

OVIPOSITION AND MATING TENDENCIES
OF *CHEYLETUS MALACCENSIS*
(ACARINA: CHEYLETIDAE)

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ABSTRACT

Oviposition by parthenogenetically reproducing females of *Cheyletus malaccensis* Ouds. began as early as the third day after the final molt and ran its course in 40 to 56 days. In one trial comprising 19 unmated females, these mites averaged 294.2 eggs each. The greatest number laid by 1 female was 406. Attempts to mate females were most successful when males were presented in the period between final molt and the onset of oviposition. Functional matings by ovipositing virgins were not observed when males were introduced during the first 30 days of the laying period. However, a few virgins continuously confined with their own sons accepted mates during the declining phase of oviposition. Females of this species establish nests within which eggs are laid. Eleven virginal females were isolated and manipulated daily only as required to determine nest occupancy. This lot averaged 64.7 days total adult life span, 3.1 days in the preoviposition period, and 50.9 days for the total nesting period. Two of these deposited all of their eggs in the first and only nest, 7 made 2 nests and 2 made 3 nests.

The relative ease with which cultures of *Cheyletus* species can be maintained in the laboratory provides a good basis for experimentation on some of the vital activities of these predators. Several contemporary investigators have described the life histories of cheyletids (Hafiz 1935; Edwards 1952; Beer and Dailey 1956; Hughes 1961; Summers, Witt, and Regev 1972), principally for species of *Cheyletus*. The reproductive biology of species studied in the laboratory is somewhat complicated by the occurrence of parthenogenesis, heteromorphic males (or no males), and belligerent behavior of nesting females.

Observers generally agree that, among cheyletids, tetranychids and allied forms, mating is most apt to occur between mature males and recently molted, teneral females. The occurrence of mating at any other time during the life span of females has not been amply studied.

The present study extends our earlier observations on oviposition, the time of mating and the duration of nesting of *Cheyletus malaccensis* Ouds., an arrhenotokous species.

METHODS

The procedures and rearing cells employed in this study were the same as those described by Summers and Witt (1973) in a study of a thelytokous species, *C. eruditus* (Schr.). The number of eggs laid by isolated, virginal females of *C. malaccensis* was determined by a method of egg destruction. Since they deposit most of their eggs in 1 or 2 nests, the eggs in an inhabited nest were counted every day and some of the oldest ones removed or destroyed so that about 10 eggs were left after each inspection. This daily adjustment

increased the accuracy of counting and was done so as to retain the newest eggs and eliminate as far as possible those almost ready to hatch. The hatching of eggs in the interval between examinations required that the very delicate shells be counted and then removed from the nest to avoid confusion in later examinations. The regular removal of older embryonated eggs also reduced the feeding by just-hatched larvae on other, unhatched eggs.

OVIPOSITION

Data on duration of oviposition and numbers of eggs produced were assembled by totaling the daily production of 19 unmated females according to days of adult life, *i.e.*, days after molting (Fig. 1). This lot of individuals averaged 294.2 eggs per female and the maximum number obtained from 1 individual was 406. As estimated by the method of egg destruction, these unmated females showed greater productivity than previously reported for *C. malaccensis* (Summers, Witt, and Regev 1972) or *C. eruditus* (Summers and Witt 1973). The mites in this lot began to lay as early as the third day, established a minor peak on the sixth day and continued thereafter to lay at a fairly steady rate through the nineteenth day—approximately 12 eggs per day per female as an average. The compiled data show that laying was 50% complete on the fifteenth day for this composite sample of females, 75% complete on the twenty-second day and entirely ended for 14 of 19 individuals on the fortieth day. One female continued to lay until the fifty-sixth day.

Discontinuity in the rhythm of daily oviposition appeared as early as the eighth day but the interruptions did not increase noticeably until after the fourteenth day. Old, almost expended females became restless and erratic in egg production. The formation of new nests was not necessarily an accompaniment of irregularity in laying; a few individuals made new nests during an irregular period, others became erratic layers without changing nests.

In order to establish the length of the calendar period during which females were to be exposed to mates, it was desirable to learn the shortest time required for their male progeny to mature and to eliminate them before mother to son mating could occur. The minimum developmental time for individuals of each sex was approximated by recording the first day of oviposition for each of a number of isolated females and then searching the cultures daily after the eighth day for the first adults of each sex to appear. The results shown in Table 1 indicate that first individuals of both sexes appeared within 12 to 22 days. Although the means for the 2 samples show that more of the first males appeared earlier than first females, the data are inconclusive on this point. Two limitations of these data are: 1) the growth

TABLE 1.—SHORTEST TIME REQUIRED FOR ADULT PROGENY OF EACH SEX TO APPEAR IN CULTURES AS TIMED FROM THE INITIAL DAY OF OVIPOSITION BY PARENTAL FEMALES.

Number of cultures observed	Condition of mother	Sex of progeny	Days for first of each sex to develop	
			Range	Mean*
41	Virgin	Male	12-22	16.4
44	Mated	Female	12-22	19.7

*D/E_a=0.99 (n.s.)

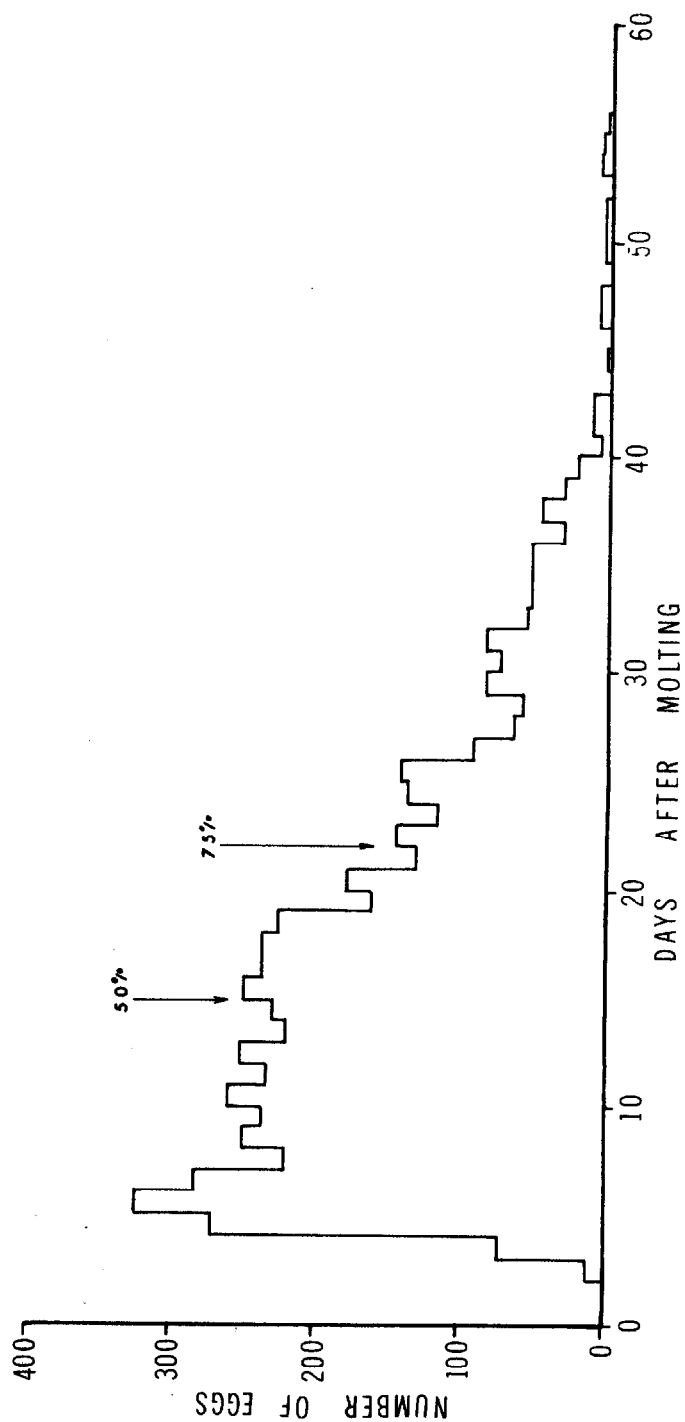


Fig. 1. Histogram showing the trend of oviposition based on daily egg production arranged according to days after molting and totaled for 19 parthenogenetic females.

periods were timed only to the nearest whole day, and 2) there is no certainty that each new individual was discovered on its natal day. However, the data provide a basis for the procedure of separating virginal or pedigreed females from their own progeny at intervals of approximately 10 days in order to avoid unplanned matings. Or, where F_1 adult progenies are being counted, the tallies of individuals harvested after twice the minimum growth period plus 1 intervening preoviposition period—approximately 28 days—are increasingly liable to contain F_2 adults.

MATING ATTEMPTS

In vigorously growing cultures it was possible to find small numbers of "courting couples", i.e., a molting deutonymph loosely attached to a bran flake and having an adult male in attendance. The males usually were nestled close beside the rigid nymphs. Under favorable culture conditions as many as 10 of these couples could be picked out per hour of diligent search through the foodstuffs of a thriving culture. The isolation of a courting couple provided an almost assured mating.

Otherwise, mating trials were initiated with molting deutonymphs not attended by males when found. These were placed singly in isolation cells sparingly provided with bran flakes, acarids and 2 males. The isolates were inspected at 24-hr intervals. Those which transformed into females were included in any series being set up at that time. Those which transformed into males were replaced with other molting nymphs destined to emerge on a subsequent day. Thus the setting up of 1 series of 20-30 virgins usually required several days of operation and the series usually contained females of different ages.

The optimum number of males required to assure insemination has not been fixed with certainty. We have routinely used an empirical procedure of confining 1 female with 2 males, 1 original suitor plus a spare male, or any 2 males picked randomly from stocks. The progeny developed thereafter were inspected at frequent intervals for the presence of F_1 daughters. As soon as 5 daughters appeared in a given culture, it was scored as affirmative for mating and discarded; otherwise the searching was continued until a decision could be made. Several cultures were judged affirmatively when 1 or 2 females other than the parent were found. Fortunately, most of the impregnated females produced more than 5 daughters.

The expected success in the mating of females during the pre-nesting period is 95% or better; in 1 such sample, 25 of 26 females were inseminated (R1, Table 2). Females of this lot were sorted into 2 subsamples; 12 of them were placed with 2 randomly picked males and 14 were caged with 1 male only. All of the females of the second subsample were isolated with a male already in attendance, i.e., as courting couples. All of the latter mated: 14 couples, 14 matings. Only 11 of 12 females isolated with 2 males produced female progeny.

This trial focussed closer attention on the question of how many males to place in confinement with deutonymphs or adult females to assure insemination. According to our direct observations of behavior, the second male may be superfluous because it harasses the courting male. The 2 males often faced and grasped each other by the raised pedipalps, claw to claw, somewhat resembling the "pied a deux" described for mating scorpions by Fabre (de Maltos and Miall 1923) or the struggles between males of pseudoscorpions (Weygoldt 1969). They engaged in a very lively "pushing" match. These episodes occurred

TABLE 2.—RECORDS OF ATTEMPTS TO MATE FEMALES OF *C. malaccensis* DURING VARIOUS PERIODS OF THEIR LIVES.

Regime (R) No.	Period of exposure to males	Number of females		Percent mated	No. of progeny observed*	
		Isolated	Mated		Males	Females
1	Pre-nesting	26	25	96	not counted	>120
2	Nesting: 1-10 days	24	1	4	590	2
3	Nesting: 10-20 days	32	0	0	859 (615)	0 (0)
4	Nesting: 20-30 days	21	0	0	175 (408)	0 (0)
5	Sons only	107	8	7	not counted	>40
6	None: virgins throughout	34	—	—	1357	0

*Number of progeny produced during the exposure time are shown in parentheses.

in the vicinity of molting nymphs, were of short duration and did not appear to injure physically either male.

Tests for mating during the nesting period were arranged by exposing virginal females to males, 2 males per female, for 10-day periods. The trials involved 3 lots of females exposed to males of undetermined ages at progressively later intervals of the nesting period (Table 2). During the time of exposure to males, each culture cell was searched at approximately 2-day intervals to confirm the presence of 2 males. Those not found were replaced. Females exposed during the earliest 10-day period (R2) were transferred to fresh cells at the end of 10 days and the progeny accumulated during the exposure time were discarded. One of these females out of 24 produced 2 daughters and was believed to have mated. Two groups of progeny were reared and counted for the second lot of females (R3). The progeny developed after the exposure time totaled 859, all males. The progeny generated within the 10-day exposure time, those left behind when the females were transferred to new cells, totaled 615, all males.

In Regime 4, the virgins were transferred to fresh cells at intervals of about 7 days prior to the exposure period. All of these progeny were discarded. The progeny developed during the exposure period (20-30 days) were saved and counted (408 males). This lot of 21 females produced only 175 sons after being established in new cells on the thirty-first calendar day of the laying-nesting period.

In a previous study, Summers et al. (1972) reported that a substantial percentage of females of *C. malaccensis* were able to mate with their own sons when mothers and progeny were imprisoned together for long periods. This observation contradicted other results in the same study and, in the light of later experience, appeared to require repetition. In Regime 5 (Table 2), individual females isolated as molting nymphs were sealed in rearing vessels and maintained with adequate food until all of the progeny matured or all of the cheyletids died, approximately 90 days. After about 45 days the cultures were transferred from rearing tubes to 50 mm Petri dishes so that the presence of new females could be more readily detected. Eight of the 107 isolated females produced at least 5 females each. These daughters were preceded by substantial broods of males in each culture and were among the final few F_1 adults to mature. The results obtained in this series support the earlier observation that females closely confined with their own sons are sometimes able to mate during the later part of their reproductive period.

It has been demonstrated in this laboratory that arrhentoky in *C. malaccensis* is based on haploid males and diploid females (Dr. S. Regev, to be published). The presence of females among F_1 progeny is taken to be proof of insemination. We have obtained limited evidence that virgins are incapable of producing daughters by some mechanism other than union of male and female pronuclei. Thirty-four females isolated as molting nymphs were tended until all of their progeny matured and were examined (R6, Table 2). Each of the females was isolated from her sons by transfers at intervals of 7 to 10 days. All of the eggs and immatures left behind in each old cell were reared to adulthood, inspected and destroyed. The entire progeny comprised males only.

NEST TENURE

Information on nest tenure was obtained from 11 unmated females cultured in paper-bottom cells. They were inspected daily but manipulated only

TABLE 3.—SUMMARY OF DATA ON NEST OCCUPANCY BY UNMATED FEMALES.

Individual identification number	Duration in days			Number of nests made	Days in first nest	Days in second nest	Days in other nests
	Adult life span	Pre- oviposition period	Nesting period				
51	61	3	43	2	29	11	0
52	35	3	31	2	21	10	0
53	82	3	46	1	46	0	0
54	75	4	56	2	15	41	0
55	46	3	40	2	25	13	0
56	81	3	60	2	10	50	0
57	49	3	43	2	19	23	0
58	81	3	74	4	11	32	8
59	50	2	46	1	46	0	0
60	76	4	61	2	19	42	0
61	76	3	60	3	20	13	10
Means	64.7	3.1	50.9	2.1	23.7	21.4	1.6

to the extent required for an observer to determine whether or not they were in their nests. The data on productivity and nest tenure are summarized in Table 3. Two of the females deposited all of their eggs in the original nests, 7 made 2 nests and 2 made 3 or more nests. Discrepancies between number of days in nests and duration of oviposition are attributable to sporadic depositions of 1 or several eggs in places not identifiable as nesting sites. As reckoned by days in successive nests, the 11 females of this lot spent approximately 96% of the laying period in the first 2 nests. Individual laying records for another lot of 19 unmated females are presented in Table 4. Under these conditions, approximately 89% of their eggs were laid in the first 2 nests, 16 females contributed 10% of the total number in their third nests, and 2 females contributed only 1% to the total when they established fourth nests.

Although we know that laying females are able to leave their nests and return, we have not recorded the frequency or duration of such excursions. There seemed to be no sustained wandering phase until oviposition had almost run its course. The abandonment of 1 nest and the establishment of another usually occurred between examination periods and sometimes without detectable breaks in the rhythm of egg deposition. Since females on nests display combativeness towards intruders, a point of interest is whether or not the aggressive behavior persists continuously or abates when females leave their nests. Available evidence seems to show that mating is not apt to occur anytime during the oviposition period.

TABLE 4.—NUMBERS OF EGGS DEPOSITED BY UNMATED FEMALES IN EACH NEST ESTABLISHED.

Individual identification number	Number of eggs laid in each nest			
	Nest No. 1	Nest No. 2	Nest No. 3	Nest No. 4
2	95	200		
3	249			
4	134	23		
5	161	158	2	
6	173	191	19	
8	123	124	57	
9	114	237	9	
10	113	128	13	
11	67	195	88	
12	110	121	8	
13	119	178	4	
14	70	195	85	
15	94	226	62	20
16	69	167	3	
17	94	187	29	
18	68	194	115	
19	74	145	85	24
20	86	153	3	
21	49	149	4	
Totals	2062	2971	586	44
% of Total	36.4	52.4	10.3	0.8

In respect to overt behavior of nesting females and to the physical arrangements of the domiciles, *C. malaccensis* (arrhenotokous) closely resembles the accounts already published for *C. eruditus* (thelytokous). We have not been able to distinguish the 2 species in cultures—except that our laboratory strain of *C. eruditus* produced no males.

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