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FACTORS AFFECTING OVIPOSITION AND FECUNDITY IN THE GRAIN MITE *ACARUS SIRO* L. (ACARINA:ACARIDAE), ESPECIALLY TEMPERATURE AND RELATIVE HUMIDITY

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ABSTRACT

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Oviposition and fecundity in the grain mite *Acarus siro* were studied at 5—30°C and 62.5—90% RH. At and above 20°C, 80% RH, mating and oviposition occurred soon after emergence, but at lower temperatures and humidities egg laying was progressively delayed from one to several days. Females needed to mate repeatedly in order to achieve maximum egg production, optimum conditions for which were 15°C, 90% RH, where total output per female averaged 435 with a maximum of 858. Oviposition rates were highest at higher temperatures, the mean daily rate at 20 and 25°C, 90% RH, rising to maximum levels of 28/29 eggs per female per day on day six.

Oviposition followed clearly defined patterns, favourable conditions producing rapid increases in the mean daily oviposition rate to high peak levels reached at an early stage in the oviposition period. Less favourable conditions resulted in reduced outputs and lower, more uniform rates of egg laying. The mean oviposition period, varying with humidity, fell from 72—122 days at 5°C to 9—13 days at 30°C and the mean incubation period from 42—70 days at 5°C to 3—4 days at 30°C. Egg viability increased with increasing humidity but was little affected by temperature and unaffected by age of the female at time of oviposition.

Males tended to live longer than females at most conditions; longevity — depending on humidity — averaging 13—15 days at 30°C and 129—175 days at 5°C. Adult life for females averaged 12—19 days at 30°C and 88—169 days at 5°C. An 'index of suitability', calculated from egg number, viability and duration of the egg stage and oviposition period, indicated that the most favourable conditions for oviposition and hatching were 20—25°C and 80—90% RH.

INTRODUCTION

The grain or flour mite, *Acarus siro* L., is a common and serious pest of stored products in many countries. Although primarily a pest of stored grain and flour, it is not restricted to these commodities but infests a wide range of foodstuffs, especially cereal products, seeds and cheese.

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It is often reported to be cosmopolitan in distribution but, because its development is prevented or restricted by unfavourably high temperatures or low relative humidities, it is a major pest only in countries of temperate climate. It has been the subject of frequent investigation in Europe, North America and the U.S.S.R., but most studies have concentrated either on the occurrence and distribution of the species in different commodities, especially in relation to the moisture content of these materials, or on problems of prevention or control of infestation in granaries, silos or other storage places. Its biology has been relatively little studied, and a detailed knowledge of its powers of development and increase under various physical conditions is lacking.

This paper describes some of the factors affecting oviposition and hatching and presents data on the fecundity and longevity of the grain mite under a wide range of physical conditions.

MATERIALS AND METHODS

An account of the methods used for the mass culture of *Acarus siro* and for the micro-culture of this species, the latter in order to study isolated individuals, eggs or small groups of mites, has been published elsewhere (Solomon and Cunnington, 1964; Cunnington, 1965) and only a brief description need be given here.

Cultures of *Acarus siro* were reared on wheat germ flakes in small glass flasks tightly plugged with non-absorbent cotton wool maintained at 17.5°C and 75% RH. Adult mites were removed from the cultures as required and transferred to micro-cells, two to three pairs per cell, in which they were confined during exposure to the experimental conditions.

The cells were examined daily and the eggs removed, in groups of ten, to fresh cells kept in a separate desiccator maintained under the same experimental conditions, and allowed to develop to the adult stage. For each experiment, 100—250 eggs, depending on conditions, were used, after which the parent mites were discarded. Immediately on emergence the adults were paired and each pair transferred to a fresh cell. Daily observations were continued on each pair until the deaths of the adults, the number of eggs laid being recorded and the eggs removed before hatching. Males which died before the female were replaced. Except for a few experiments to determine choice of oviposition site, wheat germ was used throughout as food, one or more flakes being placed in each cell according to the number of eggs or mites it contained. Separate experiments were carried out at 15 and 25°C, 90% RH, to determine whether viability of the eggs was affected by the age of the female at the time of oviposition. At 15°C, 90% RH (mean length of life of the female 42 days) eggs laid at ages 18, 25, 35 and 40 days were kept to determine the percentage hatch.

At 25°C, 90% RH (mean length of life of the female 22 days) the eggs kept were laid when the females were 6, 10, 15 and 20 days old. The range

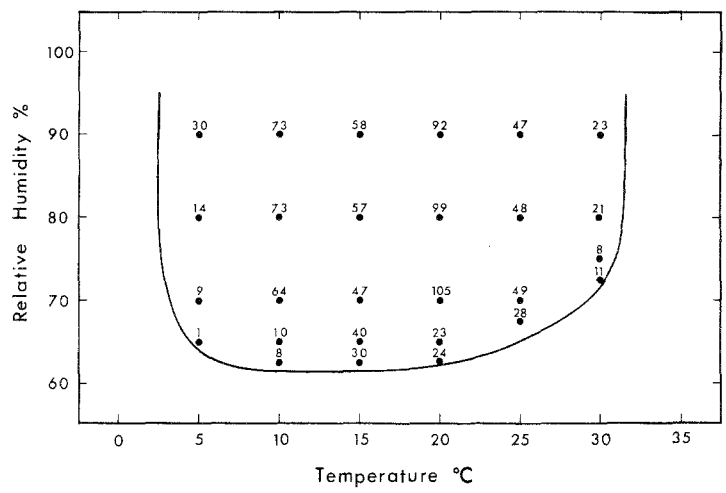

Fig. 1. Physical limits for complete development of the grain mite *A. siro* L. Figures represent the numbers of mated pairs bred under each set of conditions used to determine the data given in Tables 2—7.

of experimental conditions tested and the numbers of adult pairs bred under each set of conditions, on which the data given in Tables 2—7 are based, are shown in Fig. 1.

Relative humidity inside desiccators and culture jars was controlled by using graded solutions of potassium hydroxide (Solomon, 1951). Temperature control facilities included constant temperature rooms, thermostatically controlled ovens and incubators, and suitably adapted domestic refrigerators. The efficiency of temperature control varied, but the range rarely exceeded ± 1°C and was usually less than ± 0.5°C in constant temperature rooms and ovens.

Most experiments were repeated several times, using mites from different cultures. To exclude or nullify variations arising from the choice of adult, experiments at all temperatures except 5°C were carried out simultaneously at 70, 80 and 90% RH, using parent mites from the same source and with all experimental details identical. This ensured that the influence of humidity over the range 70—90% was not obscured by other variables. Limitation of space did not permit such multiple experiments to be carried out at 5°C for each humidity and for other temperatures at humidities below 70%, where parent mortality was often extremely heavy. In these experiments many females laid either few or no eggs before dying, so that frequent replacement was necessary to obtain sufficient eggs for experimental use.

Where replicated experiments gave markedly inferior results, that giving the highest average egg output per female was taken as the natural performance of the species and failure to achieve this maximum output in other experiments was assumed to be a consequence of unknown environmental

factors that must be ignored when comparing the optimal performance of the species under various physical conditions.

The numbers of pairs given in Fig. 1 are not constant because adult emergence depended on the mortality of the juvenile stages, which varied widely according to conditions and was often extremely heavy at marginal temperatures and humidities.

RESULTS AND OBSERVATIONS

Mating and sex behaviour

Coition is effected by the male mounting the back of the female in such a manner that the posterior parts of the idiosoma of both animals are in contact, with their heads facing in opposite directions. The male penis is then in the correct position for insertion into the bursa copulatrix of the female.

The male is enabled to maintain this position and secure a firm grasp of the female with the aid of the anal and genital suckers and of the tarsal suckers on the fourth pair of legs. During coition movement is often maintained, the female leading and the male walking backwards.

Duration of the coition period varied and was partly dependent on external conditions. At 20°C, 90% RH, where continuous observation was possible without serious disturbance of the experimental conditions, what appeared to be normal copulation usually lasted for 2—3 hours but was sometimes completed after about 30 min.

Under optimum conditions (20—25°C, 80—90% RH) mating and oviposition usually occurred within the first twenty-four hours of adult life. The shortest interval between emergence and egg laying, approximately 6 hours, was recorded at 25°C, 90 RH. At temperatures below the optimum few adults mated during the first day of adult life, but subsequent matings were more frequent than at higher temperatures but spread over a longer life span.

The influence of mating on oviposition

Both males and females were seen to mate frequently. To determine whether repeated fertilisation was necessary to enable the female to achieve maximum egg production, single pairs of newly emerged adults reared at 15°C, 90% RH, were confined in micro-cells divided into two groups. In Group 1, males and females were left undisturbed throughout the experiment, except for periodic removal of the eggs, while in Group 2 males were removed immediately after a single mating.

The results (Table 1) showed that females able to mate repeatedly throughout adult life laid considerably more eggs than did those restricted to a single mating. Separation from the male, however, considerably prolonged

TABLE 1

The influence of mating on oviposition

Group	Mean egg output per female	Mean oviposition period (days)	Mean duration of adult life female (days)
1. Males not removed	236.7	21.5	33.2
2. Males removed immediately after mating	129.2	13.8	61.6

Data based on 10 pairs in each series; experiments performed at 15°C, 90% RH.

the life of the female. In a few cells in which the male was reintroduced 12—21 days after the cessation of egg laying, oviposition recommenced, but the data were too few to show whether such periods of infertility affected the total egg-laying capacity of the female.

The effect of temperature and humidity on observed frequency of mating

The mean frequency with which mating was observed at each set of conditions is given in Table 2. Although the highest number of matings between a single pair (40) was seen at 15°C, 70% RH, mating occurred more frequently at 5 and 10°C at and above 80% RH, than at any other combination of temperature and humidity. Individual frequencies above 10 occurred commonly, with maximum frequencies of 31 and 32 respectively at each temperature. There was a marked fall in the observed

TABLE 2

Observed mean frequency of copulation among single pairs at different temperatures and humidities (mean ± S.E.)

Relative humidity (%)	Temperature (°C)					
	5	10	15	20	25	30
90	11.7 ± 1.4	8.7 ± 0.7	5.3 ± 0.5	2.5 ± 0.4	1.8 ± 0.2	0.9 ± 0.1
80	8.9 ± 1.7	6.0 ± 0.7	8.6 ± 1.1	2.0 ± 0.3	1.5 ± 0.2	0.5 ± 0.1
70	7.0 ± 1.4	3.0 ± 0.3	8.2 ± 1.1	3.6 ± 0.5	1.5 ± 0.2	—
65		3.4 ± 0.4	3.8 ± 0.9	1.7 ± 0.3	—	—
62.5		3.8 ± 1.1	1.4 ± 1.3	0.7 ± 0.3		
75						0.5 ± 0.1
72.5						0[a]
67.5					2.1 ± 0.3	

[a]Not observed.

frequency of copulation at temperatures above 15°C and at humidities below 80%.

Oviposition

The egg, usually ovoid in shape, when first laid is smooth, shiny, opalescent and uniformly opaque but becomes transparent as development proceeds. At the end of the incubation period, which varied widely depending on conditions, the larva emerged by an irregular ruption of the chorion, which was left empty, transparent and strongly iridescent.

There is no specialised mode of egg laying or choice of oviposition site. The female extrudes her eggs by expansion and contraction of the muscular walls of the large oviduct, the extruded eggs being pushed behind the body and left. The newly laid egg appears to be covered with a sticky transparent coating, probably secreted by the epithelial layer of the oviduct, which causes it to adhere readily to other eggs or mites or to any smooth surface. In the experimental cells large number of eggs were always found attached to the underside of the circular glass cover slip forming the top of the cell.

In cultures of wheat germ, flour or other finely divided materials, the eggs were found scattered haphazardly on and among the food material and on the sides and walls of the vessels in which it was contained. In cultures of wheat grains, although some eggs were found loosely adhering to the sufaces of the grains, many were deposited within the hollowed-out portion of the embryo on which the mites were feeding or in small cracks or fissures in the seed coat of damaged grains.

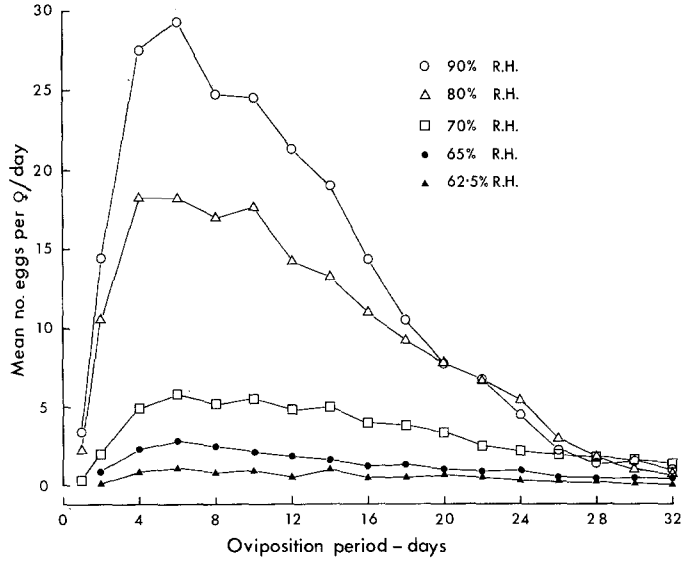

Fig. 2. The effect of relative humidity on the rate of oviposition at 20°C.

The pattern of oviposition (the oviposition curve)

Oviposition follows clear and distinct patterns (Figs. 2 and 3). Under favourable conditions, the mean daily egg-laying rate increases rapidly from an initially low to a high peak rate reached at an early stage in the oviposition period. This peak level is maintained only for a short time, e.g. for 3—4 days at 20°C, 90% RH, after which it falls more or less rapidly, according to conditions, until oviposition ceases and the female dies. Under less favourable conditions, such as low temperature or humidity, output

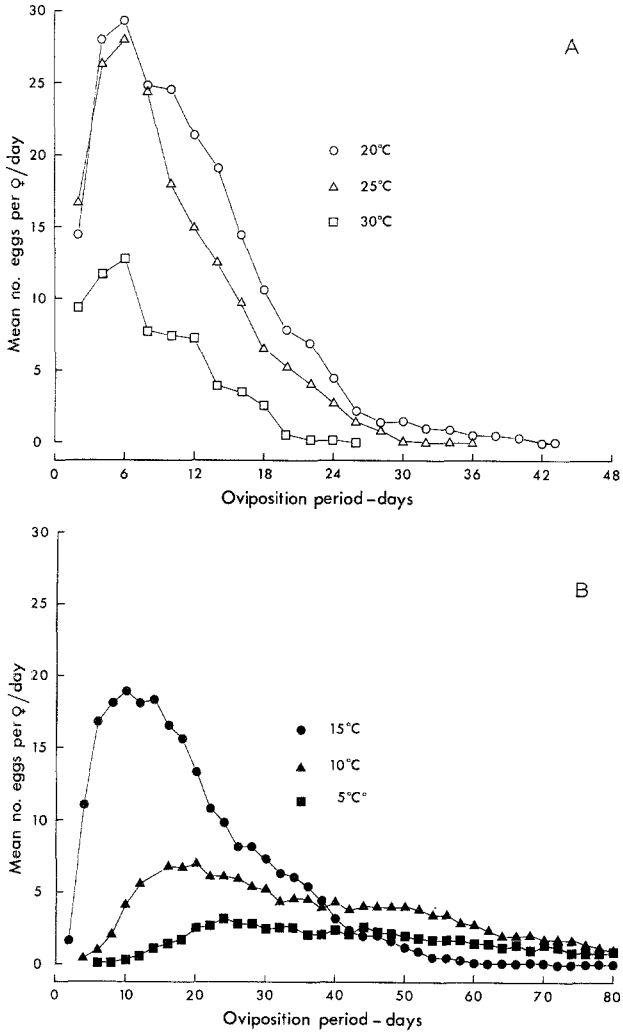

Fig. 3. (A) The effect of temperature on the rate of oviposition at 90% RH (range 20—30°C); (B) the effect of temperature on the rate of oviposition at 90% RH (range 5—15°C).

is considerably reduced and oviposition continues but at a lower, more constant rate throughout the oviposition period.

The effects of temperature and humidity on egg output and rate of oviposition

The effects of temperature and humidity are interdependent, but for the purposes of presentation I have found it convenient to deal with them separately as far as possible. Their effects on rate of oviposition are illustrated in Figs. 2 and 3 and on egg production in Fig. 4, where mean egg output per female has been written on to a grid of temperature vs. humidity and isoperiodic lines drawn through convenient values determined by linear interpolation from the means plotted.

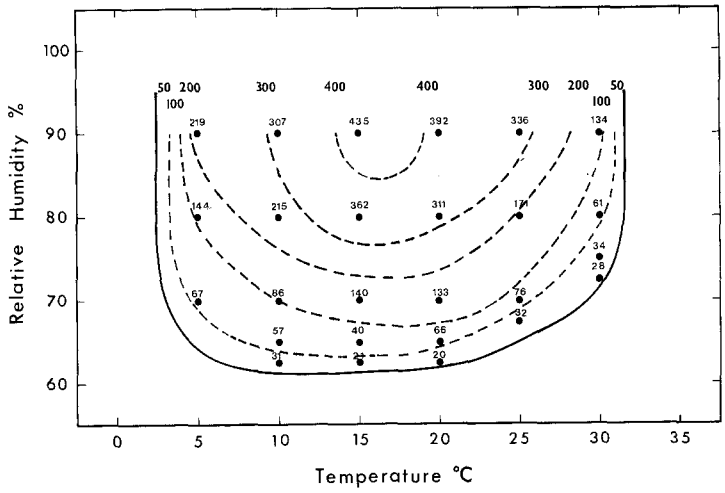

Fig. 4. The effect of temperature and relative humidity on mean total egg output per female.

Both total output and rate of ovipostion varied directly with relative humidity, the threshold of which varied with temperature. Mean total egg output per female increased from 20—30 eggs at 62.5% RH to 134—435 eggs, depending on temperature, at 90% RH. The oviposition rate was similarly affected. For example, at 20°C mean peak rates increased from 1.3 eggs per female per day at 62.5% RH to 29.3 eggs per female per day at 90% RH.

Temperature also had a pronounced effect, except when masked by the unfavourable effects of low humidity. The optimum temperature for total output (Fig. 4) was 15°C, where at 90% RH the number of eggs laid per female averaged 435 with a maximum of 858. A deviation from optimum temperature conditions either towards higher or lower temperatures caused a reduction in the number of eggs laid.

The effects of temperature on rate of oviposition as distinct from total output varied according to whether the ambient temperature was above or below 15°C, the approximate mid-point of the developmental temperature range. Temperatures above 15°C induced high rates of oviposition but curtailed the oviposition period, temperatures below 15°C depressed the rate of oviposition but greatly prolonged the duration of the oviposition period and length of adult life. The optimum temperature for rate of oviposition as distinct from total output was 20°C, where at 90% RH mean number of eggs per female per day rose to a maximum of 29.3 on day 6. As with total output, deviation from optimum temperature conditions towards either higher or lower temperatures caused oviposition rates to fall, peak levels decreasing rapidly at the lower temperatures.

Viability

Viability varied directly with relative humidity but differences in percentage hatch at 80 and 90% RH over some parts of the temperature range were small and probably not significant (Table 3). It was little affected by temperature except at the extremes of the temperature range where the percentage hatch fell sharply below 80% RH. At intermediate temperatures the fall was less rapid and relatively high levels of viability were maintained at humidities above 65%. The lowest humidity at which hatching occurred was 62.5% at 10—20°C. At 5°C no eggs hatched below 65% and at 30°C none below 72.5% RH. Viability was unaffected by age of the female at time of oviposition, the percentage hatch varying erractically between 80 and 92% and showing no significant difference between groups.

TABLE 3

Egg viability at different temperatures and humidities

Relative humidity (%)	Temperature (°C)											
	5		10		15		20		25		30	
	No. eggs	Hatch %	No. eggs	Hatch %	No. eggs	Hatch %	No. eggs	Hatch %	No. eggs	Hatch %	No. eggs	Hatch %
90	210	79.5	250	92.0	359	93.3	727	87.5	424	88.7	542	82.7
80	120	71.7	250	86.8	358	95.8	200	83.5	450	81.1	247	83.6
70	125	44.8	240	82.9	577	78.3	445	73.5	352	74.7	—	—
65	150	6.7	208	62.1	250	61.4	580	70.7	—	—	—	—
62.5	—	—	246	44.3	105	45.3	385	52.6	—	—	—	—
75											193	34.7
72.5											153	4.6
67.5									242	34.5		

Duration of the egg stage

The incubation period varied widely, depending upon conditions, from as little as 3 to as many as 85 days. These figures represent the individual

TABLE 4

Number of eggs and duration of egg stage (days; mean ± S.E.) at different temperatures and humidities

Relative humidity (%)	Temperature (°C)											
	5		10		15		20		25		30	
	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean
90	80	41.9 ± 0.7	39	14.7 ± 0.3	335	8.2 ± 0.1	634	4.9 ± 0.03	343	4.1 ± 0.06	435	3.4 ± 0.03
80	80	47.2 ± 1.9	35	16.3 ± 0.3	343	7.6 ± 0.04	367	5.0 ± 0.06	365	4.2 ± 0.05	226	3.6 ± 0.05
70	12	61.8 ± 3.5	136	20.6 ± 0.4	452	9.3 ± 0.3	327	5.4 ± 0.05	165	4.1 ± 0.1		
65	10	70[a]	246	24.1 ± 0.3	147	10.7 ± 0.1	382	6.2 ± 0.06				
62.5	—	—	53	21.5 ± 0.5	36	12.1 ± 0.3	64	6.1 ± 0.1				
75											37	3.8 ± 0.1
72.5											7	4.0 ± 0.1
67.5									85	4.7 ± 0.07		

[a]Approximate.

minimum and maximum periods recorded during experiments. Mean values, based on the total number of eggs incubated at each set of conditions, are given in Table 4.

Duration of the egg stage varied inversely with both temperature and humidity. At 5°C mean values ranged from 41.9 days at 90% RH to approximately 70 days at 65% RH, and at 30°C from 3.4 days at 90% to 4.0 days at 72.5% RH. They increased progressively with falling humidity at each temperature except at 10°C, 62.5% RH, where there was a slight reversal of the general trend, but increases were relatively slight at temperatures above 20°C.

Adult longevity and duration of the oviposition period

The effects of temperature and humidity on adult life and duration of the oviposition period are summarized in Tables 5 and 6. Over most of the developmental temperature range longevity varied inversely with temperature and was prolonged at low temperatures. At 5°C, 90% RH, the mean length of life ranged from 169 days for females to 175 days for males, while the longest-lived male and female at these conditions survived for 355 and 309 days respectively. At 30°C adult life was much reduced, mean values at 90% RH ranging from 15 days for males (maximum 28 days) to 19 days for females (maximum 35 days).

The effect of humidity varied with temperature. At and above 15°C longevity was little affected by humidity, except where development occurred below 70% RH, where adult life was much reduced. At lower temperatures longevity was directly related to humidity, the adults living progressively longer at the higher humidities.

Except at 30°C, where the adverse effects of high temperature reduced adult life to minimum levels with little difference between the sexes, and at 62.5% RH at 20°C, where the unfavourable effects of low humidity at this temperature produced a similar result, longevity of the males was consistently higher than that of the females.

Duration of the oviposition period was directly related to length of life of the female and reflected the effects of temperature and humidity in a similar manner. At and above 20°C, where egg laying usually occurred within the first 1—2 days of adult life, pre-oviposition periods were short and rarely exceeded more than half a day. Below 20°C, they increased progressively with falling temperature, mean periods at 5°C ranging from 13.3 days at 90% to 15.0 days at 70% RH.

Post-oviposition periods showed wide individual variation. Under favourable conditions egg laying continues throughout the whole or most of the adult female's life but at low humidities, where egg laying is often spasmodic and irregular, or at low temperatures where adult life is prolonged, many females survived for long periods after oviposition ceased. The longest period recorded (194 days) occurred at 5°C, 90% RH. This

TABLE 5

Duration of adult life (days; means ± S.E.) for males and females at different temperatures and humidities

Relative humidity (%)	Temperature (°C)					
	5		10		15	
	♂	♀	♂	♀	♂	♀
90	174.9 ± 15.5	169.0 ± 10.9	114.4 ± 7.9	81.2 ± 5.0	78.6 ± 6.0	42.4 ± 3.6
80	161.4 ± 26.4	127.2 ± 16.8	91.5 ± 7.9	59.6 ± 4.7	101.2 ± 7.6	50.2 ± 4.1
70	129.2 ± 19.8	88.4 ± 13.8	72.7 ± 7.5	48.9 ± 3.9	97.6 ± 6.7	46.9 ± 4.0
65			61.7 ± 8.1	35.0 ± 6.6	36.7 ± 9.1	27.9 ± 8.5
62.5			49.7 ± 10.7	32.6 ± 8.4	46.4 ± 6.2	26.5 ± 3.1
75						
72.5						
67.5						

TABLE 6

Duration of the oviposition period (days; mean ± S.E.)

Relative humidity (%)	Temperature (°C)					
	5	10	15	20	25	30
90	121.6 ± 9.0	66.9 ± 4.4	35.8 ± 2.7	23.6 ± 1.7	17.8 ± 1.2	13.0 ± 1.3
80	85.9 ± 9.5	45.0 ± 3.9	43.9 ± 3.8	22.2 ± 1.2	16.9 ± 1.3	9.0 ± 1.3
70	71.7 ± 16.2	35.9 ± 3.7	40.4 ± 3.5	28.9 ± 1.9	17.1 ± 1.7	
65		40.6 ± 9.1	43.7 ± 8.4	21.8 ± 3.0		
62.5		22.4 ± 7.9	20.9 ± 3.2	14.2 ± 2.9		
75						9.8 ± 2.8
72.5						9.7 ± 1.2
67.5					15.8 ± 1.9	

was more than three times the duration of the oviposition period of the particular female concerned, although the number of eggs laid (211) was not markedly fewer than the mean figure of 243 obtained at these conditions. In this, as in other similar cases, the males were periodically replaced during the post-oviposition period to ensure fertilisation of the female by healthy males.

DISCUSSION

The frequency with which *Acarus siro* mates throughout adult life was earlier noted by Boczek (1957) who concluded that a single fertilisation

20		25		30	
♂	♀	♂	♀	♂	♀
62.9 ± 5.7	28.1 ± 2.0	35.5 ± 2.5	22.4 ± 1.7	15.3 ± 1.7	18.9 ± 1.4
73.2 ± 3.9	23.7 ± 1.9	39.0 ± 2.5	20.2 ± 1.6	12.7 ± 2.1	12.1 ± 1.9
52.0 ± 5.1	36.2 ± 2.2	37.4 ± 4.0	22.5 ± 2.3		
41.9 ± 6.3	22.7 ± 3.1				
22.1 ± 4.9	21.4 ± 3.2				
				14.5 ± 2.5	23.6 ± 5.2
				21.0 ± 2.0	16.6 ± 7.7
		38.7 ± 2.8	27.5 ± 2.7		

was insufficient to enable the female to achieve maximum egg production, a conclusion confirmed by experiment during the present work. Boczek also noted that external conditions strongly influenced mating, which, he stated, was prolonged at low temperatures but shorter and more frequent at high temperatures. These observations were not wholly borne out during the present study, where mating was observed more frequently at temperatures below 15°C than at those above it. Indeed, the frequency of mating over the whole developmental temperature range (Table 2) at first suggests that it is inversely related to temperature, but when frequencies were correlated with the duration of the oviposition period or life span of the female, mean intervals between mating were shortest at 15°C, the approximate mid-point of the developmental temperature range, and increased progressively at temperatures above and below this point. Humidity appeared to have relatively little effect on the frequency of mating except at temperatures below 15°C, where frequencies were noticeably higher at 90% RH than at lower humidities.

Newstead and Duvall (1918) stated that coitus was maintained for several hours but Boczek (1957) reported that under favourable conditions it normally lasted about an hour but was extremely variable and at low temperatures might be prolonged for several days. This statement may be queried. It was presumably based on daily observation in which mating was recorded in the same cell on successive days. While it is possible that a single copulation over a prolonged period was being observed, it is equally possible that separate successive copulations were taking place. The opposite may be true of some of the observations recorded at 5 and 10°C (Table 2), where apparent separate matings may have represented a single prolonged

mating viewed over several days. Since the frequency of mating is dependent not only on the duration of the coition period but also on the length of adult life and extent to which both factors are influenced by external conditions, the precise significance of the results is difficult to interpret.

At the time these experiments were completed, direct transference of the sperm into the female reproductive system was thought to occur by insertion of the male aedeagus into the bursa copulatrix of the female. Later work (Griffiths and Boczek, 1977) showed that sperm transfer in *Acarus siro* involved the transfer of a spermatophore, a single mating resulting in the production of one spermatophore. At 25°C, 80% RH, this produced an average of 78 eggs (maximum 125) over a period of 23 days. A second mating increased production by 30 eggs. Following this disclosure, further studies of the relationship between mating, spermatophore production and fecundity need to be made before the effects of temperature and humidity are clearly understood. Nevertheless the observations described here remain valid.

The fecundity of *Acarus siro* has been relatively little studied. Newstead and Duvall (1918) investigated the bionomics of the species (under the synomyn *Aleurobius farinae*) on grain and reported that the female laid 20—30 eggs at the rate of 3—4 per day. Idhe (1953) studied its development on cheese and found that at 42°F (5.6°C) egg output varied from 100 to 220 eggs per female at 70 and 100% RH, respectively. At 55°F (12.8°C) output was slightly less. Boczek (1957) studied its biology on grain and other foodstuffs and reported that under optimum conditions (20—25°C, 80—85% RH) egg output per female averaged 231 with a maximum of 367. Recently, Peace (1983) investigated its reproduction on cheddar cheese held at 11—13°C, 85—88% RH, and reported a mean egg output of 66.6 and 27.5 eggs per female on sound and mouldy cheese (infected with *Penicillium verrucosum*) respectively.

Such differences in results may be due to several factors; to differences in methods, food or strains, or to the inherent variability of the species even under optimum conditions. Boczek and Czajkowska (1976) found that egg production in *Acarus siro* varied widely on different foodstuffs and was highest on foods rich in carbohydrates and proteins. On cheese, the physical conditions of storage and the chemical and physical changes occurring during ripening and contamination by moulds are probably the chief factors in influencing oviposition. On grain, the moisture content at harvest and the particular combinations of temperature and humidity to which the grain is subject during storage are probably the most important, factors.

The effects of temperature and humidity on the various aspects of oviposition and adult life are summarized in Table 7. These data show that fecundity, viability and rate of oviposition all vary directly with relative humidity but are differentially affected by temperature. Egg production and viability are at a maximum at 15°C, but the oviposition rate is highest

TABLE 7

Summary of the effects of temperature and humidity on ovipostion and adult life of the grain mite *Acarus siro*

	Temperature (5—30°C)	Relative humidity (62.5—90%)
Mean egg output per female	Optimum at 15°C; decreases at higher and lower temperatures	Varies directly with RH; maximum at 90%
Viability %	Optimum at 15°C; falls sharply at near-threshold temperatures below 80% RH; remains relatively high at most intermediate temperatures at humidities above 65%	Varies directly with RH; low humidities unfavourable
Mean incubation period	Varies inversely with temperature	Varies inversely with RH, but differences small at temperatures above 15°C
Duration of adult life	Varies inversely with temperature; prolonged at low temperatures	Below 15°C varies directly with RH; above 15°C relatively little affected except by unfavourably low humidity below 70%
Duration of the oviposition period	Varies inversely with temperature	Varies directly with RH below 15°C; little affected at other temperatures except by low humidity below 70%
Rate of oviposition	Optimum at 20—25°C; falls rapidly at lower temperatures	Varies directly with RH; maximum at 90%

at 20—25°C. Above and below their optimum temperatures all three characteristics show a more or less rapid decline in performance.

On the basis that the most favourable conditions for oviposition and hatching are those which permit the maximum number of viable eggs to be laid and hatched in the shortest time, the effects of temperature and humidity can be more readily understood if the different kinds of information are condensed into one and expressed as a single parameter. Fisher (1938) used this concept to introduce an 'index of suitability' to express the effects of temperature and humidity on oviposition and hatching in the Death Watch beetle, *Xestobium rufovillosum* de Geer. Fisher's index expressed the ratio of the mean numbers of eggs laid per female per day to length of egg period and was calculated by dividing the number of viable eggs produced (NV) by the sum of the durations of the oviposition periods and the egg stage ($L + T$). The most favourable conditions were those which produced the highest index.

Stanley (1946) proposed a similar parameter, an 'environmental index',

to compare the success of development of insects in a number of environments. His method divided the percentage of individuals completing a stage or stages of the life cycle (S) by the mean time required to complete the development of the stage or stages (T).

Howe (1971) criticised Stanley's index on the grounds that it lacked biological meaning but demonstrated that it could have biological significance if recalculated in the form (log S)/T from the statistic '+'$_m$, the intrinsic rate of increase of a population with a stable age distribution. However, because (log S)/T is related to population increase, which is influenced most by those individuals that emerge and proceed to lay eggs early, it is more heavily weighted by the development period than is S/T. Its use, therefore, although appropriate for expressing the suitability of an environment for the development of an insect or other pest which is able to complete its life cycle within the environment, is less suitable for dealing with data relating only to a single stage in the life cycle, especially to oviposition and hatching. The egg stage is often less affected by environmental conditions than the succeeding larval and nymphal stages, the mortality of which has an important bearing on the evaluation of '+'$_m$.

Fisher's index $NV/L + T$, although lacking the precise biological significance of Howe's (log S)/T, nevertheless represents a simple if crude measure of the rate of increase of the species under investigation so far as this is dependent on conditions favourable for oviposition and hatching of the egg.

Using Fisher's method, a series of indices was calculated from the data in Tables 3—6 and the figures written, as were those for egg output, on to a grid of temperature versus humidity. As before, convenient values were determined by linear interpolation from the figures plotted and iso-

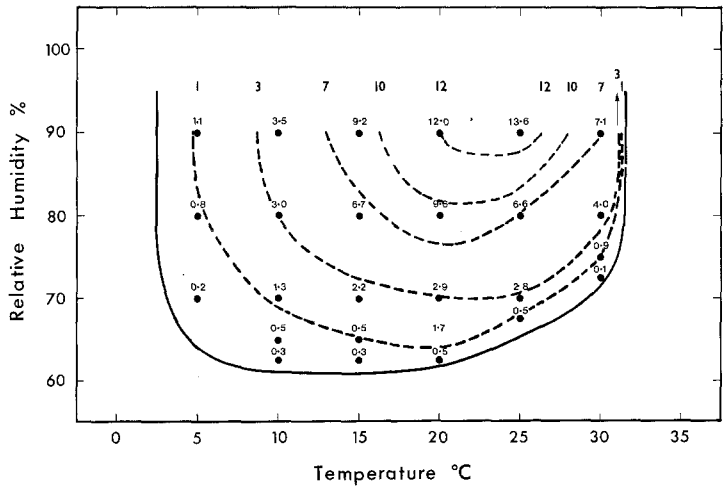

Fig. 5. The 'index of suitability' for oviposition and hatching. The most favourable conditions are those producing the highest index.

periodic lines drawn through them (Fig. 5). These show clearly the effects of temperature and humidity on oviposition and hatching and demonstrate the major role which humidity plays in the ecology of *Acarus siro*. Over the whole developmental temperature range the level of oviposition and viability of the eggs at any given temperature is determined by the ambient humidity. High relative humidities stimulate oviposition and hatching, low humidities depress both total output and oviposition rate. These results conflict with those of Boczek (1957), who stated that within the range 75—100% humidity had little effect on oviposition.

The optimum temperature for oviposition and hatching indicated by the 'index of suitability' is not 15°C, at which egg production was highest, but 20—25°C, at which oviposition rates were at a maximum. This suggests that, although the physiological processes involved in egg laying function best at the lower temperature, the most favourable conditions for rate of increase of the mite, so far as this is dependent on the most favourable conditions for oviposition and hatching, are 20—25°C, 90% RH.

The numerical value of the indices relate only to conditions governing oviposition and would need modification were the whole life cycle of *Acarus siro* to be considered and such factors as rates of development and mortality taken into account. Nevertheless, the results agree well with those of Newstead and Duvall (1918), Solomon (1946, 1962), Boczek (1957) and others, who conclude that, provided the relative humidity is suitably high, the optimum temperature range for the rapid multiplication of *Acarus siro* is about 18—25°C and suggest that optimum conditions for rate of increase of the mite will not differ greatly from those for oviposition and hatching of the eggs.

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