

Bioclimatic Studies of the Aphid Parasite *Praon exsoletum*.¹ 2. Thermal Limits to Development and Effects of Temperature on Rate of Development and Occurrence of Diapause²

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ABSTRACT

Using bioclimatic chambers, fluctuating temperatures and humidities were examined for their effects on the development of the immature stages of *Praon exsoletum* (Nees) (Hymenoptera: Aphididae), a parasite of the spotted alfalfa aphid, *Therioaphis trifolii* (Monell) (= *T. maculata* (Buckton)) (Homoptera: Aphididae). Comparisons with response of the host to the same temperature conditions were made. The thermal limits for development of the parasite are diurnal means of 10 and 27°C, and development is fastest at 23°C. The host develops over a wider range, namely 6–32°C, and most rapidly at 26°C. At any temperature level the host grows more rapidly, and at 26°C it completes development in 6 days in contrast to the 15 days required by the parasite. Diapause is induced in the parasite by low temperatures, beginning at diurnal means of 16°C and less, but it can be suppressed by long photoperiods (14 hrs or more). The host does not enter diapause under these

same conditions. The age of the female parasite does not affect the incidence of diapause of her progeny, nor do the growing conditions of the host plants. Cool fluctuating temperatures accelerate parasite development relative to that occurring in constant-temperature conditions, and they also permit development to occur at thermal levels well below the constant-temperature threshold. On the other hand, high fluctuating temperatures are injurious to the parasite. The parasite can develop only over a restricted range of medial temperatures and to that extent can be rated a mesotherm, in contrast to the eurythermic host. Typical winter conditions in the Central Valley of California were simulated in a bioclimatic chamber and were found not injurious to the parasite. Instead it was found able to complete diapause and emerge as an adult in midwinter at a monthly mean temperature of 8°C.

One of the fundamental ecological requisites of poikilothermic animals is a thermal environment favorable for their survival at all times and warm enough some of the time for the completion of their development from birth to reproductive maturity. Temperature has long been accepted as one of the major limiting factors to the geographic range of distribution of insects (Uvarov 1931, Messenger 1959). Temperature is also involved directly or indirectly in the natural control of abundance of insect species in their occupied habitats (Uvarov 1931; Birch 1948, 1957; Klomp 1962, Huffaker and Messenger 1964).

When purposeful introduction of insect parasites into certain geographic areas for the control of other species of insects is considered, the same limitations and influences of temperature on establishment, spread, and population increase must apply. In addition, the thermal relationships of the host insect become important. So in seeking to understand what biological control performance may be expected of an imported parasite, one must consider whether the parasite can develop in the habitats of concern, whether adjacent host-occupied habitats into which the parasite is expected to spread are thermally favorable, and, once established in a local area, whether populations of the parasite can increase at rates sufficient to overcome and suppress populations of the host. Of particular importance in this regard is whether host and parasite respond in the same quantitative way, or differentially so, to changing temperature during the seasonal cycle. If there is a differential response to temperature, the question arises as to whether it favors the parasite, or instead allows the host to escape regulatory control.

This paper, the second in a series involving a study of the bioclimatic characteristics of *Praon exsoletum* (Nees), an imported parasite of the spotted alfalfa aphid, *Therioaphis trifolii* (Monell) (= *T. maculatus* (Buckton)), describes laboratory research on the relation between temperature and development of the parasite. The experimental host-parasite system, and the general experimental approach used in the current study, have already been described (Messenger and Force 1963). The temperature and humidity patterns used, and the response of the host aphid to temperature also have been reported earlier (Messenger 1964a). The purposes of the present work are to estimate the temperature limits to development of the parasite, to determine its rates of development at various favorable temperature levels, and to compare its temperature responses with those of the host to bring to light any differential reactions which may serve to explain in part the distribution and abundance patterns of the 2 insect species in nature. The bioclimatic objectives of these studies are to provide a basis for estimating those geographic areas and seasons of the year in which *P. exsoletum* can complete development, and those in which it cannot.

Developmental rates also constitute 1 of the 3 main components used in the mathematical computation of the innate capacities for numerical increase of populations of organisms (Birch 1948). Previous work (Messenger 1964b) indicated that the innate capacities for increase of this parasite are useful for judging its bioclimatic responses to climatic factors. A later paper in the present series will devote itself to this aspect.

EXPERIMENTAL METHODS AND MATERIALS

Two series of tests were carried out in this temperature-development study. In one, fixed levels of

¹ Hymenoptera: Aphididae.

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fluctuating temperature and humidity patterns were used. In a sense, these exposure conditions might be considered as typical of certain seasons of the year, but lacking any seasonal trends to warmer or cooler levels. In the other series, temperature and humidity patterns typical of the months of autumn, winter, and spring in the California Central Valley (specifically Stockton, Lodi, Manteca) were simulated to provide information on overwintering development under such patterns.

In the 1st series, fluctuating temperature patterns were constructed to provide standardized diurnal cycles of 24-hr periodicity and fixed diurnal ranges of usually $\pm 5.5^{\circ}\text{C}$ ($\pm 10^{\circ}\text{F}$). These diurnal cycles were repeated each day throughout any particular test. To provide different mean temperatures for subsequent tests, the same diurnal cycle was used, but with different temperature values. Hence, while mean temperatures were varied, the diurnal ranges and times of daily maxima and minima were the same in most cases.

For each temperature pattern just described, a synchronized relative humidity pattern was also prepared. These patterns were designed to correspond roughly with the humidity patterns commonly occurring in central California, where low winter temperatures are accompanied by high humidities, and warmer summer temperatures by lower humidities. For temperature patterns with means below 15°C the daily pattern of humidities averaged 70%, with diurnal range ± 25 percentage units. For mean temperatures above 25°C the mean humidities were 50%, with diurnal range ± 30 percentage units. Intermediate mean temperatures were accompanied by intermediate humidities. The actual, synchronized diurnal patterns of both temperature and humidity are given in an earlier paper (Messenger 1964a).

In the 2nd series, the winter simulation series, mean daily, mean daily maximum, and mean daily minimum temperatures for October through May were determined from U.S. monthly Weather Climatological Data reports for California. Standardized daily temperature and humidity cycles were constructed for each month, and the simulation study consisted of running each such cycle repetitively for each month in sequence. Table 1 gives the temperatures and

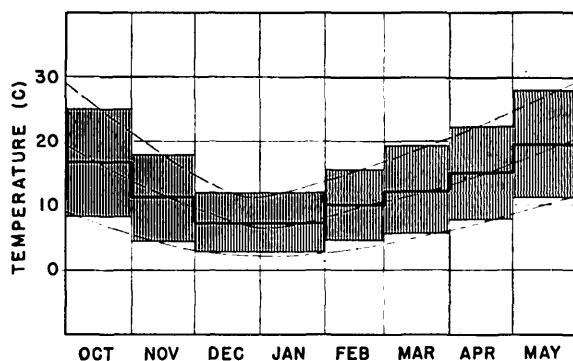


FIG. 1.—Histograms showing temperature patterns programmed in the over-wintering study. Heavy solid line shows monthly mean temperatures simulated, shaded zones show corresponding simulated diurnal ranges; upper, middle, and lower dashed lines show long-term mean daily, mean daily maximum, and mean daily minimum temperatures for each month as recorded by the U.S. Weather Bureau for the Stockton-Lodi-Manteca area of California.

humidities simulated for each month in these studies, and Fig. 1 shows the mean temperature variations through the winter. Long-term mean values (daily average, daily maximum, and daily minimum) for the area considered (the Stockton, Lodi, Manteca area of the Central Valley of California) are also shown in Fig. 1.

Relative humidity values used in synchrony with these "Stockton-Lodi-Manteca" temperature patterns were obtained from the same publication source, but refer only to Stockton. The daily maximum and minimum humidity values simulated for each month were derived from similar mean daily high and low values recorded at the Stockton Airport Weather Bureau Station, and averaged over a 15-year time span (1948-63) for the particular months being studied.

Bioclimatic chambers, 230 ft³ in internal capacity, were used to provide programmed patterns of temperature, relative humidity, and light (see Messenger and Force (1963) for a brief description of this equipment and illustrations of the typical diurnal patterns followed).

Culture methods for the spotted alfalfa aphid and the parasite, *P. exsoletum*, are also described in the aforementioned paper. Separate cultures of each species were produced in cages in each test environment, so all insects used were well acclimatized to the conditions under investigation.

Development of individuals of each species was observed in small glass test units held in each bioclimatic chamber. These units, measuring 35 mm diam and 150 mm long, each contained a small bouquet of alfalfa foliage on which the aphids lived and fed, and on which parasitized aphids mummified. The duration of development of the test insects was taken to be the time interval between larviposition or oviposition, as the case may be, and the emergence of adults. Since the adults of a replicate sample usually emerged over a more or less short span of time, the median emergence time was used as the endpoint of the developmental period.

Table 1.—Temperature and relative humidity patterns programmed in the overwintering study of *P. exsoletum*.

Month	Temperature		Relative humidity	
	Daily mean (°C)	Diurnal range (in °C)	Daily mean (°C)	Diurnal range (in % units)
Oct.	16.7	8.3	59	21
Nov.	11.1	6.7	69	16
Dec.	8.0	4.4	80	10
Jan.	8.0	4.4	80	10
Feb.	10.0	5.5	69	18
Mar.	12.2	6.9	64	18
Apr.	15.0	7.5	64	18
May	19.4	8.3	60	20

Table 2.—Effect of fluctuating temperatures on the development of *P. exsoletum*.

Mean temp (°C)	No. individuals	Median developmental period (days) ^a			
		Egg-larval	Pupal ^b	Total ^b	No. emerged
5	25	— ^c	—	—	0
8	31	29	—	—	0
10.5	187	21	24	45	135
			(78)	(99)	(52)
12.5	404	16	18	34	254
			(38) ^d	(62) ^d	(149) ^d
16.1	333	11	10	21	315
			(46)	(57)	(38)
21.1	45	7	7	14	42
			—	—	(3)
23.9	79	6	8	14	73
26.7	39	6	9	15	28
29.4	130	7	—	—	0 ^e
32.2	200 eggs	—	—	—	0
	50 pupae	—	—	—	0

^a Time for 50% of sample to transform to next stage.^b Values represent nondiapauses cases; values in parentheses represent diapausing individuals.^c — a test was run, but development through the indicated stage was not completed.^d Diapause completed when transferred at day 45 to the insectary at 22°C.^e 5 individuals reached pupal stage and then died, the rest died in egg or larval stages.

During development the aphid passes through 4 instars before becoming adult. Parasite egg and larval development occur within the living host on alfalfa leaves; parasite pupae develop within cocoons formed on the leaves under the dead aphid skins. To study aphid development, young adult aphids were transferred from the stock culture to the test unit bouquets and allowed to feed and deposit young for several hours. Then the adults and all the young but one were removed from each bouquet. For parasite development, newly emerged adults were collected from the stock culture and several male and female pairs were placed in a petri dish containing several hundred 3rd-stage aphids feeding on alfalfa leaves. The female parasites were allowed to oviposit for several hours, with each parasitized aphid being removed just after it was stung and placed on the alfalfa bouquet of a test unit until the appropriate number of parasitized hosts had been accumulated. Observations of host or parasite developmental progress were made once daily.

P. exsoletum under certain conditions undergoes diapause, usually as a response to cold and probably also to photoperiod. In nature, *P. exsoletum* diapauses within its cocoon during the winter season. In cer-

tain of the temperature studies described here a portion of each test sample of developing parasites went into diapause. While this phenomenon was not explored in detail in this study, where such a response occurred the data for incidence and duration of diapause were recorded. Certain minor experiments aimed at uncovering the cause of diapause in certain test environments were also conducted and the results are reported here.

RESULTS

Fluctuating Temperature Study.—Table 2 records the number of parasites tested in each temperature pattern, the time elapsing from egg deposition to cocoon spinning (called the egg-larval period), the time from cocoon spinning to adult emergence (called the pupal period), the total developmental time, and the number of adults emerging. Each developmental period was computed from the times 50% of the individuals under test transferred from one developmental stage to the next.

A fluctuating temperature averaging 5°C proved to be too cool for parasite oviposition. At a mean temperature of 8°C oviposition did occur, and parasite eggs would hatch and larvae would complete development and spin cocoons. However, at this thermal level no parasite pupae would develop to adulthood. The lowest temperature mean at which full immature development took place was 10°C. At this temperature ca. ⅓ of the sample passed into diapause.

When parasite eggs laid at 8°C mean temperature were transferred within their hosts to a 5°C mean temperature level, no hatching took place; thus 5°C is not only inhibitory to oviposition but also is below the temperature threshold for development and hatch of eggs of *P. exsoletum*.

The highest temperature allowing for complete development of *P. exsoletum* was 26.7°C, while exposure to 29.4°C was inhibitory. At this latter temperature, parasite eggs and larvae were able to complete development to the next stage, but pupae were not. At 32.2°C females were able to oviposit, but neither eggs nor larvae could complete development.

At the lower temperature levels (21.1°C and below), some individuals in each sample of parasites tested passed into a state of diapause. The incidence of diapause was somewhat variable and not uniform with respect to temperature. For example, with photoperiod the same in each case (12 hr light:12 hr dark), at 12.5°C a slightly larger proportion of the developing parasites diapaused than at 10.0°C. Because of concern

Table 3.—Influence of plant rearing conditions on development of *P. exsoletum* at 12.5°C.

Temp under which plant reared (°C)	No. individuals	Mean developmental period (days)			No. non-diapause	No. diapause
		Egg-larval	Pupal	Total		
12.5	81	17	15	32	32 (39.5%)	49 (60.5%)
29.4	57	16	17	33	23 (40.5%)	34 (59.5%)

Table 4.—Effect of maternal age on incidence of diapause in *P. exsoletum* held under 2 different conditions of temperature and photoperiod.

Age of mother ^a	Held at 16.1°C and 12L:12D		Held at 22°C and 14L:10D	
	Non-diapause	Diapause	Non-diapause	Diapause
3	28	6	21	0
10	24	5	15	1
17	30	8	17	0
24	14	6	7	0
31	5	2	6	0
38	6	6	7	0

^a Time in days from date of emergence as adult. Data are averages of 3 replicates.

that some factor(s) in the experimental technique contributed to this variation, several small-scale studies were carried out on diapause induction. One such possible factor, mentioned by Schlenger and Hall (1959), is the physiological state of the alfalfa plants on which the parasitized aphids grew. These workers concluded that, under decreasing photoperiod and temperature (autumn), plants became "conditioned" to induce, presumably through the aphids feeding on them, a state of diapause in *P. exsoletum* parasitizing these aphids.

To test this possibility, in part, aphids reared at a mean of 12.5°C on plants grown at either this temperature or at a mean of 29.4°C were exposed separately to ovipositing *P. exsoletum* which were also reared at a mean of 12.5°C. Table 3 shows the results of this study; the proportion of parasite progeny diapausing in each case was almost identical (60.5% and 59.5%, respectively). This result suggests that the rearing temperature of the plants (when photoperiod is held constant) exerts no pronounced effect on diapause incidence in these bioclimatic experiments. It is possible that a plant effect does in fact occur as noted by Schlenger and Hall (1959), but that the overriding influences of temperature and photoperiod make this effect difficult to detect.

A direct effect of temperature and/or photoperiod on the induction of diapause in *P. exsoletum* is suggested by the following results. Large numbers of aphids growing on the same alfalfa plant were divided into 2 groups and parasitized by the same population of ovipositing females. One group was held in the bioclimatic chamber to which all 3 organisms (plant, aphid, parasite) had become acclimatized (temperature 16.1°C, photoperiod 12L:12D). The other group of parasitized aphids was removed from the chamber immediately after parasitization and stored in the insectary at 21°C and photoperiod 14L:10D. The results indicate that while only ca. 12% of the progeny diapaused in the chamber, less than 0.25% diapaused under insectary conditions where the temperature was somewhat warmer and the photoperiod somewhat longer. The main point of this test was to show that the plants, cultured at 16.1°C and 12L:12D for some 3-4 months, did not convey any noticeable diapause effect when transferred for a short period (11-12

days) to a temperature 5.5°C higher or a photoperiod with 2 more hours of light.

Simmonds (1946, 1948) showed that the age of the ovipositing parasite affects the incidence of diapause in her progeny. Older females gave rise to a larger proportion of diapausing progeny than did younger females. To examine this effect of maternal age on the incidence of diapause in *P. exsoletum*, parasite females were allowed to oviposit in separate batches of hosts daily, with about half of each batch being held for development at 16.1°C and 12L:12D, while the remainder were held at 22°C and 14L:10D. Table 4 shows the results of these experiments, which show that (a) there is no obvious effect of parental age on the incidence of diapause; and (b) the lower temperature and shorter day again promoted diapause while the warmer, 14-hr day almost completely inhibited diapause.

Winter Temperature Study.—Table 5 gives data on the survival and duration of nondiapause development of *P. exsoletum* at each monthly temperature level for the simulated winter of the Stockton-Lodi-Manteca area. The rather close correlation of these results with those from the fixed-temperature studies can be seen by the open circles in Fig. 2.

For each replicate of immature parasites exposed each month to the autumn and winter month regime, a substantial portion entered diapause and therefore failed to emerge along with the nondiapause individuals. In most instances, diapause development was completed, and active morphogenesis resumed, only after exposure to the winter temperatures was completed. In these cases, adult emergence occurred in April and May, some 5-6 months later. However, some of those parasites that diapaused in October eventually completed development and emerged as adults in midwinter (January, February). These data suggest that for *P. exsoletum*, postdiapause development can occur at temperatures averaging as low as 8°C.

DISCUSSION

Fig. 2 presents time-temperature curves and rate-temperature curves for both aphid and parasite. All temperature levels indicated are means of regularly fluctuating temperature patterns. At each temperature level studied, *T. trifolii* completed development to the

Table 5.—Nondiapause development of immature stages of *P. exsoletum* exposed to fluctuating temperatures typical of the long-term mean values for winter in the mid-Central Valley of California.

Month	Monthly mean temp (°C)	No. in test	Median development period (days)			No. emerging (nondiapause)
			Egg-larval	Pupal	Total	
Oct.	17	40	9	10	19	12
Nov.	11	47	17	21	38	19
Dec.-Jan.	8	41	30	29	59	21
Feb.	10	50	19	21	41	23
Mar.	12	36	16	16	32	12
Apr.	15	22	10	10	20	13
May	19	25	7	10	17	18

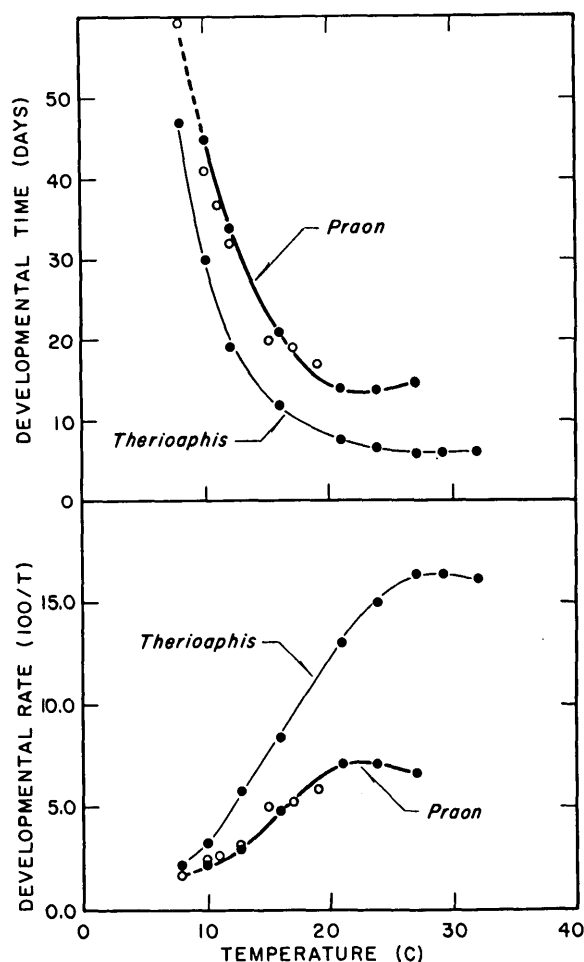


FIG. 2.—Developmental times (upper graph) and rates (lower graph) for both *P. exsoletum* and *T. trifolii* when exposed to different fluctuating temperatures. Solid circles, fixed fluctuating temperature patterns; open circles, over-wintering temperature patterns.

adult stage much sooner than *P. exsoletum*. It can be seen also from this figure that the temperature-tolerance range for development was wider for the host aphid (8–32.2°C) than for the parasite (10–26.7°C).

It is interesting from a physiology standpoint to compare the times required for completed development of *P. exsoletum* exposed to constant temperatures with those times recorded here for development under variable temperatures. Fig. 3 shows such a comparison where the constant-temperature data have been taken from Force and Messenger (1964). At all mean temperatures below ca. 24°C the exposure to fluctuating temperature results in an acceleration in rate of development relative to that occurring under constant conditions. At mean temperatures above this level, variable temperatures decelerate the rate of development, most probably because of physiological injury resulting from the few hours of exposure each day to excessively high temperatures above 30°C. This observation confirms again the earlier finding

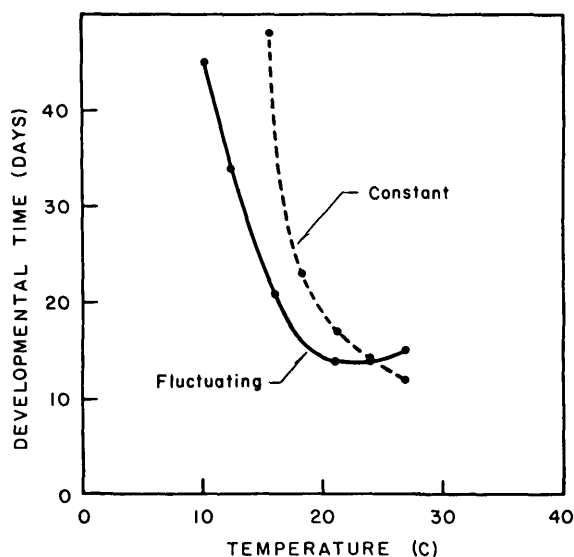


FIG. 3.—Comparison of developmental times for *P. exsoletum* when exposed to fluctuating temperature patterns on the one hand, and constant temperatures on the other. Constant temperature data taken from Force and Messenger (1964).

that *P. exsoletum* is a species quite sensitive to warm temperatures.

Aside from the differential effects of fluctuating vs. constant temperatures as just described, it is also important to note that the parasite is capable of developing over a wider range of temperatures when the latter fluctuate than when they are constant. This widening of the temperature-tolerance range is particularly noticeable at the lower thermal levels. Indeed, the lowest temperatures at which development is found to go to completion vary by as much as 6°C depending on whether conditions are held constant or fluctuate diurnally. The widening of the tolerance range does not involve an extension of the upper thermal limit for this species of insect.

The shape of the development-temperature response curve, and the accelerative effects of variable temperatures on development, are similar to those we have already shown to hold for several species of Diptera and for the spotted alfalfa aphid itself (Messenger and Flitters 1958, 1959; Messenger 1964a). While of course the quantitative details vary with each species, the fundamental relationships of development to temperature, either diurnally fluctuating or constant (i.e., time-temperature relation approximating the form of a catenary rather than a hyperbolic curve, rate-temperature curve flatter and wider for the fluctuating condition than the constant condition) is now found to apply to a parasitic hymenopteran.

So far as the bioclimatic responses of *P. exsoletum* and *T. trifolii* are concerned, I conclude that the parasite is not capable of developing at temperatures as low as the aphid can, or as high. Also, the parasite at any temperature level is not capable of developing as rapidly. This conclusion suggests that the

generation time for the 2 species is different, which hypothesis in turn introduces the problem of life cycle synchrony between host and parasite and any consequences a partial lack of synchrony may hold for successful biological control of the aphid. At the lower temperature levels a substantial proportion of the immature parasites become inactive or arrested in development (diapause), while no equivalent effect occurs with the host.

The results of the overwintering study indicate that *P. exsoletum* is easily capable of surviving the relatively mild winter temperatures of the mid-Central Valley of California. These studies show also that adults are able to emerge in midwinter, and that post-diapause development can take place at temperatures as low as 8°C. As has already been reported (Messenger 1964a) the host insect can develop more or less continuously in the Central Valley.

These findings show that, so far as temperature is concerned, *P. exsoletum* will probably not be able to occupy as many habitats as *T. trifolii*, or to develop at equivalent rates in those habitats thermally favorable to both species. On a relative basis, the aphid may be rated a eurytherm, the parasite a mesotherm. On this basis alone it is possible to explain the relative geographic distributions of these 2 species in California as recorded by van den Bosch et al. (1964).

Having made these conclusions, it is necessary to point out that they can be expected to apply accurately only to the ecotype of *P. exsoletum* which currently exists in California. Van den Bosch (1957) found this species to occur generally from Italy east to Iran, mostly in areas with relatively cold winters and warm semihumid summers; the stocks imported into California and colonized there were derived from these populations. Recently, van den Bosch (unpublished data) detected *P. exsoletum* in moderate numbers in the very hot, very dry Baghdad area of Iraq. It is possible that colonies of the parasite deriving from this latter ecotype may exhibit altogether different responses to temperature than those reported in the present paper.

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