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Influence of the environment and the host on parasitization by *Varroa jacobsoni* Oud.

P. GARCIA FERNANDEZ
DPTO. PRODUCCION ANIMAL
CENTRO DE INVESTIGACION Y FORMACION AGRARIA
CONSERJERIA DE AGRICULTURA Y PESCA
JUNTA DE ANDALUCIA
CAMINO DE PURCHIL S/N
18014 GRANADA
SPAIN

SUMMARY - This is a review of the influence of external factors, such as climate and phenology, and some intrinsic factors, such as host specificity, adaptation to parasitism, etc., on *Varroa jacobsoni* parasitization of the honey bee. This ectoparasitic mite of the Asian bee (*A. cerana)* has been invading new hosts, species, subspecies and races of bee in a progressive expansion that has led to this disease becoming a real pest for bee-keepers practically worldwide. The influence of various ecosystems and hosts on the development of this mite has led to a different pattern in its population dynamics. *V. jacobsoni* was well adapted to its original host (*A. cerana*), but when it infected other honey bee species, which live in different geographical and climatic conditions, these show a different susceptibility to the mite. Over the last thirty years there has been a great deal of research into the development of *V. jacobsoni* according to its different geographical location, its infestation of species, subspecies and races of honey bees, their intrinsic characteristics (sex, age, behaviour, etc.) and tolerance of the mite, and the existing climate and seasonal patterns. However, more local studies should be made on the development of the parasite in the different races and subspecies of bees that inhabit the Mediterranean basin, which is the region that concerns us here.

Key words: *Varroa jacobsoni* (Acari: Mesostigmata), influence of climate, host (races of Honey bees).

RESUME *- "Influence de l'environnement et de l'hôte sur l'infestation par* Varroa jacobsoni *Oud.". Cette communication est une révision de l'influence des facteurs externes, tels que le climat et la phénologie, et de quelques facteurs intrinsèques, comme la spécificité de l'hôte, l'adaptation au parasitisme, etc. sur l'infestation de l'abeille mellifère par* Varroa jacobsoni. *Cet acarien ectoparasite de l'abeille asiatique (*A. cerana*) a envahi de nouveaux hôtes, espèces, sous-espèces et races d'abeilles dans une expansion progressive qui a fait que cette maladie soit devenue un véritable fléau pour les apiculteurs pratiquement dans le monde entier. L'influence de quelques écosystèmes et hôtes sur le développement de cet acarien a mené à une situation différente dans la dynamique des populations.* V. jacobsoni *était bien adapté à son hôte original (*A. cerana*), mais quand il a infesté d'autres espèces d'abeille mellifère, qui habitent dans des conditions climatiques et géographiques différentes, celles-ci ont montré des susceptibilités différentes à l'acarien. Pendant les trente dernières années, un grand nombre de recherches ont été menées sur le développement de* V. jacobsoni *selon ses différentes localisations géographiques, son infestation des espèces, sous-espèces et races d'abeilles mellifères, leurs caractéristiques intrinsèques (sexe, âge, comportement, etc.) et la tolérance de l'acarien, ainsi que le climat et les tendances saisonnières existantes. Cependant, d'autres études locales devraient être menées sur le développement de l'acarien chez les différentes races et sous-espèces d'abeilles qui existent dans le bassin méditerranéen, qui est la région qui nous occupe ici.*

Mots-clés *:* Varroa jacobsoni *(Acari: Mesostigmata), influence du climat, hôte (races d'abeilles mellifères).*

The host

The family *Apidae* is of the Hymenopteran order and has 3 subfamilies: *Apinae* (1 genus), *Bombinae* (3 genera) and *Meliponinae* (18 genera). Each one of these evolves from a different geological period of the Tertiary. The *Apinae* have only one genus, various species and numerous subspecies, in contrast to the other subfamilies with 3 and 18 genera respectively.

These three families are very dissimilar, each having adapted to different environments (Richards and Davies, 1984):

Meliponinae:	Small stingless perennial bees living in fairly large colonies with sophisticated nests in pantropical areas.
Bombinae:	Large, highly pubescent bumblebees with small seasonal colonies, living in cold climates (including Arctic and Alpine areas).
Apinae:	Generally large bees which can be highly independent of their environmental conditions as a result of their well-developed social organization, often achieving homeothermy.

The honey bee species are within the *Apis* genus, all of which are closely related and have a very similar anatomy. The most important of these are: *A. dorsata*, the giant bee; *A. florea*, the small bee *A. cerana*, the Asian bee, and *A. mellifera*, the western bee of Europe and Africa (Dade, 1985). These species have evolved into a large number of geographical subspecies. In the Mediterranean basin, *A. mellifera* has developed 13 geographical races, which include two groups: the eastern group: *A. m. anatoliaca, A.m. adami, A.m. cypria* and *A.m. syriaca*) and the sub-Saharan group (*A.m. lamarckii*), the eight remaining species are classified according to their geographical location (Ruttner, 1988):

A.m. sahariasis *A.m. intermissa*	North-eastern Africa
A. mellifera iberica *A. mellifera mellifera*	Western Mediterranean and Northern Europe
A.m. sicula *A.m. ligustica* *A.m. cecropia* *A.m. mancedonica* *A.m. carnica*	Central Mediterranean and South-eastern Europe

In a biometric study on *Apis m. iberica*, we found a considerable morphological variability in this race in Southern Spain, coinciding with the three types of population dynamics manifested by *V. jacobsoni*, which appear to correspond to the three different existing climates (Orantes Bermejo and García Fernández, 1995).

These temperate climate races have a seasonal brood-rearing cycle which depends on the flowering cycle of each region. Only a few races of bees have adapted to hibernation. These are *A.m. mellifera* and *A.m. carnica* and, probably, *A.m. anatoliaca*. A number of inherent characteristics are vital to the colony for it to be able to hibernate (Ruttner, 1988), such as: (i) large size; (ii) efficient thermo-regulation; (iii) production of winter bees; (iv) early swarming; (v) long, hard period with no brood production; and (vi) certain degree of resistance to diseases (nosemiosis).

It is generally accepted that the *Apis* species is of tropical origin. However, *A. mellifera* and *A. cerana* are found in both tropical and temperate areas, having adapted to the latter by reducing their flight tendencies and number of swarms and limiting the swarming period to the first half of the flowering season. They also develop colonies with large populations and plentiful provisions (Ruttner, 1988).

Swarming is a genetic characteristic, peculiar to each species - tropical bees have a great tendency to swarm, whereas in temperate areas this is limited to the flowering season (Ruttner, 1988).

It is of interest to ascertain the brood cycle of a race or colony, as this is related to the development of *Varroa* and, in turn, to the flowering cycle. Thus, the phenology of a region is an additional piece of helpful information. When a race does not adapt to a region, it is because its brood rhythm has not adapted to the flowering rhythm of that region (Ruttner, 1988).

The parasite

Varroa jacobsoni Oud. belongs to the class *Aracnoidea*, subclass *Acari*, superorder *Anactinotrichida*, order *Gamasida* and family *Varroidae* family. This ectoparasitic mite of the honey bee has a relatively high specificity for its host. It originally parasitized *A. cerana*, but went on to invade the area where *A. mellifera* was distributed, and now infests all these subspecies and races (Krantz, 1978; Robaux, 1986).

Mites form an extensive zoological group with several hundred species, adapted to every kind of environment and habitat. Some are free-living, either in the ground or in water (lakes and oceans). Others are saprophytes and feed on decomposed matter, fungi, algae and bacteria. However, it is the parasitic mites that are of particular interest to humans, due to their repercussions in both human and animal health. This is because the majority of them feed on blood or tissue, apart from transmitting numerous infectious and parasitic agents (viruses and bacteria) (Krantz, 1978).

In many ways, *Varroa jacobsoni* is comparable to other species included in the order *Gamasida*.

The influence of the host

Three categories of individuals exist in the parasite/host relationship: infected, susceptible and unexposed individuals (Croll, 1973).

It is well-known that *Varroa* has a greater preference for drone brood than for worker brood (Schulz, 1984; Fuchs, 1990) to the extent that eight times more mites are generally found in drone cells than in worker cells (Fuchs, 1990; Fries *et al.* 1994). *Varroa* invades 11.6 times more drone cells than worker cells in *A. mellifera* colonies (Boot *et al.*, 1995). This may be used as a means of control method, known as the "drone brood trapping method". The queen may also be parasitized.

Varying susceptibility and infestation by *Varroa* in the various subspecies and races of bees have been studied (Boecking and Ritter, 1994).

Büchler (1990) observes differences between various strains of European bees, mainly dependent on the brood's attractiveness to *Varroa* and the duration of the capping period.

Differences in the susceptibility of the host

A varying susceptibility to *V. jacobsoni* has been noted in European hives of *A. mellifera,* both in natural and experimental colonies (recently reviewed by Büchler, 1994). The different infestation levels may be due to the following characteristics, which are linked to the behaviour and biology of either *Apis mellifera* or the mite:

(i) Influence of the bee's race on mite population dynamics: it is known that European races are less resistant than African races (Camazine, 1986; Rosenkranz, 1986; Moritz and Mautz, 1990; Moretto *et al.*, 1991b).

(ii) Variability in the reproductive rate of the mite, a reduction being observed in certain subspecies and races of bees (Camazine, 1986; Kulincevic and Rinderer, 1988; Orantes *et al.* 1994 on European and African bees; Ruttner and Markx, 1984 on South American bees).

(iii) High infertility rate in *V. jacobsoni* females (Büchler, 1992).

(iv) Hygienic behaviour, removal of the infected brood.

(v) Grooming by worker bees. For the first time, Peng *et al.*, (1987b) describe the response of *Apis cerana* to *Varroa* through deparasitization by worker bees. Moretto *et al.*, (1993) observe that africanized bees are seven times more efficient than Italian bees in identifying *Varroa* as a parasite and getting rid of it. In general, these africanized races are more resistant to *Varroa* than European races (Ruttner and Markx, 1984; Engels *et al.*, 1986; Moretto *et al.*, 1991a). This characteristic has also been monitored in the different species *A. cerana, A. mellifera, A. dorsata* and *Tropilaelaps clareae* (Büchler *et al.*, 1992).

(vi) Differing duration of the brood's postcapping period according to the different subspecies and races of bees. In africanized bees, the number of *Varroa* descendants in each reproductive cycle is lower than in European bees (Moritz and Mautz, 1990); the duration of this period is considered to be an inheritable characteristic (Moritz, 1985). However, other authors do not attribute such importance to this fact due to its great variability (Büchler and Drescher, 1990).

(vii) Brood attractiveness. *Varroa* is more attracted by drone larvae (Le Conte *et al.*, 1989; Boot *et al.*, 1995).

(viii) Length of the foraging period prior to brood parasitization: the longer this is, the greater the infertility of the mite (Rosenkranz and Sturner, 1992). Mites reproduce well when they are introduced immediately before brood capping.

(ix) Effect of climate on the development of parasite populations (de Jong *et al.*, 1984; Moretto *et al.*, 1991b; Ritter and de Jong, 1984; Marcangeli *et al.*, 1992; García Fernández *et al.*, 1995).

(x) Seasonal influences (Kulincevic *et al.*, 1988; Kulincevic *et al.*, 1992; Otten and Fuchs, 1990; Büchler, 1993).

It is necessary to investigate which of the above characteristics are inheritable and to establish the strains or stocks of bees that are tolerant or resistant to *Varroa* by selection trials (Boecking and Ritter, 1994).

In vitro culture experiments have been carried out with *Varroa* using artificial diets, with a view to finding out the nutritive needs of the mite and the effect of different nutritive components on its development (Bruce and Chiesa, 1986; Bruce *et al.*, 1988; Milani and Chiesa, 1989).

Interspecific relationship of *Varroa* with its original host (*A. cerana*)

Varroa jacobsoni was originally a parasite of the Asian bee *A. cerana* and as this bee's defence mechanisms against the mite were well-developed, a balanced host-parasite relationship was maintained. The limited reproduction and great adaptation of the mite to its original host led to a series of interrelationships: the development cycles of *V. jacobsoni* in *A. cerana* are limited to a seasonal presence in drone broods and do not develop in worker broods (Ritter *et al.*, 1980; Koeninger *et al.*, 1981, 1983; Tewarson, 1987; De Jong, 1988; Tewarson *et al.*, 1992; Rath, 1991, 1993; Rosenkranz *et al.*, 1993). Moreover, the high temperatures in the brood nest of *A. cerana* (35.1ºC + 0.2ºC) when the ambient temperature is hot (up to 38.8ºC), could contribute to the limited reproduction of the mite (Rath, 1991, 1993). Mite parasitization rates of the drone brood make it impossible to open the sealed cells from inside as would normally occur. As a result, the mites die inside the cell (Koeninger, 1983; Rath, 1991, 1992). Another adaptation developed by *A. cerana* to improve its tolerance of *Varroa* is the removal of the infected drone brood, which can be detected by the particular appearance of the cell cap (Rath, 1991, 1992). Finally, *V. jacobsoni* are damaged and sometimes killed by *A. cerana* worker bee grooming (Peng *et al.*, 1987a, 1987b; Rath, 1991; Büchler *et al.*, 1992).

Another result of these adaptations is that the mite may live for long periods of time without reproducing and can be dispersed from one colony to another (Rath, 1991).

An *A. cerana* colony may be infested with as many as 800 mites per hive without causing any imminent danger to the hive. This demonstrates the high degree of adaptation of the relationship between *V. jacobsoni* and its host (Rath and Drescher, 1990). These behavioural characteristics of the Asian bee are an excellent model to use when investigating natural tolerance of *Varroa jacobsoni* in *Apis mellifera* (Boecking and Ritter, 1994).

Interspecific relationships between *Varroa* and *A. Mellifera*

The interspecific relationships between *Varroa* and *A. mellifera* are not balanced so that when this host is parasitized by the mite, it soon dies of varroosis. However, tolerance of *Varroa* in africanized and European bees has been observed in Brazil, Tunisia and Uruguay (De Jong *et al.*, 1984; Ritter and De Jong, 1984; Camazine, 1986; Ruttner *et al.*, 1984; Ritter, 1990; Ritter *et al.*, 1990). Similar cases to those found in Brazil and Uruguay should be further researched as the infected colonies there did not need chemical treatment (De Jong *et al.*, 1984; Ritter, De Jong, 1984; Ruttner *et al.*, 1984; Engels *et al.*, 1986). In these cases, the colonies of *A. mellifera* show a reduced fertility of *V. jacobsoni* in the worker brood in comparison to the drone brood.

Effect of climate on the biology and development of *Varroa jacobsoni*

In general, temperature is an important factor in determining the distribution of the ectoparasites. Temperature is a limiting factor in the distribution of invertebrate poikilothermic hosts such as the honey bee, meaning that unlike other subfamilies of the family *apidae*, *apinae* (*A. mellifera*) are not seasonal, being the most evolved group among the *Apoidea*. They survive from year to year and hibernate with their stores of provisions for winter consumption (Richards and Davies, 1984).

The environment inside the hive is well-controlled by the bees, being very stable, particularly the temperature of the brood nest. However, factors such as humidity and food supply vary considerably according to local and seasonal conditions, which may also influence the growth of the mite populations. Furthermore, seasonal changes in bees may directly or indirectly affect the mites (De Jong *et al.*, 1984; Ritter and De Jong, 1984; Moretto *et al.*, 1991b, 1995).

As mentioned above, the honey bee is distributed in temperate and tropical regions throughout the world. However, given the characteristics of its colonies, the microclimate inside the hive is regulated so that any fluctuations in temperature are minimal (homeothermy). In the palearctic region, seasonal variations exist that affect flowering. In our Mediterranean climate, there is a cold, rainy period from October to February and a hot, dry period from June to September. This means that there is a seasonal fluctuation in flowering which affects the development of the bee colonies and this, in turn, influences the proliferation of the parasite (*V. jacobsoni*) (De Jong *et al.*, 1984; García Fernández *et al.*, 1995).

In climates with cold winters, when the bee's development cycle is interrupted during hibernation. The clustering of bees inside the hive may encourage reinfection by *Varroa*. However the interruption in brood production has the opposite effect. In these climates with cold winters, the winter bees are physiologically different from the summer bees, having a fatter body, low levels of juvenile hormone, and a reduced life span. The seasonal variations in the brood affect the development of the mite, increasing sharply in spring and autumn and decreasing in summer.

In cold climates, unlike tropical ones, mite populations rapidly reach high levels that are sufficient to cause the death of the colony in late summer and autumn (De Jong *et al.*, 1984; Moretto *et al.*, 1995).

Temperate climates are particularly propitious for the development of *V. jacobsoni*, as winter bees have a longer life-span than spring and summer bees. Adult bees infected with *Varroa* during their development have a shorter life-span than uninfected bees. Many of them therefore die early in autumn thus reducing the population of the colony at a critical time (De Jong and de Jong, 1983; De Jong *et al.*, 1984).

Other authors argue that climatic changes do not affect *V. jacobsoni* reproduction as the temperature in the brood nest hardly changes (Rosenkranz, 1990a, 1990b). However, indirect climatic effects on brood production can play an important role in mite fertility (De Jong, 1984; Ritter and De Jong, 1984; Engels *et al.*, 1986; Ritter *et al.*, 1990; Moretto *et al.*, 1991a; Marcangeli *et al.*, 1992; Orantes *et al.*, 1994).

Results obtained in southern Spain on the effect of climate on *Varroa* population dynamics

Studies undertaken by us in southern Spain show that there exists a direct climatic influence on the development of *V. jacobsoni* (García Fernández *et al.*, 1995; Orantes *et al.*, 1994). We found that (Table 1):

(i) Brood parasitization rates (BPR) vary considerably between the three climates studied: Continental Mediterranean: CM(BPR) = 17.8, Mediterranean Continental and Oceanic: MCO(BPR) = 34.2 and Mediterranean Subtropical: MS(BPR) = 24.8 (per 100 worker bee cells), significant differences existing between all of them.

(ii) Adult bee parasitization rates (APR) also had very different patterns in the three climates: CM(APR) = 4, MCO(APR) = 10 and MS(APR) = 6, significant differences existing between climates CM and MCO.

This demonstrates that the Mediterranean Continental and Oceanic climate of western Andalusia and the subtropical climate existing on the coast, with milder temperatures and a higher humidity, are more favourable for the development of *V. jacobsoni*.

Climate also affected parasite population dynamics in our studies. We found three different behavioural patterns (Figs 1 and 2):

(i) In the subtropical climate (Costa del Sol), the population dynamics are progressive and exponential, development of the population starting very early - November to December - and reaching its maximum in April. This means that the colonies die before the beginning of the summer.
The parasitic action of *V. jacobsoni* is favoured by the mild climate in which flowering continues all the year round, whether it be of autochthonous plants, plastic-covered production or subtropical crops.

(ii) In the Continental Mediterranean climate, which corresponds to the Penibetic and inland areas, a bimodal model was observed, with the appearance of two maximums, one from November to January of low intensity, which coincides with the early-flowering almond trees, rosemary, gorse, etc., and a second one in June, provoking death in the colonies during the following months.

(iii) In the MCO climate, the evolution of mite populations is deferred between one and three months with respect to the CM climate, perhaps due to the absence of early-flowering plants in these regions, but in general, the pattern of the population dynamics is the same. However, the parasitization rates (APR) in this climate are double those found in the CM climate:

APR (MCO) = 2PR (CM) ; BPR (MCO) = 2PC (CM)

Table 1. Mean values of the parameters of *V. jacobsoni*, the different bee colonies in the sampling stations being grouped according to existing climate

	Group 1 Continental Mediterranean	Group 2 Mediterranean Continental and Oceanic	Group 3 Mediterranean Suptropical
Mortality	10.723 n=69	7.940 n=126	16.987 n=36
APR (%)	4.09 n=69	9.97 n=130	6.11 n=86
PC (%)	17.835 n=49	34.23 n=73	24.82 n=26
BPR (%)	-	15.56 n=108	-
No. Bees	7.686 n=69	13.414 n=130	3.733 n=36
No. Brood PC	4.251 n=49	4.255 n=73	3.200 n=26
No. Brood BPR	-	4.255 n=73	-

Mortality = No. of dead *Varroa* found at the bottom of the hive; APR (%) = Adult parasitization rate; PC (%) = Mean No. of varroa in 100 brood cells; BPR = Percentage of cells infested by *Varroa*; No. bees = No. of bees analysed to calculate APR; No. brood PC = No. of brood cells analysed to calculate PC; No. brood BPR = No. of cells analysed to calculate BPR; n = No. of samples.

In southern Spain, the population dynamics of *V. jacobsoni* is 2 or 3 months ahead of Central Europe. Thus, we found maximum populations from March to June, whereas in continental Europe these occur from June to August (Ritter, 1988).

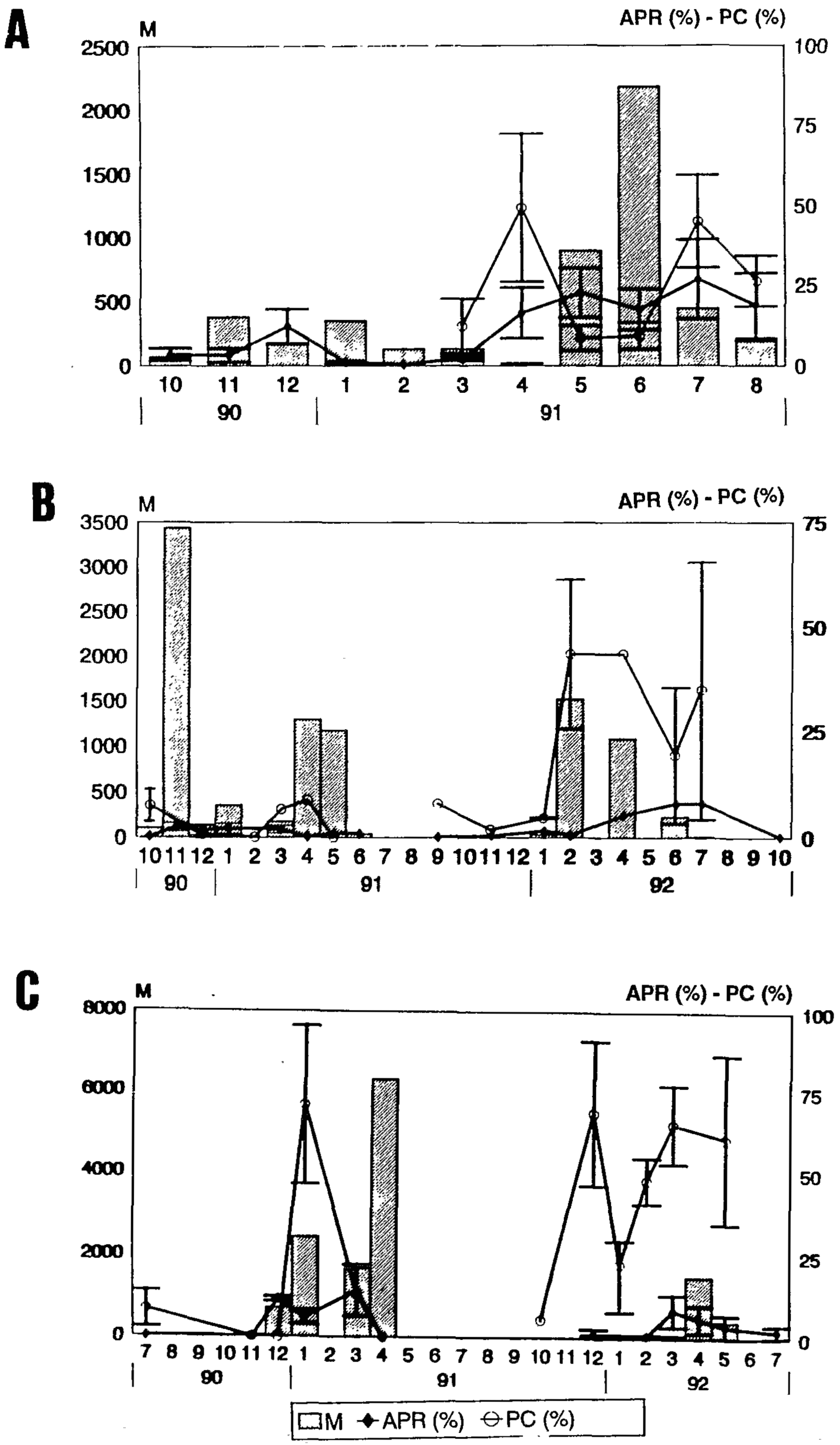

Fig. 1. Population development of *Varroa jacobsoni* in southern Spain in the three regions studied (A= Mediterranean Continental and Oceanic); B = Continental Mediterranean; C = Mediterranean Subtropical).

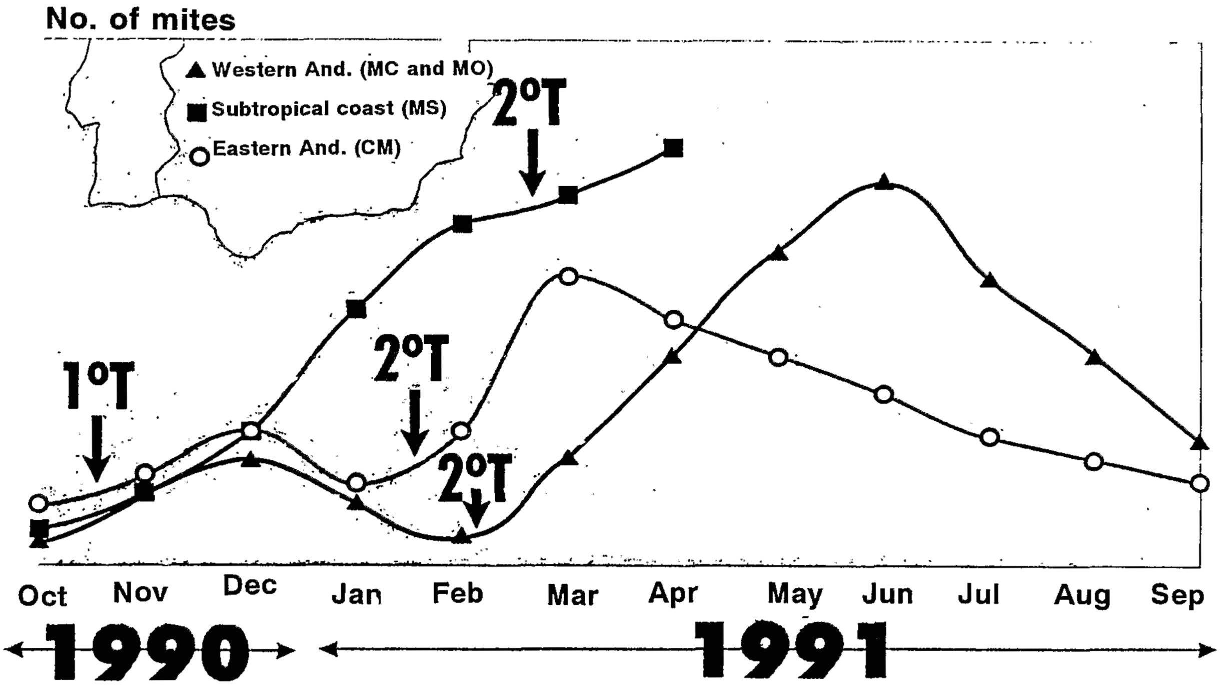

Fig. 2. Population development of *Varroa jacobsoni* in southern Spain in the three regions studied, indicating the dates of treatment with acaricides.

With regard to the fertility pattern of *Varroa* in our climates, it was observed that reproductive rates (RR) in western Andalusia were very similar to those found by other authors on the Mediterranean littoral (RR = 2.7) (Ifantidis, 1984; Calatayud and Verdú, 1992) (Table 2). We also found fluctuations in mite infertility rates (percentage of infertile females): 32% in worker bee cells and 28% in drone bee cells (see Fig. 2). Other authors found somewhat higher values for Europe and Africa (20-50%) (Camazine, 1986; Kulincevic *et al.*, 1988) and much higher values in bees in South America (70-90%) (Ruttner and Marks, 1984). Infertility rates of *Varroa* must be investigated further in our races of bees, as this should make it possible to select bees which are more tolerant to this mite.

Table 2. Reproductive rate of *V. jacobsoni* for the colonies situated in Western Andalusia (Lepe, Hornachuelos, Castellar de la Frontera, Dos Hermanas and Trasierra) during the sampling period (March - August 1991)

Brood cells type	*Varroa* found					Reproductive rate	
	Totals	Progeny	Reproducing females (A)	Non-reproducing females (B)	A/B	RR	N*
Workers	458	299	108	51 (32%)	2.1	2.7	152
Drones	228	175	38	15 (28.3%)	2.5	4.6	53

*No. of brood cells examined. N does not coincide with A+B: the difference is the number of brood cells which were considered to have been penetrated by more than one *Varroa*.

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