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RELATIVE SUCCESS OF THE MITE Acarus siro L.
ON STORED ONTARIO CHEESE OF DIFFERENT AGES

by

DIANE MARGARET McCLYMONT, B.Sc.

A thesis submitted to the Faculty of
Graduate Studies and Research in partial fulfilment
of the requirements for the degree of
Master of Science

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ABSTRACT

The development and behaviour of Acarus siro L., the most common species of mite on cheese stored in eastern Ontario were studied. These mites were reared on cheddar cheese of different ages, on the mould Penicillium verrucosum complex, and on cheese covered with this mould, to determine whether age of cheese, presence of mould, or plastic packaging affected their survival.

The life history data indicated that A. siro is capable of developing on any age of cheese produced at any time throughout the year with approximately the same egg production, size, survival, and rate of development. These mites could increase on the mould and on mouldy cheese but not as well as on uninfected cheese.

The mites were vulnerable to oily substances particularly abundant on young and plastic-wrapped cheese. They could not eat their way through the plastic coating but could survive on cheese where the coating was damaged.

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INTRODUCTION

Mites have infested stored cheeses for hundreds of years and are still a problem today. They are successful because they are small (100-700 μm) and easily dispersed. They can survive for long periods of time on scraps of cheese or other food and, in moist environments, can live for up to 100 days without food (Boczek and Sosnowska 1975, Ihde 1953). Under favourable conditions of temperature, relative humidity, and abundant food, such as in a cheese warehouse, they can increase to tremendous numbers.

Mites have never been detected on cheeses less than three weeks old. Once the cheeses dry and their protective coating is damaged, mites quickly become established. As they feed and reproduce, cast skins, dead mites, eggs, excreta, and bits of food accumulate and appear as a light-brown dust with a pungent mint-like smell. In heavy infestations, usually on older cheeses, the dust may accumulate to a depth of 2 cm or more. If the dust is brushed away, the surface of the cheese appears heavily pitted where the mites have been feeding. As Robertson (1952), White (1979, pers. comm.), and Wilkin (1979) have shown, up to 10-25% of a cheese can be destroyed by mites when control measures are not applied. Mites not only eat cheese and decrease its quality; they often cause allergies or stomach disorders to persons handling or ingesting the infested food (Robertson 1952, TerBush 1972).

In order to determine the degree of mite infestations under present-day storage conditions, six cheese warehouses in eastern Ontario were inspected by the author during 1978-79. Eighty-five percent or more of cheese is now stored in vacuum-packed plastic-coated blocks (McWater 1980, pers. comm.). These blocks were found, for the most part, to be free of mites but, wherever the plastic coating was damaged, extensive mould growth (mainly Penicillium spp.) was present. The traditional wax-coated

cheeses were, however, often attacked by mites. In five of the six warehouses inspected, these cheeses had various degrees of mite infestations although these were not always immediately apparent. For example, most "90-lb rounds" of cheddar were stored in cylindrical cardboard boxes, and it was only when these cheeses were removed from their boxes that mite infestations were apparent.

Young cheeses (<1 year) generally did not show any infestation to the naked eye (Fig. 1a). Older cheeses, especially those with injury to the wax coating, showed various degrees of infestation ranging from small patches (Fig. 1b), to an entire surface, usually the bottom (Fig. 1c), or almost all of a cheese. Generally, older cheeses had more widespread infestations. In severe infestations, mite dust had spread to the adjacent floor, shelving area, or other cheeses. Microscopic examination of a portion of this dust revealed thousands of mites per cubic centimetre (Fig. 1d). These mites were primarily Acarus siro L. (Acaridae) with some Glycyphagus domesticus (DeGeer) (Glycyphagidae).

From these observations, there arose several questions not adequately answered in the literature: First, why are mites abundant only on older cheese? Is it simply a matter of time before their numbers increase or are they unable to survive on young cheese? Second, can mites survive on plastic-wrapped cheese particularly where the wrapping is damaged and mould is present?

This thesis has attempted to answer these questions through the following studies:

1. An investigation of the development and behaviour of A. siro, the most common species of mite on cheese of eastern Ontario.
2. Experimental rearings of A. siro on different ages of cheddar cheese to determine egg production, survival at each stage, and rate of development.

Fig. 1a. A six-month-old cheese showing no infestation of mites.

Fig. 1b. A one-year-old cheese showing a small light-coloured patch of infestation (i).

Fig. 1c. A three-year-old cheese whose entire bottom surface (cheese turned upside-down) is covered with an infestation of mites (i).

Fig. 1d. A portion of cheese dust with mites (m).

3. Experimental rearings of A. siro on a strain of Penicillium verrucosum complex and on cheese covered with this mould, also to determine egg production, survival at each stage, and rate of development.

LITERATURE REVIEW

I Identification and Distribution

References to mites infesting cheese date back hundreds of years (DeOng and Roadhouse 1922, Wilkin 1979). Saunders (1880) published the first Canadian record of infestations of mites on cheese caused principally by A. siro.

Michael (1901, 1903) and Banks (1906) published reviews of existing information on mites including those living on cheese but these authors indicated considerable confusion about identification of species. Although Jary (1936, 1937 a,b) attempted to clarify some misidentifications it was not until the 1940s that comprehensive taxonomic studies began (Zakhvatkin 1941, Nesbitt 1945, Robertson 1946a,b). Revisions of the genus Acarus (Acaridae) (Griffiths 1960, 1962, 1964a,b, 1970) and of the genus Tyrophagus (Acaridae) (Robertson 1959, 1961, Johnston and Bruce 1965, Griffiths 1979b), and the manual by Hughes (1976) are the sources generally referred to for identification of cheese mites.

Table I lists the species of mites normally found in cheese infestations. This list is by no means complete and includes only those species verified in the above revisional works. The most frequently quoted species are A. siro, Tyrophagus putrescentiae, Tyrolichus casei, and G. domesticus (Wilkin 1979).

Usually two or more species have been found on cheese at the same time (Robertson 1952). There may be a complete replacement of one of these species by another over several months or years. For example, by 1977 A. chaetoxysilos was the dominant species in English cheese warehouses, whereas four years earlier it was observed only occasionally (Wilkin 1973, Pest Infestation Laboratory 1977).

Table I
Species of mites, feeding cheese

Family		Acariidae										Larropodiphidae	Larropodiphidae (L. Y.)	Others	References
		Species	Acarus siro	Acarus chelonys	Acarus immobilis	Acarus terrestris	Acarus chelonys	Acarus terrestris	Acarus chelonys	Acarus terrestris	Acarus chelonys				
Country or Continent	Species	Acarus siro	Acarus chelonys	Acarus immobilis	Acarus terrestris	Acarus chelonys	Acarus terrestris	Acarus chelonys	Acarus terrestris	Acarus chelonys	Acarus terrestris				
Canada	X														Seuders 1980 Jensen 1937ab Sinha 1965
USA	X														Dicks et al. 1953 Hillenbrand 1957 Robertson 1959 Hillenbrand and Dicks 1963 Griffiths 1964b Robertson 1961 Caccese and Fair 1975 Griffiths et al. 1974 Robertson 1952, 1959, 1961 Griffiths 1964b Wain 1973, 1979 Paul, Infection Laboratory 1977 Robertson 1952, 1959, 1961 Griffiths 1964b
South America															Caloglyphus micro- gryphoides (Zachvatkin) (Acariidae)
England	X														Tydeus sp. (Tydeidae)
Holland	X														
Germany	X														
France	X														Zachvatkin 1961 Robertson 1959
Czechoslovakia	X														Zachvatkin 1961 Hennard et al. 1977
USSR	X														Zachvatkin 1967, 1969
Egypt	X														Zachvatkin 1961
New Zealand	X														Weir et al. 1966
Australia	X														Robertson 1964b, 1959, 1961 Robertson 1959, 1961
Japan	X														Sasa 1964 Yoshizawa et al. 1970

In addition, different species may be found under different environmental conditions. In New Zealand, Robertson (1946a,b) found that A. siro, G. domesticus, and Lepidoglyphus destructor were common in warehouses kept at temperatures between 5.5-10°C, whereas Tyrolichus casei and Tyrophagus longior were more common in warmer ones maintained at 7-21°C. She also noted (1961) that T. putrescentiae is more frequently found in tropical and subtropical parts of the world, T. palmarum in temperate areas, and T. longior in temperate-to-cool areas.

II Development

Michael (1884) described the life cycle of a typical cheese mite. He traced its development through egg, larva, protonymph, facultative hypopus, tritonymph, and adult, and noted an inactive period at the end of each stage. He agreed with Mégnin (1880) that the hypopus (a non-feeding, heavily sclerotized nymph) is a developmental stage of a mite rather than a separate species or other form as commonly believed at that time. Subsequent authors have described aspects of the life cycle of acarid mites but have added little new information (Eales 1917, Newstead and Duvall 1918, Belyaev et al. 1932, Jary 1936, 1937a,b, Robertson 1948, 1952, Ihde 1953, Hilsenhoff 1957, Hilsenhoff and Dicke 1963, Cotton 1963, and Hughes 1976).

As the number of mites living on a cheese increases, an infestation develops, visible as a fine dust. The development of these infestations on cheese has been described by Saunders (1880), DeOng and Roadhouse (1922), Dustan (1937b), Thomas (1942), Robertson (1948), and Kosikowski (1967). Generally older wax- or rind-coated cheeses have greater infestations (Wilkin 1979, Molina et al. 1974).

III Health Hazards

Until recently, in certain parts of southeastern Germany, mites were purposely introduced onto Altenburger cheese to impart a special flavour. People eating the cheese for the first time or in large quantities often developed stomach or intestinal disorders (Hinman and Krampmeier 1934, TerBush 1972). Saunders (1880) thought mites were harmless even though they were often eaten in large quantities. At the turn of the century, people were of various opinions as to whether these disorders were caused by the mites or the cheese (Michael 1903). By 1945, the controversy still existed (Lapage 1945). Manson-Bahr and Muggleton (1945) considered Acarus spp. capable of development in the gastrointestinal tract but concluded they have no pathological significance. Recently, Chmielewski (1970) showed that some mites can pass live through a mammalian gut and reviewed their known detrimental effects. Warner and Bohane (1978) and Braude et al. (1980) demonstrated the adverse effects upon animals of eating mite-infested food.

In addition, it was often recorded that persons handling infested cheeses often suffered with skin, eye, and lung irritations (Hirst 1912, 1917, Eales 1917, Findlay 1921, Cleveland 1940, Dowling and Thomas 1942, Thomas 1942, Forman 1944, Nixon 1944, Robertson 1946b, 1952, Anderson and Fishman 1948, Booth and Jones 1954, Pirilä and Kilpiö 1954, Daniel et al. 1955, Chandler and Read 1961, Alexander 1972, TerBush 1972, Southcott 1976, and Krantz 1978). Recently Molina et al. (1974) and Wraith et al. (1979) have shown that many people are sensitive to allergens produced by some mites including those associated with stored cheese. Nevertheless cases have been reported where condemned lots of cheese have been salvaged by cheese connoisseurs (Kosikowski 1967).

IV Damage and Control

Early opinions about the significance of mite dust were often contradictory. Wallace (1915) reported the belief that mite dust was found only on good cheese. Michael (1903) and Zakhvatkin (1941) noted that young cheeses were sometimes dusted with mites to give them a well-aged appearance. In contrast, many considered that mites caused some damage to cheese. Eales (1917) reported an average loss in cheese mass of 2.5% because of mite damage.

As cheese production and trade increased, mite infestations were recognized as causing economic losses (up to 10-25%) especially during World Wars I and II when large amounts of cheese were stored without adequate refrigeration (Eales 1918, DeOng and Roadhouse 1922, Robertson 1948, 1952). As a result, efforts were concentrated on studying the habits of mites in order to control them.

Wallace (1915) and Eales (1917, 1918) noted that mites were more abundant on old or damaged cheeses. Eales (1917) showed that mites could survive for long periods of time in cheese debris and that they could be transported by flies, people, and air currents. Cranfield et al. (1934) noted that unpressed cheeses were more susceptible to attack than pressed ones but that any dry cheese could be attacked. DeOng and Roadhouse (1922) and Dustan (1937b) showed that cheese coated with paraffin was susceptible to attack especially where cracks developed. Dustan (1937b) stated that mites could live at temperatures between 0-15.5°C on cheese. Above this temperature fats unfavourable to the mites were extruded from the cheese.

Solomon (1943, 1944) reviewed some of the early literature concerning cheese mites and their control. Although many of the early control measures were only partially effective, Dustan (1937 a,b) recommended

several including treatment with methyl bromide which is still the most common fumigant used on cheese (Davis 1965a,b, Kosikowski 1977). Other control measures have been suggested by Muggeridge and Dolby (1947), Robertson (1946b, 1952, 1955), Dicke et al. (1953), Hilsenhoff (1957), Marzke and Dicke (1959), Hilsenhoff and Dicke (1963), Kosikowski (1967), Schmidt and Cremmling (1975), and Wilkin (1973, 1979).

Robertson (1946b, 1948, 1952, 1955) studied cheese-mite infestations in New Zealand, England, and the Netherlands and recommended control procedures.

She (1946b, 1948) found infestations throughout New Zealand and noted that warehouses provided favourable conditions for mites - suitable temperatures and relative humidities, dim lighting, and small crevices where mites could breed. Often badly infested cheeses were stored for long periods of time near others and provided a constant source of spreading mites. She showed that all species of cheese mites could live on many other types of stored foods. She emphasized the importance of thorough cleaning of warehouses and equipment to reduce the problems of infestation. Mites, because of their small size, may not be suspected until they are already too well established in inaccessible parts of a cheese to be killed readily.

In England, Robertson (1952) observed the same problems, and noted that Stilton (mould-ripened) cheese was probably the most susceptible to mites because of its open texture, its need to be cured at a high temperature ($>15.5^{\circ}\text{C}$) and relative humidity (90-95%), and its long process of ripening.

In the Netherlands, Robertson (1955) found that mite infestations were rarely a problem because of excellent sanitary procedures and ageing

techniques. Cheeses that were destined for the tropics were wrapped in pig bladders for protection from moulds and mites and to allow for the escape of moisture and gases.

In the United States of America, Hilsenhoff (1957) and Hilsenhoff and Dicke (1963) studied the development of cheese mites at different temperatures and relative humidities in order to find an alternative method of control to fumigation. They showed that the rate of development and viability of mites increased with increasing temperature and relative humidity and that, while mites could live at 0°C, their eggs did not hatch. Their recommended storage conditions (0°C and 61% relative humidity) were impractical for proper ageing of cheese.

Previous to the mid-1950s, most cheddar was coated with wax or left to develop its own rind. During ripening these cheeses invariably developed mite and mould infestations.

In the 1950s, however, plastic packaging, especially cryovac, became popular in Canada, the United States of America, Australia, and New Zealand. Morris (1957) and Dolby (1960) reviewed the advantages and disadvantages of this type of packaging. The major advantage was the inability of mites to penetrate the plastic coating unless some fault or hole was present (Morris 1957, Kosikowski 1967, Wilkin 1979).

Cheese mites are now considered a serious problem only on cheeses ripened in the traditional way, that is, coated with wax or their own rind. Wilkin (1979) has reviewed the present-day problems of cheese-mite infestations in England and has recommended new control methods to supplement good sanitary practices and fumigation.

V Recent Studies

Although the economic losses caused by mites on cheese were reduced, mites still caused considerable damage to other stored foods

(Freeman 1973, 1974). Thus biological studies of these mites were continued.

Cunnington (1965, 1969, 1976) and Solomon (1962) studied the physical limits for the complete development of A. siro and T. putrescentiae. Sinha (1964b) showed that A. siro could live at -18°C for at least 168 days if preconditioned at 6°C . Sokolov (1935) showed that most mites of this species died at -30°C after 24 h exposure. Cunningham (1965) emphasized that adult mites varied considerably in their resistance to unfavourable conditions. Those from dense overcrowded populations were less resistant than those from less crowded ones. Solomon (1962, 1969b) estimated the maximum rate of increase in numbers of A. siro living on grain. At 25°C , this species could increase 4-fold per week at 80% relative humidity and 7-fold at 90%. These mites were, however, already shown not to be able to survive on cheese above 15.5°C because of extruded oils (Dustan 1937b, Robertson 1944).

Numerous other studies were undertaken on cheese mites. These studies included rate of development (Boczek 1957, Davis and Brown 1969, Davis 1972, Berreen 1974), ageing (Boczek and Czajkowska 1973, Boczek and Sosnowska 1975, Czajkowska 1975, Czajkowska and Boczek 1975), inbreeding and hybridization (Boczek and Pankiewicz-Nowicka 1976), effect of methyl bromide on egg development (Boczek et al. 1975, Barker 1967), effect of food on fecundity (Boczek and Czajkowska 1976, Curry 1971), and effect of predators (Solomon 1962, 1969a, Burnett 1977).

Recent work on cheese mites has centred around their survival and attraction to moulds (Griffiths et al. 1959, Rivard 1958, 1961a,b, Sinha 1964a, Sinha and Mills 1968, Thomas 1971, Thomas and Dicke 1971, 1972). Some of the attractive components of moulds have been characterized by Žďárková (1971) and Yoshizawa et al. (1970, 1971, 1972).

Curtis et al. (1978) have studied the production of a volatile compound produced by cheese mites. Kuwahara et al. (1975) and Kuwahara (1976) have studied their alarm pheromones, citral and neryl formate, whereas Okamoto et al. (1978), and Matsumoto et al. (1979) have studied the antifungal effects of these pheromones.

MATERIALS AND METHODS

I Determination of Cheese Maturity

All cheeses used in this study were obtained from one producer and were stored at -6 to -8°C until used. An estimate of the maturity of each cheese was determined by the macro-Kjeldahl method (as described by Kosikowski (1977)). This technique measures the mass of soluble protein and expresses it as a percent of total cheese mass in duplicate samples of 3 g each.

These analyses were performed on all cheeses at the beginning of each experiment and six weeks later on control samples that were maintained under the same conditions as in the rearing experiments but without mites. Approximately six weeks was the longest time that any cheese remained in the rearing cells before it was entirely consumed. Analyses of soluble protein were also performed on cheeses infested with mites and cheeses inoculated with a mould in the Penicillium verrucosum complex.

This mould, isolated from a cheddar cheese made in eastern Ontario, was identified by Dr. R.A. Samson, Centraalbureau voor Schimmelcultures, Baarn, Netherlands, as Penicillium verrucosum complex intermediate between the variety verrucosum and the variety cyclopium with closer affinities to cyclopium. This mould and its synonymies have been described by Samson et al. (1976). Members of this group have been recorded previously from cheese (Raper et al. 1968, Thomas 1971, Renaud et al. 1977, Northolt et al. 1980).

II Stock Cultures

All experiments and observations were conducted on a single strain

of the mite A. siro collected from an eastern Ontario cheese warehouse. Identification of this species was confirmed by Dr. E.E. Lindquist, Bio-systematics Research Institute, Agriculture Canada, and by Dr. P.R. Wilkin, Slough Laboratory, Ministry of Agriculture, Fisheries and Food, England.

Stock cultures of A. siro were maintained in 100-mL jars containing approximately 10 g of ground wheat germ and yeast in the proportion of 1:1 and previously sterilized with propylene oxide. Recommended dosages, mode of action, and effects of this fumigant on foods have been described by Griffiths (1969), Bruch and Koesterer (1961), Block (1977), Phillips (1949), and Perkins (1969).

These cultures were kept at 20-22°C in desiccator jars (diameter 23 cm) containing a saturated solution of sodium chloride that maintained the relative humidity at 78-79%. Once a week, the lids of the desiccator jars were removed for several minutes to allow outward diffusion of any carbon dioxide that had accumulated. Approximately once a month, half of each culture of mites was discarded and replaced with fresh food to maintain healthy mites.

For the cheese stock cultures, small cubes of cheese, <4 mm per side were surface-sterilized by exposure to 6×10^{-3} J of ultraviolet radiation on each of the six sides. This is sufficient radiation to kill 99.9% of surface bacteria (Hescox and Carlberg 1972, Reagan et al. 1973). Mould mortality was confirmed by plating samples of cheese on potato dextrose agar and incubating them for one week at 20°C. Mode of action and effects of ultraviolet radiation on foods have been described by Block (1977) and Reagan et al. (1973).

One 125-mL flask was set up for each of the 12 types of cheese to be used in the study. Cubes of cheese and approximately 0.05 cm^3 of the

wheat germ and yeast mite culture were transferred to each flask which was then closed with a cotton plug to prevent the movement of mites from one flask to another. The flasks were kept at 11-13°C in a desiccator jar (diameter 23 cm) containing a saturated solution of sodium chloride that maintained the relative humidity at 85-88%. These conditions are thought to simulate those on a cheese being aged in an Ontario warehouse. The mites were allowed to complete at least one generation on these cheeses before use.

III Rearing Cells

All experimental studies were conducted on mites living in small, 2.5-mm diameter rearing cells, 10 in each 2x8x0.05-cm clear plexiglass slide (Fig. 2a), made according to the specifications of Radinovsky and Krantz (1961). A smooth ring of Pliobond adhesive (T.M. Goodyear Inc.) was applied to the top of the slide around the outside of each cell and allowed to dry for several days. Each cell was then washed, rinsed with distilled water, dried at 55°C, and surface-sterilized with 6×10^{-3} J of ultraviolet radiation directed at each of five angles.

Approximately 10 mg of experimental food, previously sterilized according to the procedures described in Section II, Stock Cultures, was added to each cell. The cells were then closed with a 5-mm strip of cellophane that stuck to the adhesive. The cellophane could be removed and replaced when necessary. Each cellophane "lid" was pierced 5 to 7 times with a minuten insect pin to make holes large enough to allow air exchange but small enough to retain the smallest mites. These cells were irradiated with a further 6×10^{-3} J of ultraviolet radiation and allowed to equilibrate to 85-88% relative humidity in a desiccator jar (Fig. 2b) for one day before the mites were added.

Fig. 2a. Ten rearing cells (r) in a plexiglass slide.

Fig. 2b. A desiccator jar used to maintain the relative humidity in the rearing cells at 85-88%.

2 b

IV Determination of Relative Humidity

The relative humidity in the desiccator jars was measured with a Lufft hygrometer. The relative humidity inside the rearing cells was estimated by measuring it in an enlarged version of a cell large enough to house the hygrometer and the same proportion of cheese as in a typical rearing cell. For the sake of comparison the relative humidity of an infested cheese was estimated by taking hygrometer measurements of a wax-coated cheese with several sites of damage and enclosed in a cardboard container held in a chamber at the same temperature and relative humidity as in a warehouse.

V Rearing and Observation Techniques

Mites were allowed to develop for at least one generation on each type of food to be tested. Resting tritonymphs were removed from a stock culture of the particular food and placed in intermediate rearing cells until the adults emerged. Within two days of emergence, one female and one male were placed in each of 10 or more cells prepared as described in Section III, Rearing Cells. Cells were kept at 11-13°C and 85-88% relative humidity in a desiccator jar (Fig. 2b) as described in Section II, Stock Cultures.

Every three or four days, the total numbers of eggs, larvae, protonymphs, tritonymphs, and adults, live, resting or dead, for each cell were counted (Fig. 3a,b,c) with the aid of a stereoscopic microscope at 40x magnification until all of the first generation reached adulthood or died. If a cell became contaminated by mould or if a female died before her egg-laying period was almost complete, this count was omitted and replaced by another so that there was a replicate of 10 counts for each study. If a

Fig. 3a. One rearing cell showing a female (F) and her eggs (e).

Fig. 3b. A male (M) and female (F) in the mating position.

Fig. 3c. Part of a rearing cell showing a male (M), female (F), and some of their eggs (e).

Fig. 3d. A rearing cell containing mould-covered cheese (P).

male died or did not appear to be healthy, he was replaced with one of approximately the same age. When the amount of food in any cell became low, several more milligrams of the same food were added.

Observations of the behaviour of these mites on cheese in rearing cells were made using a stereoscopic microscope at 40-70x magnification. More detailed observations were made with a compound microscope at 100-800x magnification using mites in a depression slide. Observations on the orientation of the mouth parts were made using a Semco scanning electron microscope at 15 kV on mites sputter-coated with gold. Internal development studies were made with a compound microscope at 100-1000x magnification using mites mounted in glycerine on glass slides. Size measurements of living mites were made on a minimum of 100 mites at each life stage using an ocular micrometer and a stereoscopic microscope at 40x magnification. Body measurements were made on adult females reared on each of the four age classes of cheese, wheat germ and yeast, or mould and then mounted in Hoyer's medium on glass slides. The total lengths of the idiosoma, tarsus II, and the dorsal setae - $d_1, d_2, d_3, d_4, l_2(=l_a), l_3(=l_p), l_5(=sae)$ (terminology of Griffiths 1979 a,b), were measured in micrometres using a compound microscope at 160x magnification.

VI Egg-laying Studies

A Wheat Germ and Yeast

The total numbers of eggs laid by females living on wheat germ and yeast, as a control for comparison with existing studies, were determined using at least 10 pairs of adults. Every two weeks each pair of adults was moved to a new cell with new food and the egg count continued until each female died.

B Cheese

The total numbers of eggs laid by females living on 12 different types of Canadian cheddar cheese were determined as above using at least 10 pairs of adults for each type of cheese. The 12 types of cheddar cheese, all obtained from one manufacturer, consisted of four age categories: curd, mild, medium, and old, and within each category, cheddar made at three different times of the year: summer, winter, and an intermediate season.

VII Life History Studies

The total numbers of offspring at each stage: egg, larva, protonymph, tritonymph, and adult, their time of development, and their survival rate were determined as described in Section V, Rearing and Observation Techniques. The adult pairs were not moved to new cells as was done in the egg-laying experiments.

A Cheese

The above life history information was determined for 12 sets of 10 pairs of adults living on each of the types of cheddar described in Section VIB, Egg-laying Studies.

B Penicillium Mould on Cheese

The same information was determined for three sets of 10 pairs of mites living on mouldy cheeses as follows. Ten replicates of 10 mg from each of three age categories of cheddar: mild, medium, and old, were placed in rearing cells and inoculated with a single-spore isolate of the mould Penicillium verrucosum complex. The mould was allowed to grow until it covered the outside of the cheese and then a pair of mites was added to each cell (Fig. 3d). When the mould was eaten, new mould-covered particles of cheese were added.

C Penicillium

The same information was also determined for mites living solely on the Penicillium verrucosum complex. Mould hyphae and spores were removed from a large culture of the same isolate used in Section VII B, Penicillium Mould on Cheese. This mould was sterilized with 3 mL of propylene oxide in an anaerobe jar for 24 h, aired for seven days, and equilibrated for at least one day at 85-88% relative humidity according to a procedure described by Griffiths (1979c, pers. comm.). Several milligrams of the mould were added to two series of 10 cells, the first series for mites from a curd culture, and the second for mites from a medium cheddar culture. More mould was added when the old was eaten.

VIII Statistical Analyses

For each experiment the cumulative numbers of offspring per 10 pairs of adults were plotted against time in days. From this information, the cumulative percentages of offspring per 10 pairs of adults were plotted against the logarithm of time on probability graph paper. From these plots, the mean and standard deviation for each curve were estimated.

Four of the variables measured: 1) number of offspring produced, 2) number of offspring that reached adulthood, 3) proportion of offspring that survived to adulthood, and 4) time to emergence of the first adult per pair, were tested against age of cheese, season of manufacture, block effect, and interaction, by a series of analyses of variance for unbalanced models using dummy variables according to the procedure described by Kendall and Stuart (1958). Values for variables 1, 2, and 4 were transformed to natural logarithms; those for variable 3, the proportion of offspring that survived to adulthood, were transformed to arcsin values in radians, to stabilize the variance. Because of the unbalanced nature of the experiment it was not always possible to separate the variances of the season of manufacture

from those of the blocks. For these variables, the sums of squares were estimated. As a result, the sums of squares as well as the degrees of freedom do not add up to the totals.

The body measurements: length of the idiosoma, length of tarsus II, and proportional lengths of the dorsal setae to the idiosomal lengths were compared by means of one-way analyses of variance according to the procedure of Snedecor and Cochran (1967).

Studentized range tests were calculated according to the procedure of Snedecor and Cochran (1967) when significant values were found in the analyses of variance.

LIFE CYCLE AND FEEDING BEHAVIOUR OF Acarus siro

The following information applies to A. siro living on cheese at 11-13°C and 85-88% relative humidity. These are my observations unless otherwise stated. The life cycle is illustrated in Fig. 4.

I Life Cycle

The oval eggs, 100-150 μ m long, are opaque white when first laid but as they mature they become translucent beginning at one end until approximately seven-eighths of the egg is clear (Fig. 3a,c). At 100-1000x magnification the opaque part appears to be composed of yolk (Fig. 5a) and the translucent part corresponds to the area of cell differentiation that begins at the anterior end (Fig. 5b-e) and progresses ventrally and posteriorly.

At about the time when cell differentiation has progressed to one-quarter of the length of the egg, a pair of cone-shaped structures appear at a point one-sixth of the way from the anterior end of the egg on the dorsolateral surface (Fig. 5c). At first they are colourless but they soon become dark (Fig. 5d). Evans et al. (1963) have termed these structures "les calottes chitineuses". Fain (1977) and Fain and Herin (1978) considered these structures to be part of a prelarval stage which otherwise in this species consists only of a thin membrane in close contact with the egg-shell.

As soon as the "calottes chitineuses" are visible, larval segmentation begins (Fig. 5c). The first two lobes to appear become the chelicerae (Fig. 5d). Then the palpal lobes appear, followed in succession by each pair of legs, I-III (Fig. 5e,f). Claparède (1868) also observed these five pairs of appendages in a related species. As the yolk regresses, the anal opening

Fig. 4. Life cycle of *Acarus siro* on cheese.

Fig. 5. Egg development.

can be seen. Setae, including the coxal rods, develop quickly (Fig. 5g). Just before the larva is ready to hatch, the chelicerae and legs become pigmented and their reddish-brown colour can be seen through the egg-shell. The egg stage lasts 10-18 days. Eales (1917) and Dustan (1937b) reported 10-12 days, Ihde (1953) 14 days, and Hilsenhoff (1957) 13.5 days.

The egg shell splits in a lateral plane approximately three-quarters of the way around the egg from the vicinity of the one calotte to the other (Fig. 5h). Fain (1977) and Fain and Herin (1978) suggested that these structures are used to help break open the egg shell. The larva hatches rear end first, as shown in Fig. 5h. It pushes the egg shell off by alternately expanding and contracting its idiosoma and by slipping its legs and chelicerae backward and then pushing forward on the egg shell.

At first, the larva is very pale and small, as short as 140 μm . Gradually the limbs darken and the larva grows to a maximum length of 220 μm . This six-legged larva spends most of its time feeding and walking.

Several days before the end of this stage, the larva becomes swollen and ceases to feed or move. The legs remain bent with their empodial claws appressed to the ends of the tarsi (Fig. 4). Eales (1917) called this phase a quiescent period. Boczek et al. (1969) noted that the alimentary canal is empty and the anterior part is contracted during this period. During the latter part of this quiescent or resting phase, development of the protonymph can be seen. The legs are particularly evident, closely pressed to the idiosoma inside the larval skin. The larval stage was observed to last from 6-16 days. Eales (1917) reported 7 days, Ihde (1953) 9.5 days, Hilsenhoff (1957) 9.7 days, and Belyaev et al. (1932) 11-12 days at 8-10°C.

The eight-legged protonymph hatches posterior end first in the same way as the larva emerges from the egg. It feeds and develops in the same

way as the larva and was observed to range in size from 160-300 μm , and to last 7-20 days. Ihde (1953) reported a mean of 6.5 days and Hilsenhoff (1957) 5.5 days. Several days before the end of this stage, the protonymph also develops into a resting phase.

A tritonymph emerges from this resting phase in the same way as the earlier stages. No hypopal (deutonymphal) stage was observed between the protonymph and the tritonymph in this strain of A. siro. Hughes (1976) mentioned that the hypopus of A. siro is rarely found. Griffiths (1979c, pers. comm.) suggested that the hypopal stage has been lost in strains that have lived in stored products with a fairly constant supply of food for a long time.

The tritonymph was observed to range in size from 260-400 μm , and can be distinguished from the protonymph by its larger size and by the presence of two rather than one pair of genital papillae. The tritonymph also develops into a resting phase, after 9-59 days. Ihde (1953) reported a mean of 5.5 days at 100% relative humidity and Hilsenhoff (1957) 6.5 days. From the tritonymph an adult emerges. The interval from egg-laying to adulthood ranges from 46 - 103 days.

The first adults to emerge may be either males or females and the sex ratio in all adults is close to 1:1, as has been reported by Boczek and Czajkowska (1973). Berreen (1974), however, estimated a sex ratio of 1.5 in favour of females in populations reared at 15°C and 90% relative humidity.

Males were observed to range in length from 360-440 μm , and can be recognized by the large ventral conical process on femur I, the sclerotized genital structures, and the pairs of anal and tarsal suckers (Fig. 6). Females can be distinguished by the inverted V-shaped genital plate (Fig. 7). When females first emerge they are of approximately the same

Fig. 6. Acarus siro male showing the ventral conical process (cp) on femur I, the sclerotized genital structures (gs), and the anal (as) and tarsal (ts) suckers.

Fig. 7. Acarus siro female showing the V-shaped genital plate (gp).

size as the males but as they mature their idiosoma enlarges considerably such that in some cases they appear to be almost twice the size of males. Females were observed to range in length from 380-650 μm .

Usually within a day of emergence, mating begins. A male crawls over the back of a female and turns to face in the opposite direction. He then attaches his two anal suckers onto the dorsal posterior part of her idiosoma so that his genital structures are directly opposite her bursa copulatrix. At the same time, he bends his last pair of legs forward in order that tarsi IV may cross inside legs III; he then attaches his two pairs of tarsal suckers to the sides of her idiosoma (Fig. 8 and 3b). His third pair of legs often rubs against the body of the female. Whether the male is only securing his position or fondling the female, as Boczek (1974) suggested for Tyrophagus putrescentiae, is difficult to tell.

Soon after attachment, very rapid pulsations of the sclerotized male genital structures can be seen; these pulsations last for approximately 2 min. Then the ejaculatory bulb expands and is everted outside the body, forcing the aedeagus outwards in a semicircular path into the bursa copulatrix of the female. Within 1-2 s the bulb collapses and the aedeagus retracts. The expansion and collapse cycle is repeated many times, initially once every 3-5 s, with the period between pulsations gradually increasing. Copulation continues for a minimum of 10 min; Griffiths and Boczek (1977) reported that it may last for up to 45 min. During the entire mating process, the female may rest or walk, stopping only occasionally. Sometimes the male becomes dislodged. He either quickly resumes the mating process or abandons it.

Griffiths and Boczek (1977) stated that at each successful mating one spermatophore is transferred to the female. The spermatophore solidifies in the sclerotized bell-shaped area of the seminal receptacle and

Fig. 8. Mating position of Acarus siro.

then moves into the lumen of the sac where its contents are released leaving a characteristic bow-shaped tail. By counting the number of tails, they estimated that on the average one spermatophore was transferred every 24 h at 20°C, although considerable variation was noted. Boczek and Griffiths (1979) showed that for single-pair cultures, the mean number of spermatophores per female was 24.5 (range, 16-40) when kept together for 27 days at 20°C. For stock cultures, the mean number of spermatophores was lower 12.5 (range, 0-62).

After mating has been completed, the male often remains attached to the female for days or longer and can walk (backward) and feed. I observed that a male may still be attached to a female when she is old or almost dead. Thus the statement by Davis and Brown (1969) that females in copulating pairs are newly emerged is not always true.

Use of the large conical spur on femur I of the male was observed only once. A male climbed onto a female's back, seized each of her front legs and held them between each spur and the tightly bent genu and tibia. He then proceeded to hit her mouth parts with rapid movements of his chelicerae. From these observations one could suppose that these acts were either some form of courtship or male aggression.

Egg-laying begins 5-15 days after the emergence of the female and only if a male is present. Virgin females do not lay eggs and if mating is not continued the female stops laying. Griffiths and Boczek (1977) showed that with one mating (one spermatophore) an average of 78 (maximum 125) eggs was produced; a second mating produced an additional 30 eggs. In the current study, the number of eggs laid ranged from 32 to 393 per female.

When a female is ready to lay an egg, her idiosoma becomes more arched and the edge of an egg appears at the genital opening (Fig. 9). The egg may remain there for several minutes and then quickly comes out.

Fig.9. Egg-laying in Acarus siro.

Other than the arching of the idiosoma, there was no visible movement by the female during egg-laying. The eggs are laid on the food or any other substrate, either singly or in piles of 3-50 or more. Sometimes eggs are carried passively on the backs of other mites where they have been accidentally placed.

The genital papillae of a female are often used to probe the substrate especially during the egg-laying period. They are extruded, either singly, as a pair, or as both pairs, and can be seen to move in several planes. They were also observed to be extruded in other stages but not as frequently as in the adult stage. Their exact function is not known but they appear to be sensory structures as shown by SEM images (Baker and Nesbitt 1980, pers. comm.). Additional suggested roles for these structures in other groups of mites include humidity detection (Knülle 1959, Krantz 1970), respiration (Vercammen-Grandjean 1975), and osmoregulation (Alberti 1977, 1979).

The lateral opisthosomal glands are highly refractile (Hughes, 1976), as though they contain an oily substance. Michael (1901) and Solomon (1946) postulated that these glands secrete oil. If so, this secretion may explain the glossy appearance of all stages, which is gradually lost in dead specimens. Kuwahara (1976) has reported that these organs produce alarm pheromones (citral and neryl formate) in Tyrophagus putrescentiae.

As mites become older, their sclerotized structures, particularly the limbs and genital papillae, become very dark. In this study, mites were observed to live for up to one month after egg-laying ceased. Davis and Brown (1969), however, stated there was only a brief or no post-ovipositional period. In the current study, males tended to outlive females but not by a significant period of time. Males lived 50-139 days, mean 100 and females 30-129 days, mean 85. Boczek and Czajkowska (1973) found that

on casein and yeast diets females lived longer than males but on rye germ for a shorter period of time than males. Both sexes tended to live longer on high protein foods.

II Feeding

The structure of the mouthparts has been described by Griffiths (1979a). Briefly, the ventral base of the gnathosoma is made up of the coxae of the palps fused with the sternal segments to form a sclerotized pre-oral trough with a median dorsal ridge within which the two chelate chelicerae lie (Fig. 10 and 11). The cheliceral bases are supported dorsally by the anterior region of the prodorsum (Fig. 12) and ventrally by a subcheliceral plate (Fig. 13). Between the chelicerae and above the median ridge of the trough lies the labrum, a long tongue-like process with spinules on either side (Fig. 13). The oral opening is just posterior to the base of the labrum. Anterior to the oral opening and between the palps, the gnathosoma forms a snout-like structure with two lobes called rutellae (Fig. 11 and 13). On the dorsal margin of the rutellae (close to where they are attached to the palps) are two pairs of cone-like projections called strigili (Fig. 11 and 13). The palps are incompletely segmented and appear to have limited lateral movement.

During feeding, the first pair of legs is waved up and down, sometimes touching the chelicerae, and the palps continually probe the potential food source. To feed, one of the chelicerae moves out (forward and down), guided ventrally by the pre-oral trough and laterally by the median dorsal ridge and a palp until the movable digit has projected beyond the indentation of the rutellum. The movable digit then opens (Fig. 12) and the chelicera continues to move outward until the basal portion of the movable digit has just passed the tip of the palps. As the digit makes

Fig. 10. A scanning electron microscope micrograph showing the mouth parts of Acarus siro in anterodorsal view. (c) chelicerae, (p) palps, (LI) leg I.

Fig. 11. A scanning electron microscope micrograph showing the mouth parts of Acarus siro in anteroventral view. (c) chelicerae, (p) palps, (pot) pre-oral trough, (r) rutellae, (s) strigili, (b) base of solenidion phi which has broken off.

Fig. 12. Mouth parts of Acarus siro in lateral view.

Fig. 13. Mouth parts of Acarus siro in dorsal view.

contact with food, it closes quickly and the chelicera is retracted along the same groove until its base reaches as far back as a point mid-way along the podocephalic canal. Meanwhile the other chelicera moves out in the same way in its own groove. The two chelicerae protract and retract alternately but in rapid succession (2-5 times per second). At the same time the entire gnathosoma can move outward or inward independently of the cheliceral movements.

As a chelicera is retracted, food that is caught between the two digits is moved backward into the pre-oral cavity. The inner surface of the chelicera moves along the lateral margin of the pre-oral ridge and the toothed labrum while the outer surface comes in contact with the strigili which appear to scrape the chelicera and so remove food particles (Griffiths 1979a, Akimov 1979). Once food particles have reached the pre-oral cavity, it is difficult to see how they are passed through the oral opening. Every few seconds or so during feeding, the chelicerae stop moving and the gnathosoma stretches upward. It would appear that this is when swallowing occurs.

The movement of food through the alimentary canal has been described by Griffiths et al. (1959) and digestion by Akimov (1977). Žďárková and Reška (1976) have calculated that A. siro adults can eat their own body mass (mean 7.86 μ g) per day at 25°C.

As shown by the type of feeding mechanism just described, A. siro is a particulate rather than a fluid feeder. To show this particulate type of feeding A. siro was allowed to eat coloured wax according to the technique of Bowman (1978, pers. comm.). Small coloured particles were observed in the oral region soon after the mites began to feed. Within a day, the coloured particles could be seen throughout the digestive tract and in the faecal pellets. Solomon et al. (1964) also noted that A. siro would

ingest these particles. When mites were allowed to feed on cheese completely coated in paraffin, they usually ate a small hole in the wax. When the cheese was all consumed, a hollow shell of wax remained. In some cases, even this was subsequently eaten.

Although the protective wax coating on a cheese may slow down attack by mites (Muggeridge and Dolby 1947, Hilsenhoff and Dicke 1963), it does not prevent them from reaching the cheese, contrary to the opinion of Dustan (1937b). In most cases, however, mites begin to feed on cheese where there is already a crack or other weakness in the wax coating (Wallace 1915, Muggeridge and Dolby 1947).

In contrast, although thousands of mites were reared in cells covered with cellophane, this study yielded no evidence that they ate this plastic or tried to enlarge the small holes made for air exchange.

EXPERIMENTAL RESULTS

I Cheese Maturity

The initial soluble protein content of the cheeses ranged from a mean low of 1.82% for curd to a mean high of 9.73% for old cheddar (Table 2). After six weeks of ripening, the soluble protein content of each cheese increased to approximately that of the next age category and ranged from a mean of 5.47% for curd to 10.4% for old cheddar. By comparison curd showed the greatest relative increase and old cheddar the least. There was no detectable change in the soluble protein values of the experimental blocks on which mites had fed.

The growth of the mould Penicillium verrucosum complex on cheese increased the soluble protein content to mean values ranging from 13.3 - 24.5%, far in excess of those for naturally ripening, uninfected old cheddar. These levels were not dependent on the initial age of the cheese but rather on the extent of mould growth.

II Egg-laying Studies

The mean number of eggs laid by pairs of adults living on cheese and moved every two weeks was 163 (Table 3) (range 32-393), which was considerably lower than that for adults living on the standard diet of wheat germ and yeast (mean 266, range 69-419). There was, however, no significant difference in the number of eggs produced by adults living on different ages of cheeses nor on cheeses made at different times of the year ($P=0.05$) (Table 4).

III Life History Studies on Cheese

A Egg Production

In these studies, the adult pairs were not moved to new cells but

Table 2
Percent soluble protein of cheese of different age categories initially, and after ageing, and of mouldy cheese

Season of Production		% Soluble Protein					Mouldy (Penicillium verrucosum complex) Mean
		Initial	Mean	Overall Mean	After 6 wk of ageing	Overall Mean	
Curd	3* Summer	1.96	1.93		6.20		
	1 Winter	1.90	2.44	1.82	6.02	6.11	
	2 Intermediate	2.24	2.34		5.22		
Mild	3 Summer	1.17	1.20		5.02	5.12	
	2 Winter	1.24	4.82		5.09		17.1
	1 Intermediate	4.82	4.82		5.29	5.19	18.0 17.6
Medium	3 Summer	3.34	3.34	4.41	6.50	6.53	
	2 Winter	5.19	5.07		5.68	5.55	15.2
	1 Intermediate	4.94	6.41		5.42		19.8 17.5
Old	3 Summer	6.28	6.35		7.68	7.56	25.3
	2 Winter	5.95	5.93	6.13	7.43		23.8 24.5
	1 Intermediate	6.10	6.11		7.43	7.37	17.6
* Block Number	3 Summer	8.75	8.74		9.68	10.0	18.3 17.9
	2 Winter	8.72	11.2	9.73	10.4	7.58	16.0
	1 Intermediate	11.3	9.24		7.54		19.4 17.7
	3 Summer	11.0	11.2		7.62	7.58	
	2 Winter	9.32	9.24		9.06		17.0
	1 Intermediate	9.15	9.24		10.5	9.78	19.4 18.2
	3 Summer	11.3	11.2	9.73	11.1	11.3	10.4
	2 Winter	9.32	9.24		11.5		
	1 Intermediate	9.15	9.24		9.81	9.97	12.6
	3 Summer	11.3	11.2		10.1		13.9 13.3
	2 Winter	9.32	9.24				
	1 Intermediate	9.15	9.24				

* Block Number

Table 3

Mean numbers of eggs laid per pair of adults (n=10)

living on cheese

(pairs moved every two weeks)

Season of Manufacture	Age of Cheese				Mean
	Curd	Mild	Medium	Old	
Summer	150	182	146	166	161
Winter	145	182	147	197	168
Intermediate	159	189	142	152	161
Mean	151	184	145	172	163

Table 4

Analysis of variance for numbers of eggs laid per pair of adults

moved every two weeks

(natural logarithmic transformations)

Source	S.S.	d.f.	M.S.	F	Significance
Age of Cheese	1.0327	3	0.3442	0.85	NS, P=0.05
Season of Manufacture	0.1853	2	0.0926	0.23	NS, P=0.05
Interaction	0.3896	6	0.0649	0.16	NS, P=0.05
Residual	43.890	108	0.4064		
Total	45.498	119	0.3823		

remained in the same cell with their developing offspring. The numbers of eggs laid were much lower, mean 66.6 (Table 5) (range 33-114), than those laid by adults moved every two weeks.

An analysis of variance showed no significant effect of age of cheese on the number of eggs produced per pair of adults ($P=0.05$) (Table 6). Because of the unbalanced nature of the experiment the variances for the season of manufacture could not be separated from those of the blocks. These variables as well as the interaction showed a significant effect at $P=0.05$ but not at $P=0.045$. No clear-cut interaction effect could be seen when the means for each variable were plotted.

B Pattern of Emergence

For each of the 12 experiments, the cumulative number of offspring produced per 10 pairs of adults was calculated and plotted against time in days as shown for old cheese, winter production (Fig. 14). The five curves represent, respectively, the cumulative means of eggs, larvae, protonymphs, tritonymphs, and adults. The vertical lines represent the standard error for each set of 10 observations. All 12 graphs for the four age categories of cheese and three seasons of manufacture showed the same type of pattern.

In these experiments, 98% of the eggs were viable. Those that were not eventually turned dark and shrivelled.

Most mortality occurred during the larval stage, especially when these mites became stuck on their backs, usually where there were oily deposits from the cheese in the rearing cell. It would appear that the mites were incapable of stretching their legs sufficiently far backward to dislodge themselves; eventually they shrivelled and died. Occasionally, however, they were dislodged, probably accidentally, by another passing mite and survived.

Table 5
Mean numbers of eggs laid per pair of adults (n = 10)
living on cheese

(pairs not moved)

Season of Manufacture	Age of Cheese				Mean
	Curd	Mild	Medium	Old	
Summer	68.1 (3)*	54.8 (3)	62.8 (1)	55.6 (1)	60.3
Winter	69.9 (1)	70.6 (2)	60.6 (2)	84.7 (3)	71.5
Intermediate	75.8 (2)	66.9 (1)	58.2 (3)	70.7 (2)	67.9
Mean	71.3	64.1	60.5	70.3	66.6

*Numbers in parentheses refer to block numbers

Table 6
Analysis of variance for numbers of eggs laid per pair of adults
not moved

(natural logarithmic transformations)

Source	S.S.	d.f.	M.S.	F	Significance
Age of Cheese	0.3352	3	0.1118	1.78	NS, P=0.05
Season of Manufacture Confounded with Block	0.2872	2	0.1436	2.29	S, P=0.05
Interaction	0.8624	6	0.1437	2.29	S, P=0.05
Residual	6.6593	106	0.0628		
Total	8.3705	119	0.0703

Fig. 14. Cumulative numbers of offspring per 10 females of *Acarus siro* living on old cheddar, winter production, block-3. Vertical lines represent mean $\pm$ standard error (n=10).

Other stages also died prematurely when stuck on their backs but not as frequently as larvae. Very little mortality occurred during the resting phases or during moulting.

C Survival to Adulthood

The mean number of offspring per pair that survived to adulthood was 15.9 (Table 7) (range 0-37). There was no significant effect of age of cheese on the number of adults produced ($P=0.05$) (Table 8). As for the egg analysis, however, both the season of manufacture confounded with the blocks, and the interaction, showed significant effects at $P=0.05$ but not at $P=0.045$. There was a slight increase in adults produced on cheeses made in the spring (part of the intermediate season), as seen when the means for each variable were plotted.

The mean percent of offspring surviving to adulthood per 10 pairs was 23.9 (Table 9) (range 0-58%). As for the number of adults produced, there was only a significant interaction effect (Table 10), thought also to be because of a higher proportion of adults produced on cheese made in the spring.

D Body Measurements

There were no significant differences in any of the body measurements (length of the idiosoma, length of tarsus II, ratios of the lengths of the dorsal setae to idiosomal length) for females raised on cheeses of different ages when these measurements were compared by one-way analysis of variance and studentized range tests. These females, however, had significantly longer idiosomal lengths and larger d_2 setal ratios than those living on the standard diet of wheat germ and yeast ($P=0.05$) (Table 11).

Table 7
Mean numbers of offspring surviving to adulthood per pair of adults (n=10)
living on cheese

Season of Manufacture	Age of Cheese				Mean
	Curd	Mild	Medium	Old	
Summer	9.1 (3)*	15.9 (3)	15.2 (1)	10.8 (1)	12.8
Winter	16.0 (1)	20.8 (2)	17.0 (2)	10.0 (3)	16.0
Intermediate	22.2 (2)	10.4 (1)	21.8 (3)	21.4 (2)	18.9
Mean	15.8	15.7	18.0	14.1	15.9

*Numbers in parentheses refer to block numbers

Table 8
Analysis of variance for numbers of offspring surviving to
adulthood per pair of adults

(natural logarithmic (x+1) transformations)

Source	S.S.	d.f.	M.S.	F	Significance
Age of Cheese	1.4082	3	0.4694	0.94	NS, P=0.05
Season of Manufacture Confounded with Block	3.3163	2	1.6581	3.30	S, P=0.05
Interaction	6.8686	6	1.1448	2.28	S, P=0.05
Residual	53.120	106	0.5011		
Total	68.215	119	0.5732		

Table 9
Percent of offspring surviving to adulthood per pair of adults (n=10)
living on cheese

Season of Manufacture	Age of Cheese				Mean
	Curd	Mild	Medium	Old	
Summer	13.4 (3)*	29.0 (3)	24.2 (1)	19.4 (1)	21.2
Winter	22.9 (1)	29.5 (2)	28.1 (2)	11.8 (3)	22.4
Intermediate	29.3 (2)	15.5 (1)	37.5 (3)	30.3 (2)	27.8
Mean	22.1	24.5	29.7	20.0	23.9

*Numbers in parentheses refer to block numbers

Table 10
Analysis of variance for proportion of offspring surviving
to adulthood per pair of adults
(angle transformations)

Source	S.S.	d.f.	M.S.	F	Significance
Age of Cheese	0.2244	3	0.0748	2.36	NS, P=0.05
Season of Manufacture Confounded with Block	0.1528	2	0.0764	2.41	NS, P=0.05
Interaction	0.5559	6	0.0927	2.92	S, P=0.05
Residual	3.3620	106	0.0317		
Total	4.4634	119	0.0375		

Table 11
Comparison of two body measurements of Acarus siro females* reared on the diets
under study

Diet	Curd	Mild Cheddar	Medium Cheddar	Old Cheddar	Wheat Germ + Yeast	Mould Penicillium verrucosum complex
Letter Designation	a	b	c	d	e	f
Mean Idiosomal Length (μm)	572	556	549	570	481	461
Range (μm)	503-602	525-577	512-650	506-640	435-525	416-506
Significantly Different From ($P=0.05$)	e,f	e,f	e,f	e,f	a,b,c,d	a,b,c,d
Mean Length of Dorsal Seta d_2 as a Percent of Idiosomal Length	15.5	16.8	16.0	17.4	9.7	13.3
Range (%)	11.0-20.0	10.6-22.2	11.8-22.5	13.4-23.4	7.9-12.3	8.9-17.6
Significantly Different From ($P=0.05$)	e	e	e	e	a,b,c,d,f	e

*No. of females per diet = 10

E Rate of Development

The cumulative percentages of offspring produced at the various stages were calculated and plotted against the logarithm of time on probability paper for each of the 12 experiments (Fig. 15-26). The five curves on each graph represent the cumulative percentage of eggs, larvae, protonymphs, tritonymphs, and adults, respectively.

The cumulative curves for each stage were more or less straight and parallel to each other except for those representing the egg stage, which had slightly lower slopes.

The mean emergence time for each stage is the x-value where the cumulative frequency is 50%. The standard deviation for each curve is the difference in the x-values between the cumulative frequencies of 50% and 15.5% (or 84.5% and 50%). The means and standard deviations are presented in Table 12. For all 12 experiments, the mean development periods for each life stage were homogeneous.

The mean time from egg-laying to emergence of the first adult per pair was 74.9 days (Table 13) (range 46-123). There was no significant effect of age of cheese on this time but there was a significant block effect ($P=0.01$) (Table 14). A studentized range test showed that the values for block 1 were significantly higher (> 7.86) than those for blocks 2 or 3 ($P=0.05$) (Table 15). Because of a missing value where one pair did not produce any adults, and the unbalanced nature of the experiment, the data on season of manufacture could not be tested for significance.

IV Life History Studies on Mould

A Egg Production

The mean numbers of eggs laid by adult pairs living on cheese inoculated with mould and on pure mould of the Penicillium verrucosum

Fig. 15. Rate of development for Acarus siro reared on curd, summer production, block-3.

Fig. 16. Rate of development for Acarus siro reared on curd, winter production, block-1.

Fig. 17. Rate of development for Acarus siro reared on curd, intermediate production, block-2.

Fig.*18. Rate of development for Acarus siro reared on mild cheddar, summer production, block-3.

Fig. 19. Rate of development for Acarus siro reared on mild cheddar, winter production, block-2.

Fig. 20. Rate of development for *Acarus siro* reared on mild cheddar, intermediate production, block-1.

Fig. 21. Rate of development for *Acarus siro* reared on medium cheddar, summer production, block-1.

Fig. 22. Rate of development for Acarus siro reared on medium cheddar, winter production, block-2.

Fig. 23. Rate of development for Acarus siro reared on medium cheddar, intermediate production, block-3.

Fig. 24. Rate of development for Acarus siro reared on old cheddar, summer production, block-1.

Fig. 25. Rate of development for Acarus siro reared on old cheddar, winter production, block-3.

Fig. 26. Rate of development for Acarus siro reared on old cheddar, intermediate production, block-2.

Table 12
Mean times of emergence of each stage of *Acarus siro* reared at 11-13°C and 85-88% R.H.

Food	Season of Production	Eggs	Larvae	Protonymphs	Tritonymphs	Adults
Curd	Summer	15.8 ± 10.8*	33.9 ± 11.7	43.7 ± 11.7	56.2 ± 15.7	100.0 ± 29.1
	Winter	26.3 ± 14.7	53.1 ± 22.8	61.7 ± 18.2	78.4 ± 28.6	102.3 ± 30.2
Mild Cheese	Intermediate	18.2 ± 14.8	37.2 ± 22.6	58.9 ± 19.8	76.7 ± 28.6	112.2 ± 35.1
	Summer	17.0 ± 9.2	30.9 ± 13.9	40.7 ± 11.6	63.1 ± 16.9	101.0 ± 31.9
	Winter	19.5 ± 10.5	39.8 ± 16.6	52.5 ± 18.1	75.9 ± 16.9	100.0 ± 31.9
	Intermediate	22.9 ± 11.1	41.7 ± 11.3	56.2 ± 16.1	82.2 ± 32.7	121.6 ± 20.3
Medium Cheese	Summer	22.9 ± 13.0	41.6 ± 16.9	54.3 ± 20.3	70.8 ± 24.9	121.6 ± 36.8
	Winter	16.6 ± 11.5	30.2 ± 14.1	43.7 ± 22.9	74.1 ± 34.3	121.6 ± 42.3
Old Cheese	Intermediate	14.4 ± 7.8	26.9 ± 7.5	39.8 ± 11.1	66.1 ± 14.6	98.4 ± 34.5
	Summer	23.4 ± 18.0	43.6 ± 22.5	69.2 ± 24.9	89.1 ± 25.9	113.2 ± 22.4
	Winter	18.6 ± 9.0	37.1 ± 13.8	48.9 ± 9.5	58.9 ± 14.9	76.7 ± 15.1
	Intermediate	20.4 ± 12.5	39.8 ± 15.4	47.9 ± 11.7	58.9 ± 14.7	81.2 ± 19.3
Mouldy Cheese	Mild	20.4 ± 16.2	38.9 ± 14.6	44.7 ± 13.8	61.7 ± 19.8	85.1 ± 30.7
	Medium	20.0 ± 16.1	38.0 ± 16.1	47.9 ± 16.9	63.1 ± 20.7	81.3 ± 23.2
	Old	28.8 ± 13.9	38.9 ± 12.2	41.7 ± 13.7	57.5 ± 19.5	85.1 ± 24.4
Pure Mould	Mites from Curd	20.8 ± 11.8	30.9 ± 14.7	45.7 ± 14.2	63.1 ± 10.2	69.1 ± 10.5
	Mites from Medium	21.9 ± 11.5	32.3 ± 14.4	38.0 ± 13.8	63.1 ± 10.8	74.1 ± 11.8

*Values represent: mean ± one standard deviation in days

Table 13

Mean times in days to emergence of first adult per pair of adults (n=10)
living on cheese

Season of Manufacture	Age of Cheese				Mean
	Curd	Mild	Medium	Old	
Summer	65.6 (3)*	67.0 (3)	79.7 (1)	89.6 (1)	75.5
Winter	83.3 (1)	74.2 (2)	75.1 (2)	61.0 (3)	73.4
Intermediate	72.4 (2)	100.3** (1)	69.5 (3)	63.4 (2)	75.8
Mean	73.8	79.8	74.8	71.3	74.9

* Numbers in parentheses refer to block numbers

** Based on 9 rather than 10 pairs

Table 14

Analysis of variance for time in days to emergence of first
adult per pair of adults

(natural logarithmic transformations)

Source	S.S.	d.f.	M.S.	F	Significance
Age of Cheese	0.1772	3	0.0591	1.71	NS, P=0.05
Block	1.6044	2	0.8022	23.2	S, P=0.01
Residual	3.9071	113	0.0346		
Total	5.6697	118	0.0481		

Table 15

Mean times in days to emergence of first adult per pair of
adults (n=10) living on cheese (data arranged by blocks)

Block	Age of Cheese				Mean
	Curd	Mild	Medium	Old	
Block 1	83.3	100.3*	79.7	89.6	87.9**
Block 2	72.4	74.2	75.1	63.4	71.3
Block 3	65.6	67.0	69.5	61.0	65.8
Mean	73.8	79.8	74.8	71.3	74.9

* Based on 9 couples rather than 10

** Significantly different (P=0.05) from Blocks 2 and 3

Studentized Range Test:

$$\begin{aligned}
 \text{Significant} \\
 \text{Difference} &= Q_{0.05} \cdot \frac{s}{\sqrt{n}} \\
 &= 3.37 \frac{\sqrt{217.86}}{\sqrt{40}} \\
 &= 7.86
 \end{aligned}$$

complex were 27.5 and 24.4, respectively (Table 16). For both these diets, the numbers of eggs laid were significantly lower than those for mites living on pure cheese ($P=0.01$) (Table 17).

B. Pattern of Emergence

Mites living on cheese inoculated with mould had a pattern of emergence as shown in Fig. 27, and those living on pure mould, as shown in Fig. 28. In the remaining mould experiments, the emergence patterns were similar.

These patterns resemble those for mites living on pure cheese except that the numbers of offspring produced were lower and the curves more irregular.

As in the cheese experiments, most mortality occurred during the larval stage when mites were trapped in the mould. Although mould growth was abundant, at no time did it fill an entire cell when mites were present.

C. Survival to Adulthood

The mean number of mites surviving to adulthood per pair on mouldy cheese was 9.8, and that on pure mould 0.85 (Table 18). Mites living on cheese inoculated with mould did not produce significantly fewer adults than those living on pure cheese, but those living on pure mould did ($P=0.01$) (Table 19).

D. Body Measurements

Adults living on the pure mould were significantly smaller than those living on pure cheese but did not have significantly lower d_2 -setal ratios ($P=0.05$) (Table 11).

Table 16
Mean numbers of eggs laid per pair of adults (n=10)
living on mould, mould on cheese, and cheese

Food	Age of Cheese				Age of Cheese			
	Mild	Medium	Old	Mean	Food	Curd	Medium	Mean
<u>Penicillium verrucosum</u> complex on cheese	30.2	23.0	29.4	27.5	<u>Penicillium verrucosum</u> complex only	22.9	25.9	24.4
Cheese Control (no mould)	66.9	54.3	55.6	58.9	Cheese Control (no mould)	69.9	58.2	64.1
Mean	48.6	38.7	42.5	43.2		46.4	42.1	44.2

Table 17

Analysis of variance for numbers of eggs laid per pair of adults
(natural logarithmic transformations)

Penicillium verrucosum complex on cheese

Source	S.S.	d.f.	M.S.	F	Significance
Age of Cheese	0.7315	2	0.3657	2.79	NS, P=0.05
Presence of Mould on Cheese	9.3608	1	9.3608	71.4	S, P=0.01
Interaction	0.1343	2	0.0671	0.51	NS, P=0.05
Residual	7.0747	54	0.1310		
Total	17.301	59	0.2932		

Penicillium verrucosum complex only

Age of Cheese	0.0003	1	0.0003	0.01	NS, P=0.05
Presence of Mould	8.9817	1	8.9817	174.8	S, P=0.01
Interaction	0.1811	1	0.1811	3.53	NS, P=0.05
Residual	1.8495	36	0.0514		
Total	11.013	39	0.2824

Fig. 27. Cumulative numbers of offspring per 10 females of *Acarus siro* living on *Penicillium verrucosum* complex on old cheddar. Vertical lines represent mean $\pm$ standard error ($n=10$).

Fig. 28. Cumulative numbers of offspring per 10 females of *Acarus siro* living on pure *Penicillium verrucosum* complex and previously reared on medium cheddar. Vertical lines represent mean $\pm$ standard error ($n=10$).

Table 18
Mean numbers of offspring surviving to adulthood per pair of adults (n=10)
living on mould, mould on cheese, and cheese

Food	Age of Cheese				Age of Cheese			
	Mild	Medium	Old	Mean	Food	Curd	Medium	Mean
<u>Penicillium verrucosum</u> complex on cheese	9.8	6.7	13.0	9.8	<u>Penicillium verrucosum</u> complex only	1.0	0.7	0.85
Cheese Control (no mould)	10.4	14.1	10.8	11.8 ₂	Cheese Control (no mould)	16.0	21.8	18.9
Mean	10.1	10.4	11.9	10.8		8.5	11.3	9.9

Table 19

Analysis of variance for numbers of offspring surviving to adulthood

per pair of adults

(natural logarithmic (x+1) transformations)

Penicillium verrucosum complex on cheese

Source	S.S.	d.f.	M.S.	F	Significance
Age of Cheese	0.8126	2	0.4063	0.78	NS, P=0.05
Presence of Mould on Cheese	0.1954	1	0.1954	0.37	NS, P=0.05
Interaction	2.8256	2	1.4128	2.70	NS, P=0.05
Residual	28.257	54	0.5233		
Total	32.090	59	0.5439		

Penicillium verrucosum complex only

Age of Cheese	0.2551	1	0.2551	0.92	NS, P=0.05
Presence of Mould	55.258	1	55.258	200.3	S, P=0.01
Interaction	1.1484	1	1.1484	4.16	NS, P=0.049
Residual	9.9302	36	0.2758		
Total	66.592	39	1.7075		

E Rate of Development

The cumulative percentages of offspring were calculated in the same way as for those living on cheese. Graphs for mites living on cheese inoculated with mould are shown in Fig. 29-31, and for those living on pure mould in Fig. 32 and 33. The patterns are similar to those for mites living on cheese (Table 12) except that the rate of development is slightly but not significantly faster.

The mean time to emergence of the first adult per pair living on cheese inoculated with mould was 66.6 days while for those living on pure mould it was 79.6 (Table 20). This emergence time was significantly shorter for those living on mouldy cheese compared to pure cheese, but not for those living on pure mould (Table 21). It was observed, however, that many of the first offspring living on pure mould died before reaching adulthood.

Fig. 29. Rate of development for *Acarus siro* reared on *Penicillium verrucosum* complex on mild cheddar.

Fig. 30. Rate of development for Acarus siro reared on Penicillium verrucosum complex on medium cheddar.

Fig. 31. Rate of development for Acarus siro reared on Penicillium verrucosum complex on old cheddar.

Fig. 32. Rate of development for Acarus siro reared on pure Penicillium verrucosum complex and previously reared on curd.

Fig. 33. Rate of development for *Acarus siro* reared on pure *Penicillium verrucosum* complex and previously reared on medium cheddar.

Table 20

Mean times in days to emergence of first adult per pair of adults (n=10)
living on mould, cheese, and cheese

Age of Cheese						Age of Cheese			
Food	Mild	Medium	Old	Mean	Food	Curd	Medium	Mean	
<u>Penicillium verrucosum</u> complex on cheese	67.6	68.9	63.3	66.6	<u>Penicillium verrucosum</u> complex only	78.4	80.8	79.6	
Cheese Control (no mould)	67.0	78.9	89.6	78.5	Cheese Control (no mould)	83.3	69.5	76.4	
Mean	67.3	73.9	76.5	72.6		80.9	75.2	78.0	

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Table 21

Analysis of variance for time in days to emergence of first adult
per pair of adults

(natural logarithmic transformations)

Penicillium verrucosum complex on cheese

Source	S.S.	d.f.	M.S.	F	Significance
Age of Cheese	0.1646	2	0.0823	1.56	NS, P=0.05
Presence of Mould on Cheese	0.4178	1	0.4178	7.90	S, P=0.01
Interaction	0.3268	2	0.1634	3.09	NS, P=0.05
Residual	2.8566	54	0.0529		
Total	3.7659	59	0.0638		

Penicillium verrucosum complex only

Age of Cheese	0.0618	1	0.0618	1.51	NS, P=0.05
Presence of Mould	0.0362	1	0.0362	0.89	NS, P=0.05
Interaction	0.1012	1	0.1012	2.48	NS, P=0.05
Residual	1.4704	36	0.0408		
Total	1.6697	39	0.0428		

DISCUSSION

I Cheese Maturity

A Experimental Results

In the current experiment, the soluble protein content of cheese gradually increased with the age of the cheese from a mean of 1.82% for curd to 10.4% for old. These values are close to the range given by Kosikowski (1977) of 2% for one-month-old to 12% for one-year-old cheese.

There are many other interrelated changes occurring in cheese as it ripens. These are briefly summarized as follows from reviews by Kosikowski (1977), Davis (1965a,b), Webb et al. (1974), Schmidt and Lenoir (1974), and Butkus et al. (1974).

B Production

In milk, protein is normally maintained in solution. With the addition of a coagulating enzyme such as rennin, casein precipitates during a series of chemical reactions to form a semi-rigid network of cross-linked protein fibres that trap many of the fats, insoluble salts, and some of the carbohydrates.

When the cheese has reached a soft, custard-like consistency it is cut, heated, stirred, and the whey (the soluble portion) is drained away. In order to produce a hard cheese such as cheddar, the cheese is piled and repiled (called cheddaring), cut again, salted, and pressed to allow more whey to drain. The resultant fresh cheddar is composed of approximately 25% proteins, 32% fats, 2% carbohydrates, 37% water, and various vitamins and minerals.

C Ripening

During the ripening of cheese, physical and chemical changes take place that alter the texture and develop the flavour. These changes are caused principally by enzymes that originate from microorganisms in the milk or in added starters. Acids, moisture, salts, and minerals such as copper, zinc, and iron also aid in the ripening process. Cheddar is generally ripened at 2-16°C and 85% relative humidity for a period ranging from two months to five years.

The changes in carbohydrates, mainly lactose, occur during cheese production and the first 14-30 days of ripening. During this time the remaining lactose is converted to lactic acid, lactates, acetic and propionic acids, and carbon dioxide.

During ripening, the proteinaceous framework breaks down to peptones and polypeptides and then to amino acids, amines, carbon dioxide, and ammonia, mainly by the action of the remaining rennin and lactic acid. Further changes in the amino acids and amines are reviewed by Marth (1963), Wong (1974), and Creamer (1979).

Many of the fats are hydrolyzed to fatty acids, ketones, alcohols, and carboxylic acids such as butyric, caproic, and caprylic acids.

Some of the minerals that remain in the cheese include calcium, sodium, phosphorus, potassium, and iron. Vitamins present include riboflavin, niacin, thiamine, and vitamin A.

A ripened cheese is a highly nutritious food whose texture and flavour are the result of many factors such that no two cheeses are thought to be the same.

D Effect of Mites on Cheese Maturity

Although there was no evidence that these mites affected cheese maturity, Hilsenhoff (1957) noted that mites prefer to feed on areas of cheese where they had already fed. To date there is no evidence that these mites secrete digestive enzymes; mites are thought to ingest food principally as particles. Studies of the structure of cheese by scanning electron microscopy (Eino et al. 1979) show that it is actually a complex network containing many holes and tunnels. The diameter of many of these openings appear large enough for a mite's cheliceral digit to penetrate in order to grasp and tear off fragments of cheese. As the cheese matures, the network of holes becomes more extensive and fragile, possibly making it easier for mites, especially young ones to feed.

E Effect of Penicillium Mould on Cheese Maturity

Various authors (Bullerman 1980, Bullerman and Olivigni 1974, Gaddi 1973, and Beuchat 1978) have found that Penicillium moulds are the most common ones infecting naturally ripened cheeses. They grow especially where cheeses are damaged and some oxygen is available.

The species used in this study and belonging to the P. verrucosum complex is related to P. roqueforti (Raper et al. 1968), the mould commonly used for production of blue cheese. Both the species of mould may break down cheese in a similar way.

Kinsella and Hwang (1976) have reviewed the chemical effects of P. roqueforti on cheese. They stated that in mould-ripened cheese, 20-40% of the casein is converted to soluble proteins and the cheese fats are broken down to fatty acids, methyl ketones, and alcohols to a greater degree than in non-mould-ripened cheese.

II Egg-laying Studies

Boczek and Czajkowska (1976) noted that A. siro laid more eggs on rye germ than on a casein diet. In the current study, the same was true but the mean number of eggs (266 on wheat germ) was greater than those reported by Griffiths (1964a: 124 on wheat germ) and Boczek (1966: 200 on rye germ). Boczek and Legat (1971) noted that egg production could vary with the quality of food.

Because there were no significant differences in the numbers of eggs laid in my different cheese experiments, I conclude that neither the age of the cheese nor the season when it was made had any effect on the nutritional quality of the cheese as far as egg production is concerned.

Inde (1953) reported a higher mean number (210) of eggs laid per female living on cheese than I do in my current study (163). His rearings, however, were performed at 100% relative humidity rather than at 85-88% as in the present study. Hilsenhoff and Dicke (1963) and Cunningham (1965) noted that fecundity increased with relative humidity.

It should be noted that egg production can vary with other factors. Boczek (1957) stated that fecundity increases if a female mates at least once a week. Boczek and Czajkowska (1976) demonstrated that the age of both adults, male and female, at the time an egg is laid affects the fecundity of their offspring. It is suggested that part of the variability and significant interaction of egg production may be caused by this parental age effect.

III Life History Studies on Cheese

A Egg Production

The numbers of eggs laid in rearing cells where adults were not moved were much lower than in those cells where the mites were moved

every two weeks. Golebiowska (1963) showed that when the density of a population was higher in a rearing cell the mites were less fecund. As well as density-dependent factors, the increased fertility of the adults that were moved may be the result of the removal of waste metabolites, the presence of new food, fresh air, or the physical stimulus of being handled. I think the conditions in the rearing cells where the mites were not moved resemble more closely the actual conditions in cheese dust.

B Pattern of Emergence

In my experiments, practically all the eggs (98%) were viable. Under similar conditions, Hilsenhoff and Dicke (1963) found that only 88-90% of the eggs hatched. Griffiths (1964a) also reported a hatching rate of 90% when A. siro was reared on wheat germ. More recently, hatching rates of up to 100% have been recorded for Tyrophagus putrescentiae by Griffiths (1979b).

My study revealed that most of the mortality occurred during the larval stage when, because of the oily deposits, mites became stuck on their backs. Whether being stuck was the cause or just the outcome of another illness is not known. Hilsenhoff and Dicke (1963) and Ihde (1953) have stated that A. siro can survive in moist conditions for 32-100 days without food. As their investigations did not single out larvae in their reports, it is possible that larvae like those of insects are more susceptible to starvation than older stages (Allée et al. 1949). The fact that they were shrivelled before death would indicate either tissue catabolism or interference with their water balance.

Other authors maintain that most mortality occurs during the resting phases (Hilsenhoff 1957) or during moulting (Davis and Brown 1969). I observed very little mortality at these times.

C Survival to Adulthood

The age of cheese and for the most part, the season of manufacture, did not significantly affect the number or proportion of adults to eggs. Only on spring cheese were these values higher. Although in the past spring cheese was thought to be superior in taste (Kosikowski 1977), it is not known why a larger proportion of eggs reached the adult stage. Perhaps the amounts of other nutrients such as vitamins are higher in spring cheese, with a result of greater survival of offspring to adulthood.

I found that only 23.9% of the eggs laid survived to adulthood. Hilsenhoff (1957) also found high rates of mortality during the young stages especially when they were reared under low relative humidities. In contrast, Cunnington (1976) reported only 25% mortality of immatures when reared on wheat germ. I think that immature mortality is higher on cheese because of the extruded oils that appear to trap some mites.

D Body Measurements

Griffiths (1970) noted that females reared on a rich diet were larger and had proportionally longer dorsal setae, especially d_2 , than siblings raised on a poor diet. My study indicates that these measurements were greater for females reared on cheese than for those reared on wheat germ and yeast. Although wheat germ with yeast is generally considered to be a good food source (Solomon and Cunnington 1964, Griffiths 1966), Boczek (1957, 1964) considered that high protein foods such as cheese, powdered milk, and dried meat were better for A. sirsi. Differences in digestibility or essential amino acids may explain the results observed.

E Rate of Development

The emergence curves for each of the 12 cheeses are for the most

part straight lines which indicate their values are log-normally distributed. The rate of egg-laying was constant for most of the time. Boczek and Czajkowska (1976) found the same type of egg-laying pattern for A. siro living on high protein foods such as casein or dried cod.

The slopes for the egg-laying curves, however, are slightly lower than those for the others. These lower slopes may indicate a slower rate of egg-laying than of development of subsequent stages. Hilsenhoff and Dicke (1963) noticed that several mites feeding on a given area developed more rapidly than one or two isolated ones. It is postulated that some density-dependent factor was influencing these rates such that as the population increased so did the rate of development. Allee et al. (1949) have shown that the temperature may increase in crowded insect populations. Solomon (1949) has stated that the relative humidity of foods may increase with the presence of mites. Both of these factors have been demonstrated to increase the rate of development of mites (Hilsenhoff and Dicke 1963). Allee et al. (1949) have also shown that the rate of cell division may increase as a population enlarges.

A further increase in the rate of development was seen in the emergence curves between 95-99%. Smaller organisms of a particular species are known to develop faster than larger ones (Slobodkin 1961). If smaller mites are produced near the end of the reproductive cycle, the rate of development of the whole population at that time may be faster. Because of the crowded cultures and the fact that adult mites, especially females, increased in size with age, Slobodkin's hypothesis was impossible to confirm. I do not think that the increase in rate of development is because of sex differences. Although males may be slightly smaller than females at emergence, I did not observe an increase in the proportion of males that emerged near the end of the reproductive cycle.

The mean development times especially to the adult stage did not appear to be affected by the age of the cheese. The slower rate of development of mites used in the first experimental block is thought to have been caused by a difference in the stock culture.

The mean emergence times for each stage are slightly longer than those found by Hilsenhoff (1957) for mites reared on one type of cheese under approximately the same conditions. The longer emergence times in the current study may be caused by slight differences in stock culture of mites, different rearing cages, or differences in the cheeses.

These life history data have indicated that A. siro is capable of developing on any age of cheese produced at any time throughout the year with approximately the same egg production, survival, and rate of development.

Many of the constituents of cheese are continually changing. Thus the reasons for survival of mites may be different at different stages of ripening. In older cheeses the physical structure is most favourable for a mite. The more fragile network make ingestible particles easily available and at the same time there is less free fat to trap the mites physically.

Furthermore, in old cheese there is an increase in the more digestible compounds, some of which are beneficial and some of which may not be. For example there is a buildup of the fatty acids butyric, caproic, and caprylic acids. Rodriguez (1972) and Rodriguez and Potts (1974) have shown that these fatty acids, present at levels between 0.5-1%, inhibit development and egg-laying in T. putrescentiae. Although these fatty acids are not present in levels as high as this in cheese, they may alter productivity to some degree.

In young cheese, there is little buildup of inhibitors but many of the potential nutrients such as casein are present in less readily digestible

forms. Some related mites such as A. immobilis, especially the immature stages, are thought to be incapable of digesting complex water-insoluble proteins by themselves (Griffiths 1969). Microorganisms already present in the digestive tract of the mite or ingested along with cheese particles may assist in the digestion of such insoluble products and may render such materials available for assimilation by the mite.

IV Life History Studies on Mould

A Egg Production

There have been many conflicting opinions about the relationship between moulds and acarid mites (Griffiths et al. 1959, Rivard 1958, 1961a,b, Sinha 1964a, Solomon et al. 1964, Sinha and Mills 1968, Thomas 1971, Thomas and Dicke 1971, 1972, and Fleurat-Lessard 1974, 1976). Some authors considered Penicillium moulds detrimental to these mites while others reported that they could in various degrees support mite populations. These authors showed that A. siro is more successful on some species of Penicillium such as P. verrucosum var. cyclopium than on others.

Shimp and Kinsella (1977) have analyzed the nutritional composition of P. roqueforti mycelia and considered that they have adequate nutrients to support animal life. They stated that methionine, which is mainly involved in protein synthesis (Lehninger 1970), is the most limiting amino acid. Rodriguez and Lasheen (1971) have shown that this amino acid is essential for T. putrescentiae. The low level of methionine may be one reason why significantly fewer offspring were produced by mites living on P. verrucosum complex mould.

Section I of the discussion shows that cheese on which Penicillium mould has grown contains nutrients in a more digestible form than pure cheese. The numbers of offspring produced on mouldy cheese, however,

were not much greater than those produced on pure mould. Three possible explanations for the low production of eggs are given. In the first place it may be noted that adults had to feed on the mould for the early part of the egg-laying period before reaching the cheese. Thus, feeding on the nutritionally inferior mycelia may partially explain the low egg production. Second, not all compounds made available by the mould are beneficial to the mites. For example, these moulds increase the levels of fatty acids and ammonia in cheese; these compounds are toxic to the mites when present in high levels (Rodriguez 1972, Rodriguez and Potts 1974, Muggeridge and Dolby 1947). Third, many moulds also produce mycotoxins. Artificial culturing of some strains of Penicillium spp. including verrucosum complex have resulted in the production of mycotoxins (Bullerman and Olivigni 1974, Lafont et al. 1976, Gaddi 1973, Raper et al. 1968, Purchase 1974); some strains of P. roqueforti have been shown to produce various mycotoxins while growing on cheese (Scott and Kennedy 1976). I was unable to test the strain used in the present study for mycotoxin production.

Rodriguez et al. (1980) have shown that some mycotoxins are lethal to T. putrescentiae which could survive but not produce F_2 -progeny when reared on diets containing 1-100 ppm of penicillic acid, citrinin, or ochratoxin. In contrast, I have observed specimens of Acarus sp. feeding and reproducing for over two years on a culture of P. palitans which produced citrinin and ochratoxin. These mites have been noted to feed on the new mould rather than the old where the toxins are more abundant (vanWalbeek 1979, pers.comm.). Aucamp (1969) also stated that Tyrophagus sp. preferred young colonies of fungi (Aspergillus flavus). Therefore it is possible that these mites may eat mycotoxin-producing moulds, but may not always feed where the mycotoxins concentrate. Thus

cheese on which Penicillium mould has grown may contain compounds in a more digestible form but at the same time some potentially toxic ones especially if present in high concentrations.

Mites are known to be capable of spreading mould spores on their bodies or in faecal pellets where a portion of the spores may remain viable (Žďárková 1967, Griffiths et al. 1959, Keller and Smith 1978). It is also thought that mites can retard the growth of some moulds by feeding on them and by the presence of their alarm pheromones (Kuwahara et al. 1975, Kuwahara 1976) which have been shown to have antifungal properties (Okamoto et al. 1978, Matsumoto et al. 1979).

B Pattern of Emergence

Although the emergence pattern for mites living on pure mould was similar to that for mites on cheese, except for the reduced numbers of offspring produced, the pattern on mouldy cheese was more irregular. I think this irregular development is caused by the uneven distribution of nutrients in the mouldy cheese. Periods of slower development were thought to occur when more mites were feeding on Penicillium hyphae, whereas the periods of faster development were the result of more mites feeding on cheese already well digested by the mould.

C Survival to Adulthood and Body Measurements

The fact that significantly fewer adults with smaller body measurements were produced again indicates that the mould is nutritionally inferior or in some way inhibits mite success relative to that on cheese or mouldy cheese. The mould is, however, capable of supporting life as demonstrated by viable egg production in mites that reached adulthood.

D Rate of Development

In these experiments, the rates of development of mites living on mould and mouldy cheese were for the most part the same, but occasionally were slightly faster than for those living on pure cheese. These increased rates of development may be related to their smaller size (Slobodkin 1961).

Various authors have also noted a change in the rate of development of acarid mites living on moulds (Fleurat-Lessard 1974, Sinha 1964a, Hilsenhoff and Dicke 1963). Daneshvar and Rodriguez (1979), and Daneshvar et al. (1977) demonstrated that the rate of development of Caloglyphus berlesei (Mich.) varied with the species of mould on which it was reared.

The preceding information has shown that acarid mites can survive on mouldy cheeses for at least one generation. They frequently congregate on cheeses especially where moulds, including Penicillium spp., are present (Kosikowski 1967, Žďárková 1971). Thomas (1971) and Thomas and Dicke (1971, 1972) have shown experimentally that A. siro is attracted to many species of mould including three species of Penicillium: P. roqueforti, P. camemberti, and P. verrucosum var. cyclopium.

Yoshizawa et al. (1970, 1971, 1972) have isolated the components in cheddar and blue cheese that attract the mite I. putrescentiae. They found that this species of mite was attracted to a combination of four methyl ketones and to 3-methyl butanol, and that there was a synergistic attraction to the combination of all of these. They further demonstrated a decreasing degree of attraction in these mites to cheese inoculated with P. roqueforti, then mature cheese, and finally young cheese. These cheeses were shown to contain different levels of the five attracting compounds in the same order as their degree of attraction (Kinsella and Hwang 1976).

Yoshizawa et al. (1972) noted that these mites were also attracted to milk products and to new cheese but to a lesser degree. They postulated that the mites were less attracted to such products because of even lower levels of the four methyl ketones and to the absence of 3-methyl butanol. Such findings could explain why mites tend to congregate on old and Penicillium-infested cheeses.

CONCLUSIONS

1. Mites are abundant only on older wax-coated cheeses.

I have demonstrated experimentally, by the number of eggs laid, the number, proportion, and size of offspring surviving to adulthood, as well as the rate of development, that A. siro has the same capacity to increase when living on cheddar cheese of all ages even though these values are variable.

It was shown that these mites, especially the larvae, are particularly vulnerable to the oily substances that are more prevalent on young cheeses. As well, mites can take a long time to develop under the conditions of cheese storage such that if only a few adults colonize a new cheese, it would take from 1.5-4 months before the next generation would reach adulthood and even longer for a population to be visible.

Nevertheless, I demonstrated that the mites can produce large numbers of offspring. Thus, given time, they can increase to tremendous numbers, especially on cheese that has been aged for a long time. It was stated in the literature that as cheese ages it often becomes infected with Penicillium moulds that attract mites by the production of particular volatile compounds. I have demonstrated that A. siro is able to survive on one strain of Penicillium mould and on cheese inoculated with this mould, but not as well as on pure cheese.

2. Mites cannot survive on plastic-wrapped cheese unless the coating is damaged.

Although the study of the structure and function of the mouthparts of these mites demonstrated that they are well adapted as particulate feeders to eat their way through wax to the cheese, they cannot eat their

way through plastic used in the cheese trade. In addition, mites are vulnerable to the oily substances which are particularly abundant in plastic-wrapped cheese. If the plastic coating is damaged and the cheese dries to some extent or Penicillium moulds begin to grow, A. siro can survive.

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