daughters than in European *A. mellifera* are expected to reach maturity if mites reproduce in worker brood. In the *A. mellifera* races *scutellata* and *capensis* developmental times of 11.2 and 9.7 days respectively will also decrease N_w in comparison to European *A. mellifera* (Moritz 1985).

If the phenomenon of non-reproduction in worker cells is the result of adaptation of the mites to the bee strain, it is not necessarily an immediate consequence of a trait of the bees. Non-reproduction may well be a trait of the mites. This is in agreement with Fuchs (1994), who recently showed that variation in the percentage of mites refraining from reproduction did not depend on the origin of the worker brood when 12 distinct bee lines were tested.

In our model, we use intracolony population growth as a fitness measure and evaluate the effect of the average period on adult bees. On a larger scale however, there may be other factors selecting for a larger or shorter period on adult bees, for instance dispersal from colony to colony or absconding behaviour by the

bees. Which reproductive strategy of mites is promoted under different circumstances is an important question for further research, because whenever tolerance by honey bees of (*Euvarroa*)*Varroa* mites has been reported, it is associated with an increased specialization on drone brood cells in comparison with susceptible honey bees. Therefore, insight into which factors promote specialization on drone brood may help in breeding more tolerant European *A. mellifera* in future.

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