AN ABSTRACT OF THE THESIS OF

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Title: BIOLOGY AND BEHAVIOR OF THE MITE CHELETOMORPHA LEPIDOPTERORUM (SHAW) (PROSTIGMATA:CHEYLETIDAE) AND ITS ROLE AS A PREDATOR OF A GRAIN MITE ACARUS FARRIS (OUD.) (ASTIGMATA:ACARIDAE)

Abstract approved: Redacted for Privacy
Dr. G. W. Krantz

Cheletomorpha lepidopterorum (Shaw), a predaceous, prostigmatid mite, was studied under laboratory conditions of 20° - 30° C and 80% - 90% R. H. to determine its effectiveness as a possible biological control agent of Acarus farris (Oud.), a graminivorous mite which infests stored grains and grain products. Although Cheletophyes knowltoni Beer and Dailey had been synonymized with C. lepidopterorum, it was found that the latter could be differentiated from C. knowltoni on the basis of biological, morphological, and behavioral data obtained from four species "populations" (Kansas, Oregon, California, and World-Wide). A temperature range of 20° - 25° C and relative humidities of 80% - 90% created conditions ideally suited to the rearing of C. lepidopterorum. Egg survival under optimal temperature and humidity regimes exceeded 75%.

Mated females laid more eggs than unmated females at optimal environmental conditions.

Development time from egg to adult ranged from a low of 192 hours for a single male at 30° C, 90% R. H., to 420 hours for a male at 20° C, 90% R. H. The second nymphal stage sometimes was omitted in the male ontogeny.

Mated females produced male and female progeny, while unmated females produced a higher percentage of males.

Starved C. lepidopterorum females survived longest at 20° C, 80% R. H. -- 31.33 days. Starved males lived up to 12 days at 20° C, 80% R. H.

All stages of C. lepidopterorum were voracious predators of A. farris and reverted to cannibalism when prey was in short supply. Females consumed from .471 prey/day at 5° C, 80% R. H. to 3.844 prey/day at 20° C, 80% R. H., while males consumed slightly fewer. C. lepidopterorum females survived for over four months at 5° C.

Males guarded quiescent female deutonymphs until emergence and subsequently mated with them. Indications are that females may secrete a substance which attracts males for up to 14 days after the female's emergence. Females were receptive to mating for six days after emergence.

A. farris may feed on the immobile forms of C. lepidopterorum or as a saprophage on dead predators.

Biology and Behavior of the Mite *Cheletomorpha lepidopterorum* (Shaw) (Prostigmata: Cheyletidae) and its Role as a Predator of a Grain Mite *Acarus farris* (Oud.) (Astigmata: Acaridae)

by

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Typed by Mary Jo Stratton for James Roger Allison

DEDICATION

This thesis is dedicated to my four children, Dennis, Aaron, Ethan, and Aimee, who have been my biggest admirers and in spite of whom I have managed to finish this endeavor.

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INTRODUCTION

Acari, or mites, compose an important portion of the arthropod fauna in stored brain and grain products throughout the world. Species of all major suborders of Acari are found in stored grain, with the exception of Metastigmata (ticks). Predator species are found in the suborders Mesostigmata and Prostigmata, and graminivorous species occur in Astigmata (families Acaridae and Glycyphagidae). Mesostigmatid mites are not common or abundant enough to play an important role in the control of astigmatid mites; prostigmatid mites, however, are important predators of these slow-moving, soft-bodied mites which are considered injurious to whole grains and feed. The most widespread and effective species of grain-inhabiting prostigmatid predators belong to the family Cheyletidae.

Mites of the family cheyletidae (sensu Smiley 1970), are free-living predators. They often are associated with infestations of acarid or eriophyid mites, or with scale insects (Baker, 1949). Many cheyletids are world-wide in distribution. Cheyletid mites capture their prey with raptorial palpi, pierce it with stylet-like chelicerae, and suck the body contents.

At least six species of cheyletid mites have been reported from stored grain and grain products by Krantz (1961) and Hughes (1961). Cheletomorpha lepidopterorum (Shaw) is one of the more common and colorful of these species.

C. lepidopterorum was described in 1794 from specimens collected from a moth of the family Noctuidae. Shaw named the mite Acarus lepidopterorum. Koch (1839) found the same species in stables and hay barns and designated it Cheyletus venustissimus. Michael (1878) studied the biology of C. venustissimus in Great Britain and found that males were rare. Oudemans designated the species as the type of his monotypic genus Cheletomorpha. Volgin (1969) synonymized Cheletophyes knowltoni Beer and Dailey with C. lepidopterorum on the basis of morphological characters and was followed in this decision by Summers and Price (1970).

Various investigators, including Solomon (1961, 1962, and 1969) and Pulpan and Verner (1959, 1965), have reported the successful control of acarid mites by Cheyletus eruditus (Schrank). Certain characteristics held in common by C. eruditus and C. lepidopterorum, such as persistence, voracity, and hardiness, suggest that C. lepidopterorum might also be valuable in biological control of graminivorous mites.

The abundance of C. lepidopterorum in stored grain in the Butler bin at the Oregon State University Entomology Farm and its apparent destruction of populations of the graminivorous mites. Tyrophagus putrescentiae (Schrank) and Glycyphagus domesticus (De Geer) prompted studies on its biology, behavior, and interaction with another prey species, Acarus farris. This thesis assesses the effectiveness of C. lepidopterorum as a biological control agent.

LITERATURE REVIEW

Acarid mites have been recognized as pests of stored grain and grain products for centuries, but only in the last 60 years have ecological studies been made. Early investigations on the ecology of acarid mites were carried out in England by Newstead and Duvall (1918) and Newstead and Morris (1920), and in the U.S.S.R. by Belyaev, Shesterikova and Popov (1932) and Zakhvatkin (1936, 1941). The most recent and comprehensive studies have been by Solomon (1944, 1946a, b, 1953, 1962, 1969) and Cunnington (1965) on the grain mite Acarus siro L.

Graminivorous mites occur in stored grain and grain products where there is dockage available or concentrate their attacks on a particular part of the grain substrate. In wheat the mites damage the embryo (germ) and then move to the embryo of another seed instead of eating the exposed endosperm. Grains attacked by mites usually have a small hole in the grain-coat near the tip of the embryo, which may be completely hollowed out, leaving a cavity still largely covered over (Solomon, 1946). Thus, both the germination power and the nutritive value are lost or diminished. Mites cannot attack sound grain, i.e., grain that has not been damaged mechanically, by insects, or by disease.

Solomon (1946) found that dense infestations of mites (80,000 to

160,000 per 100 cc) caused heating in stored grain, as had Rathbone (1919) and Voloschuk (1936). Rodionov (1940), Sigrianski (1940), Christensen (1957), Griffiths, Hodson and Christensen (1959), Sinha (1966, 1968), and Anwarullah et al. (1968) found that mite infestations spread fungus spores from infested to clean areas in the grain bin. Voloschuk (1936) found that A. siro, Tyrophagus putrescentiae, and Glycyphagus cadaverum Schr. tainted grain with their excreta and skins. Pulpan and Verner (1959) found the characteristic odor of mite-infested grain occurred with the presence of 280-330 specimens of G. destructor or 100 specimens of A. siro in 500 grams of grain.

In addition to rendering grain worthless, grain mites may be a public health risk because they carry plant pathogens, transmit food-poisoning organisms, cause intestinal disorders and allergies, and are responsible for the presence of toxins in stored food. Sigrianskii (1940) reported that Tyrophagus noxius transmitted spores of Tilletia tritici to healthy wheat; spores of Botrytris allii to healthy onions, and a virus from infected potatoes to healthy ones. Mlodecki and Burzynska (1956) found that A. siro and T. perniciosus transmit the pathogens Escherichia coli and Salmonella typhimurium. Rats fed on flour infested with Glycyphagus destructor (Schrank) had experienced pathological changes in their intestinal tract. Howe (1965), from Oxley (1950), reported that mite-infested cornmeal caused diarrhea in man. Pulpan and Verner (1959) reported that 2000 specimens of

Glycyphagus destructor or 500 specimens of A. siro caused health disturbances in man and animals. Herranz and Herranz (1963) reported that the ingestion of food heavily infested with A. siro caused intestinal irritation and lesions on various organs, causing the death of a human. Dowling and Thomas (1942) reported an itch caused by contact with Tyrophagus putrescentiae, its eggs and dead bodies. Soysa and Jayawardina (1945) found mites of the genera Tyroglyphus and Tarsonemus in the sputum of asthmatic patients. Pyemotes ventricosus, a mite parasite on larvae of insects in stored produce, often attacks humans, causing itching. Yunker (1964) found that graminivorous mites in animal laboratories can cause dermatitis, respiratory, urinary, and pulmonary acariasis. Shaw (1966) reported that constant irritation by graminivorous mites caused the death of guinea-fowl chicks.

Granary mites carry spores of fungi which produce toxins in moldy grain. Zeleny (in Anderson and Alcock, 1954) reported that unsound grain is toxic to horses because of the fungi present. Spensley (1963) found that groundnuts infected with Aspergillus flavus caused the death of many farm animals.

Acarus farris (Oud.) is a member of the Acarus siro complex (Griffiths, 1964). A. farris has been recorded from cheese, insect collections, nests of birds and rodents, grain stores, stored potatoes, an old barley stack, garden humus, as hypopi on insects, and from deep

litter of chicken houses (Griffiths, 1964). It is one of the outdoor species of the A. siro complex and does not establish itself in processed cereal products. It seems to be a field species sometimes transported to storage but does not persist there (Cunnington, 1965). Whole cereals appear to be the zone where hybridization can occur between A. farris, A. immobilis, and A. siro, the three species of the A. siro complex (Griffiths, 1964). A. farris has been found in England, Holland, Germany, Kenya, U.S.A., and Czechoslovakia. Sinha and Wallace (1966) found A. farris on wheat, oats, and barley, both in outdoor and indoor bulk habitats. Frequency of association of A. farris with fungi in stored products was as follows: 94% - Alternaria tenuis; 66% - Hormodendrum cladosporiodes; 91% - Streptomyces spp.; and 71% - Penicillium spp. A. farris was found in small numbers in the deep litter of a chicken house on the Oregon State University campus. Some of the published information on A. siro is probably based on misidentification of A. farris and A. immobilis Griffiths.

Cheyletid mites were noted as predators of acarid mites in stored grain nearly 100 years ago (Michael, 1887), but their importance was not realized until the early twentieth century, when they were studied by Ewing (1912), Newstead and Duvall (1918), Newstead and Morris (1920), Sigaard (1920), Shepard (1932, 1939), Rodionov (1937, 1940), Rodionov and Furman (1940), and Solomon (1946). More

recent studies have been conducted by Boczek (1959) and Solomon (1961, 1962). These studies, with the exception of the study by Beer and Daily (1956) on Cheletophyes knowltoni Beer and Dailey, dealt with Cheyletus eruditus (Schrank).

Cheyletid mites have long been used in experimental predator-prey interaction studies. Gause (1935), Gause, Smaragdova and Witt (1936), and Smaragdova (1936) all studied the interactions between Cheyletus eruditus and Aleuroglyphus ovatus (Troup), an acarid mite which infests stored products. They found that the interaction between A. ovatus and C. eruditus did not produce the classical oscillation shown in the models of Lotka and Volterra, but rather formed a "relaxation interaction" consisting of extermination of the prey except when immigration of prey from the outside was allowed. Rodionov and Furman (1940) studied the effect of ecological variables such as species of prey and food type on interaction. They found that coarser media such as broken grains favored the predator, while a flour substrate allowed the prey species to reach a high density. C. eruditus was found to survive dry conditions better than its prey. Solomon (1943, 1946, 1961, 1962, 1969) studied interaction and competition between mite species inhabiting stored grain and grain products, these studies being on Cheyletus eruditus (Schrank) and A. siro. Boczek (1959) studied the biology and habits of C. eruditus, including also predator-prey studies on C. eruditus and A. siro. All

of these studies on predator-prey interactions were laboratory studies and, therefore, not directly applicable to the situation in grain storage areas.

Recently, however, predator-prey interaction studies in grain storage areas pointed to the use of C. eruditus as a biological control agent against acarid mites. Norris (1958) reported that A. siro was controlled in wheat stored in bags or in bulk by Cheyletus spp. Pulpan and Verner (1959, 1965) studied the effects of temperature and humidity on the interaction between C. eruditus and the astigmatid mites A. siro, A. farris (Oud.), and Glycyphagus destructor (Schrank). They observed the effect of physical conditions on the abundance of predator and prey as the seasons changed, and using this information, they successfully used C. eruditus as a biological control agent by introducing it into grain either from the grain bin or from laboratory cultures.

Cheletomorpha lepidopterorum (Shaw) is cosmopolitan in distribution (Baker, 1949; Hughes, 1961). Sinha (1966) found it to be one of the commonest stored products mites in floor debris in five rural granaries in Shiga prefecture, Japan. He also found C. lepidopterorum in large numbers infesting barley stored in bags in the Milo District (1968). Sinha's samples showed C. lepidopterorum to be scarce in fall and absent in winter. Previously, Sinha (1963) found C. lepidopterorum overwintering in small, unheated bulks of

grain in Canada. Champ (1966) found that C. lepidopterorum replaced Cheyletus malaccensis Oud. as the major predator of Tyrophagus putrescentiae in peanuts under dry conditions. C. lepidopterorum is also common in Oregon. It has been found in stored grain and grain products throughout the state, although seldom as numerous as at the Butler Bin, Entomology Farm, Oregon State University.

C. lepidopterorum, when first described by Shaw (1794) and later as the type species of the new genus Cheletomorpha, showed little morphological variation, although there is some doubt that the type specimen was examined by Oudemans in his description of the monotypic genus. In 1956 Beer and Dailey described Cheletophyes knowltoni, which was later synonymized with C. lepidopterorum by Volgin (1969) and Summers and Price (1970) on the basis of morphological characters.

C. lepidopterorum was described in the literature as a thelytokous species. Michael (1878) and Hughes (1961) found that unmated females lay fertile eggs which give rise to all-female progeny. Males occurred rarely, and when they did, appeared several at a time. Thus, the literature indicated that bisexual reproduction was rare, and parthenogenesis was the common method of reproduction.

BIOLOGY

Morphology of Cheletomorpha lepidopterorum (Shaw)

Although Volgin (1969) and Summers and Price (1970) synonymized Cheletophyes knowltoni Beer and Dailey with C. lepidopterorum, gross differences in behavior and development between Beer and Dailey's populations and the cultures from Oregon prompted a comparative morphological study of these and other available specimens. Slides and live specimens of C. lepidopterorum from Oregon were compared with slides of both males and females from California, the U.S. National Museum, and Kansas. Efforts to obtain live material from Kansas, where Beer and Dailey conducted biological and behavioral studies on C. knowltoni, were unsuccessful. In this section, I will refer to the mites by their population names; i.e., C. knowltoni will be known as the Kansas population, C. lepidopterorum from California as the California population, C. lepidopterorum from Oregon as the Oregon population, and C. lepidopterorum from other parts of the world as the world population.

Descriptions, drawings, and slides of the Oregon, California, world and Kansas populations were compared. Solenidion ωI and the guard seta were measured from each of the four populations and compared, using the Student "t" test (see Tables 1 and 2). The number of teeth on the palpal claw of males in all populations also was

Table 1. Ranges and averages of observed measurements (in microns) within four populations of Cheletomorpha lepidopterorum (Shaw).

Population	No. observed	Length					
		Solenidion ω I	Guard seta	Solenidion ω I	Guard seta	Ratio of solenidion/ guard seta	No. of teeth on palpal claw
				Females			
California	28	51.07	169.28	35.63-71.25	117.31-204.21	0.30167 or 30.17%	1
Oregon	22	56.70	175.25	43.45-78.21	147.73-195.52	0.32352 or 32.35%	1
World-wide	7	41.85	170.18	34.76-52.14	147.73-182.49	0.24590 or 24.59%	1
Kansas	11	90.46	172.58	78.21-99.93	156.42-191.18	0.52415 or 52.41%	1
				Males			
California	1	77.34	125.57	76.47-78.21	117.31-133.83	0.61591 or 61.59%	3
Oregon	20	68.11	161.86	39.10-79.95	139.04-182.49	0.42078 or 42.08%	3 (ave)
World-wide	6	63.87	144.86	43.45-78.21	121.66-158.16	0.44090 or 44.09%	2.33 (ave)
Kansas	11	87.46	167.15	78.21-99.93	147.73-182.49	0.52326 or 52.32%	1

Table 2. Comparison of four populations of Cheletomorpha lepidopterorum (Shaw) using the Student's "t" test.

Population	No. of females observed	No. of males observed	Average length					
			Solenidion ωI		Guard seta		Ratio of solenidion/guard seta	
			♀	♂	♀	♂	♀	♂
California Oregon	28 22	1 20	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
California Kansas	28 11	1 20	*	N.S.	N.S.	N.S.	*	N.S.
California World-wide	22 7	1 6	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Oregon Kansas	22 11	20 11	**	N.S.	N.S.	N.S.	**	N.S.
Oregon World-wide	22 7	20 6	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Kansas World-wide	11 7	11 6	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.

N.S. = No significant difference
* = Significant at .05 level
** = Significant at .10 level

compared. All measurements were made through an AO microscope.

The results of the morphological study on the four populations indicated some differences between the three C. lepidopterorum populations and the Kansas population. These differences included: (1) number of teeth on palpal claw of males; (2) number of setae on tarsi I-IV of females; (3) shape of tooth on palpal claw of female; and (4) shape of palpal femur of female. The females and males from the California, Oregon, and world populations differed in some ways from the Kansas population. Several leg setae of the Kansas specimens were considerably longer than those from the other three groups (Table 1). Solenidion ωI was longer in the females of the Kansas population. The males of the Kansas population had longer solenidia ωI and guard setae. The results of the "t" test confirmed that a significant difference existed between the lengths of solenidia ωI in the California, Oregon, and Kansas populations (Table 2). A significant difference was also found in the solenidion ωI/guard seta ratio of the California, Oregon, and Kansas populations (Table 2). The statistical data obtained from these four populations along with the morphological, behavioral, and biological data give an adequate basis for separating these two forms (Table 1).

The Egg

Eggs are deposited singly or in small groups over the floors and

walls of the rearing cells and covered by a few fine threads of silk. The eggs are ovoid, semitranslucent, smooth, and shiny, with the embryonic prelarva clearly visible through the eggshell beginning at the broader end of the egg (see Figure 1). The eggs averaged 150 x 100 μ (average dimensions of ten eggs). The shell reflects a brilliant bluish light when viewed through the dissecting microscope after the larvae has emerged, as reported by Beer and Dailey (1956) for Cheletophyes knowltoni (Figure 2).

The Larva (Plate 1)

The larva emerges by pushing forward through the anterior end of the eggshell with its gnathosoma and then gradually forces the rest of its body out through the rapidly-enlarging hole in the shell wall. Extrication is hastened by expansion and contraction of the body and by the use of the legs. Some larvae are unable to free themselves from the eggshell and may struggle for up to four days before dying.

The larva is hexapod, white in color, and transluscent with no evidence of the orange coloration often apparent in later stages. Successful emergence is not the final obstacle the larva must face before it can begin to function. It must also force its way through the silk covering the eggs, a slow and tedious job.

The larva of C. lepidopterorum has been described by Michael (1878) and Oudemans (1906). It is redescribed here since neither

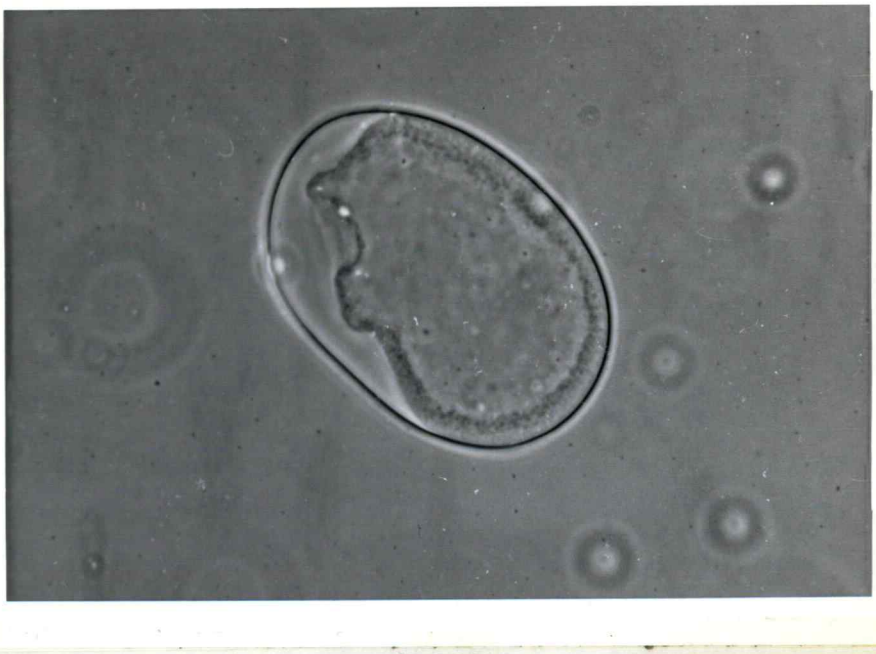


Figure 1. Egg of Cheletomorpha lepidopterorum showing embryonic development.

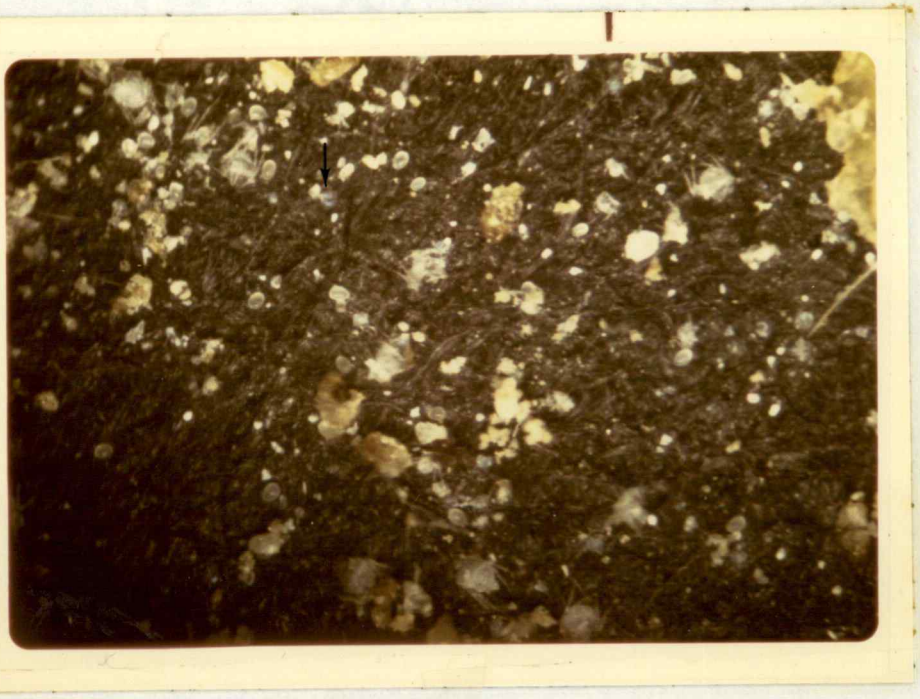
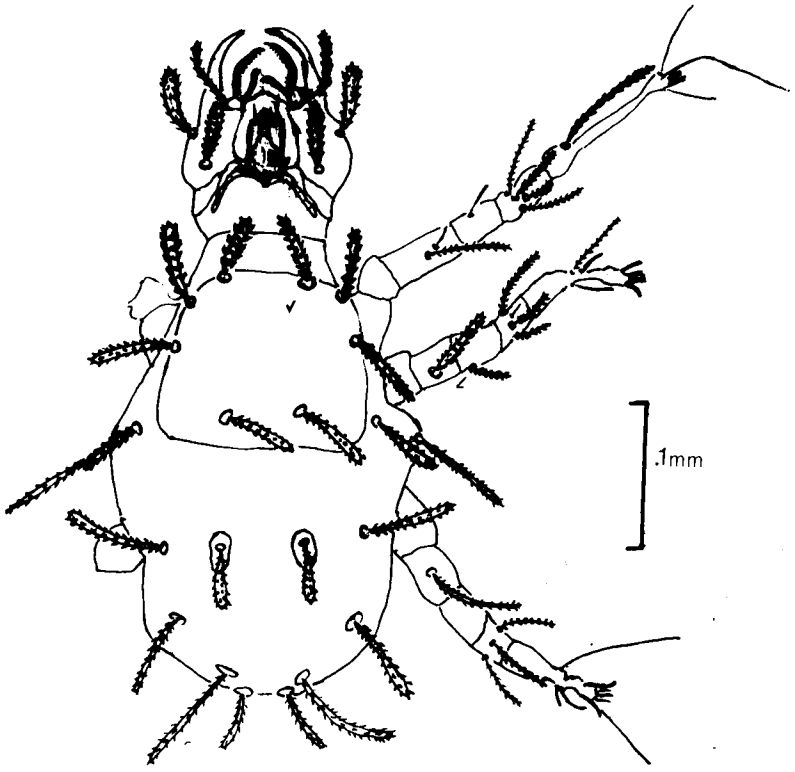


Figure 2. Eggs and cast skins of C. lepidopterorum. Arrow designates bluish-colored eggshell after larva emerged.

Plate 1. Dorsal view of larva of Cheletomorpha lepidopterorum (Shaw).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description is complete.

Palpus and rostrum robust; palpal femur and genu each with one dorsal clavate spinose setae; palpal tibia with three setae, one finely pilose dorsal seta, one lateral and one ventral simple seta; palpal claw long, slender, slightly curved with a single tooth on the basal third; palpal tarsus with two apical whiplike setae and two comb-like setae. Single pair of eyes on propodosoma. Propodosomal shield covering most of propodosoma, with three pairs of marginal subclavate spinose setae at anterior angles near eyes, one pair of submedian subclavate spinose setae on posterior margin of shield; posterior (fourth) pair of marginal subclavate spinose setae lies outside the propodosomal shield. One pair of dorsolateral lanceolate spinose setae on lateral protuberances of propodosoma. Hysterosoma with five pairs of setae, four subclavate spinose setae placed dorsally in four transverse rows and one placed terminally. Venter of hysterosoma with two pairs of submedian simple setae, the anterior pair mesad from coxae I, the posterior pair mesad from coxae III. Anal aperture surrounded by three pairs of very short, simple setae; postanal setae to the side and behind the anal aperture. Larvae averaged 243.99 μ in length by 123.83 μ in width (average of ten specimens).

Legs shorter than idiosoma. Setae on legs I-III as follows: coxae 1-0-0, trochanters 0-0-0, femora 2-2-1, genua 1-1-1, tibia

4-4-4, tarsi 8-7-7. Tarsi II and III without median setae.

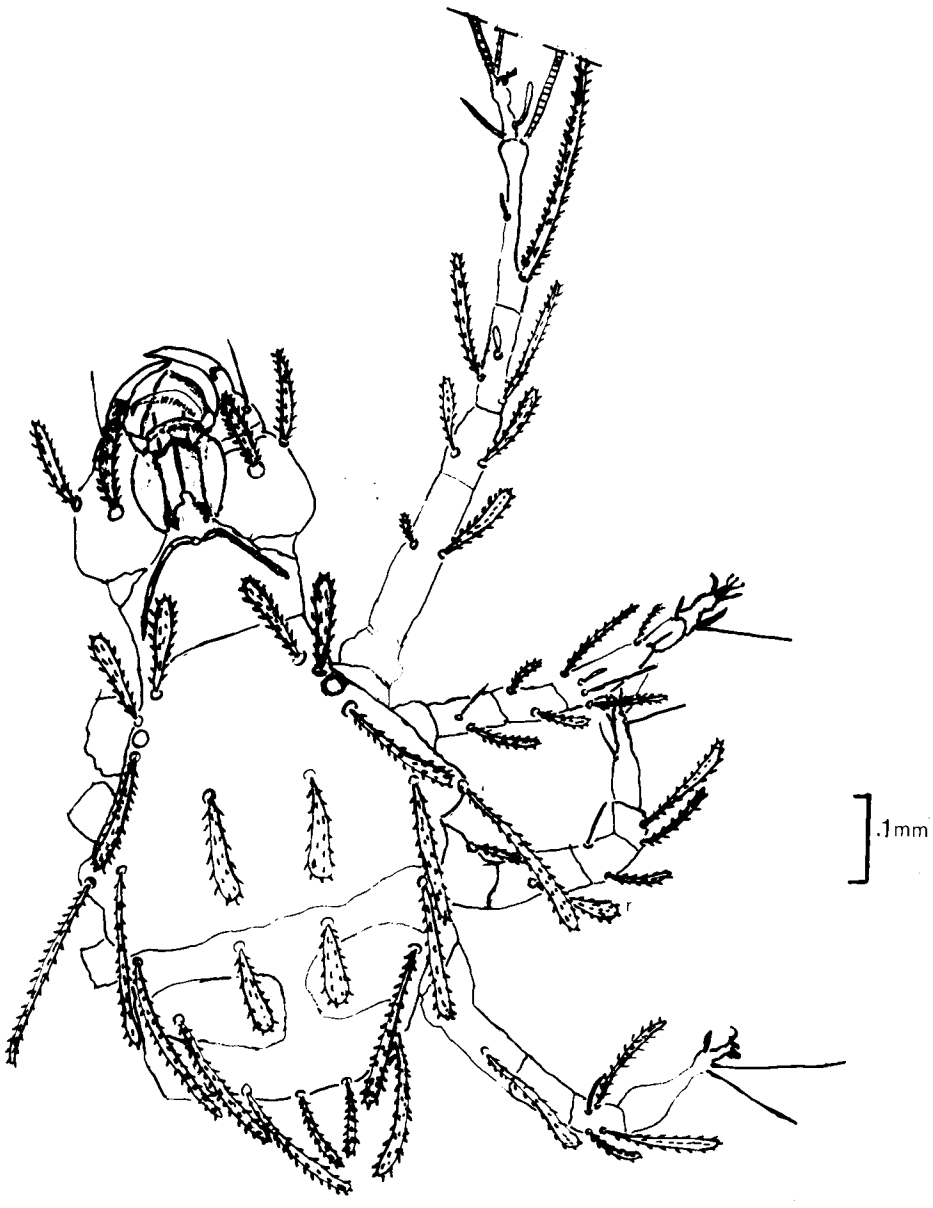
The Protonymph (Plate 2)

The protonymph is octopod, white to pale yellow in color, as is the resting larvae preceding it. The yellow color of the protonymph intensifies as the nymph approaches the resting stage.

The protonymph of C. lepidopterorum has been described by Michael (1878). I decided to redescribe it, as Michael's description is not complete.

Palpus and rostrum broad; palpal femur bears three setae, two dorsal rod-like spinose setae and one ventral simple seta; genu bare, tibia with two long and one short setae; palpal claw long, curved, slender, with a single prominent tooth at basal third; tarsus small, knob-like, with two apical whip-like setae, two apical comb-like setae, the outer comb with 16 teeth; outer comb stouter and longer than the inner comb, the inner comb with perhaps twice as many teeth. Rostrum with dorsal shield finely punctate; dorsal shield extending posteriorly to anterior margin of propodosoma; peritreme horseshoe shaped, segments elongate; rostrum with a pair of ventrolateral simple setae distally, one pair of shorter, dorsolateral simple setae subapically with a single pair of eyes. Propodosomal shield covering most of propodosoma, rounded anteriorly, broadening posteriorly, finely punctate, with four pairs of marginal subclavate spinose setae,

Plate 2. Dorsal view of protonymph of *Cheletomorpha lepidopterorum* (Shaw)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three pairs of anterior angles near eyes, one pair at posterior corner; one pair of submedian subclavate spinose setae near posterior margin of shield. One pair of long subclavate spinose setae on lateral protuberances between legs II and III. Hysterosomal shield with five horizontal rows of long subclavate spinose setae; anterior row with four setae, each borne on a minute plate, second row with two setae, each borne on a small distinct plate, third, fourth, and fifth rows with two setae each; all six of the dorsal hysterosomal plates finely punctate. Ventral side of idiosoma with three pairs of submedian simple setae, three pairs of short simple setae, three pairs of short simple setae around a terminal anus, one pair of postanal setae. Protonymphs averaged 371.05 μ in length and 179.44 μ in width (average of ten specimens).

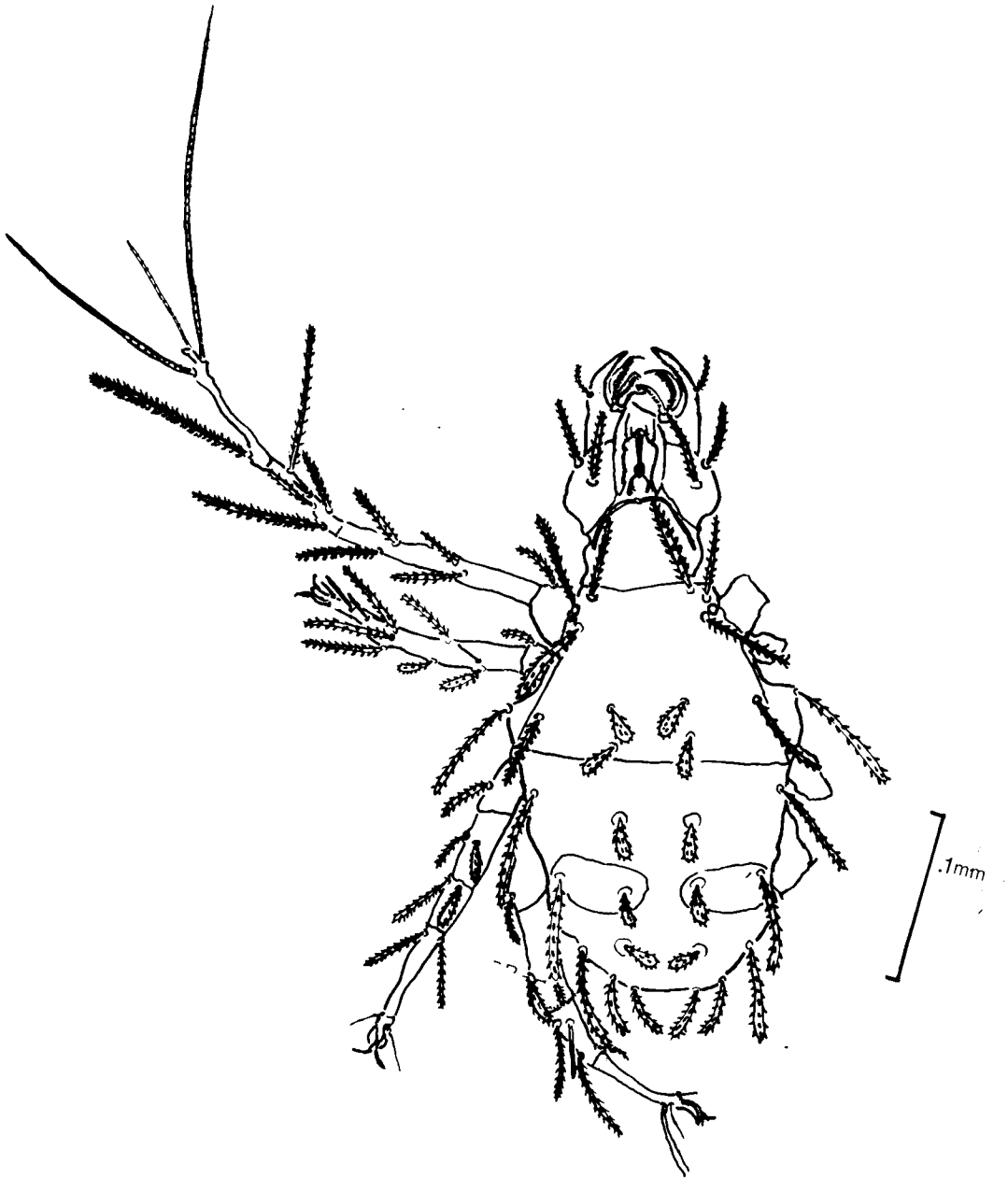
Setae on legs I-IV as follows: coxae 2-1-2-0, trochanters 0-0-1-0, femora 2-2-2-1, genua 2-2-2-0, tibia 5-4-4-4, tarsi 8-7-7-7. Tarsus IV lacks a median ventral seta.

The Deutonymph (Plate 3)

The deutonymph is octopod and pale yellow-orange in color, with coloration changing to a pale orange in the resting deutonymph.

The deutonymph of C. lepidopterorum has been described by Oudemans (1906) who believed that C. lepidopterorum had only one nymphal stage. I have redescribed the deutonymph in more modern

Plate 3. Dorsal view of deutonymph of Cheletomorpha lepidopterorum (Shaw).


.1mm

terms so as to avoid confusion in definitions and intended meanings.

Palpus and rostrum broad; palpal femur broadly rounded on outer margin, with two dorsal rodlike spinose setae, one ventrolateral finely pilose seta and two simple ventral setae; no genual setae; tibia with one long finely pilose seta and two simple setae; palpal claw long, curved, simple, having a single basal tooth; tarsus small, knob-like, with one apical peglike seta on tubercle, two apical simple whiplike setae and two apical combs, the outer comb with 18 teeth, this comb stouter and longer than inner comb, the inner tarsal comb with 48 teeth; coxa with one ventral simple seta. Rostrum with dorsal shield broadly emarginate at anterior margin; rostrum with two ventrolateral simple setae distally, two dorsolateral simple setae subapically; peritreme horseshoe shaped, segments elongated. Single pair of eyes. Propodosomal shield covering most of propodosoma, rounded anteriorly, widening posteriorly, with three pairs of long marginal subclavate spinose setae located near eyes, one pair at posterior angles of shield, two pairs of spinose, subclavate spinose setae located submesally on posterior half of shield, entire shield punctate. One pair of dorsolateral spinose setae on the lateral protuberances between legs II and III. Dorsum of hysterosoma with five horizontal rows of spinose setae; first row with four setae each borne on a minute plate; second row with four setae, two borne on each of the two moderately large and widely

separated dorsal plates; third row with four setae; fifth row consisting of two setae situated terminally on opisthosoma; all dorsal hysterosomal plates are finely punctate. Venter of propodosoma with two pairs of short stout setae; one pair of postanal setae. Deutonymphs averaged 494.36 μ in length and 234.61 μ in width (average of ten specimens).

Setae on legs I-IV as follows: coxae 2-1-2-2, trochanters 1-1-2-1, femora 2-2-2-1, genua 2-2-2-2, tibia 5-4-4-4, tarsi 8-7-7-7.

Male (Plate 4)

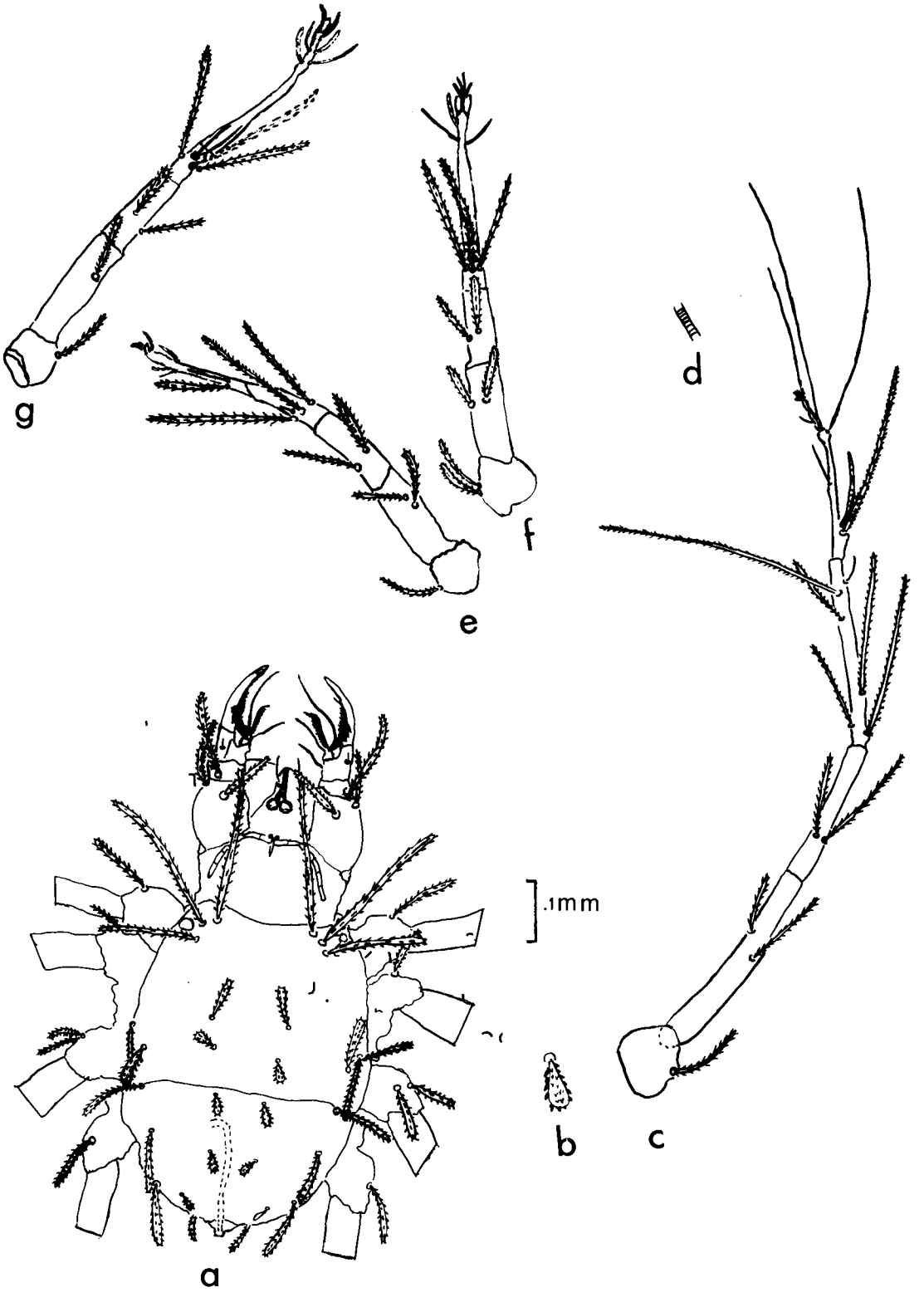
The male is octopod and pale orange, becoming darker orange as the mite ages. According to Michael (1878) the chief differences between males and females of C. lepidopterorum are that males are considerably smaller in size and more elliptical, less diamond-shaped.

The male of C. lepidopterorum has been described by Oudemans (1878), Baker (1949), Meyer and Ryke (1960), and Volgin (1969). These descriptions are adequate for most purposes, but redescription was undertaken as part of the study on population variation.

Palpus robust; femur broadly rounded on outer margin with two simple ventral setae, two stout spinose dorsal setae and one stout spinose ventrolateral seta; genu bare; tibia with one simple seta and

Plate 4. Male of Cheletomorpha lepidopterorum (Shaw).

a. Dorsal view of body
b. Median seta
c. Leg I, note the addorsal seta
d. Addorsal seta
e. Leg II
f. Leg III
g. Leg IV


g
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one short spinelike dorsal seta; palpal claw short, curved, slender, with two to four teeth at base of claw (a single mite may vary in the number of teeth on each claw); tarsus with one apical short peglike seta on tubercle, two apical whiplike setae; two apical tarsal combs, the outer comb stouter and larger than the inner comb, outer comb with 22 teeth, inner comb with about 40 teeth; coxa with one ventral simple seta near trochanter; trochanter small unornamented; rostrum robust, its dorsal shield extending rearward to propodosoma; rostrum with a pair of ventrolateral simple setae distally and a pair of dorsolateral simple setae subapically; peritreme horseshoe shaped, segments elongate. Single pair of eyes located laterad from third seta of anterior shield; dorsum of idiosoma almost completely covered by propodosomal and hysterosomal shields. Anterior shield rounded anteriorly, posterior extremity slightly wider than anterior extremity. Posterior shield with hind margin roundly truncate and anterior margin broadly and angularly truncate. Propodosomal shield bears four pairs of large subclavate spinose setae on lateral margin, three on anterolateral angles of plate, one on posterior angles. Two pairs of short, spatulate, spinose setae arranged submesally on posterior third of propodosomal shield. One pair of long, stout subclavate spinose setae slightly anterior to junction of anterior and posterior shields. Hysterosomal shield with three pairs of large subclavate spinose setae on lateral margins; three pairs of short, spatulate, spinose submedian setae; one pair of stout subclavate spinose setae

on posterior margin of body. Venter of idiosoma with two longitudinal rows of small simple setae, the first pair mesad to coxae I, the second anteromesal from coxae III, the remaining three pairs posteromesad from coxae IV. Genital opening dorsoterminal on opisthosoma with three short spines on either side; two pairs of small dorsal setae each borne on a minute plate, located between posterior margin of the large posterior plate and the cluster of setae around genital orifice. Aedeagus lancetlike. Males averaged 506.25 μ in length and 210.84 μ in width (an average of ten specimens).

Setae on legs I-IV as follows: coxae 2-1-2-2, trochanters 1-1-2-1, femora 2-2-2-1, genua 2-2-2-2, tibia 6-5-5-5, tarsi 10-8-7-7. Tarsus I with addorsals ultralong, with ridgelike annulations; pretarsus with very small multirayed empodium, with true claws absent in most specimens; pedicel attenuate; mesal paraterminal seta exceptionally long, at least five times as long as lateral paraterminal; guard seta about as long as entire tarsus; guard seta arises close to much shorter solenidion ωI.

Female

The female is long-legged and orange in color, with long body and leg setae. The newly emerged female is pale orange, becoming darker as the mite ages.

The female of C. lepidopterorum has been described by Shaw

(1794), Koch (1839), Michael (1878), Oudemans (1904, 1906), Baker (1949), Hughes (1961), Volgin (1969), and Summers and Price (1970). These descriptions are very detailed and accurate, especially that of Summers and Price, eliminating the necessity for redescribing the female.

The female is similar to the male except for size (female is much larger); palpal claw bearing a single basal tooth; body setae are shorter than in the male; the dorsomedian setae are strandlike structures. Females averaged 677.09 μ in length and 327.93 μ in width (an average of ten specimens).

Rate of Development of *Cheletomorpha lepidopterorum* (Shaw) at Three Temperatures and Two Relative Humidities

Temperature and relative humidity are the most important environmental factors influencing the physiology of insects and mites. Since mites are poikilothermic animals, their rate of metabolism and activity are functions of temperature (Patton, 1963). Mites, unlike insects, possess no heavy protective cuticle, so humidity is definitely a limiting factor. Insects inhabiting stored products can endure much higher temperatures and lower humidities than can mites in grain storage, but mites can function at much lower temperatures. (Some are active at temperatures just above freezing.) Thus extremes of temperature and relative humidity limit the activities of *C.*

lepidopterorum. Bursell (1964) doubted whether data gathered under laboratory conditions could be applied to insect populations in their normal environment where there are wide temperature fluctuations. However, much of the data should be allowable because in grain storage temperatures and relative humidities are fairly uniform.

Two series of experiments were conducted to study the life cycle of C. lepidopterorum at the following temperature-humidity combinations: 20°C, 80% R.H.; 20°C, 90% R.H.; 25°C, 80% R.H.; 30°C, 80% R.H.; 30°C, 90% R.H. One-day-old eggs were collected with a pulp canal cleaner and a moistened #0 paint brush which had most of its bristles removed, from selected females which had been isolated for 24 hours at 20°C, 80% R.H. They were carefully transferred to black bakelite rectangles 28 x 50 mm and 3 mm deep, the centers of which were drilled through to a diameter of 10 mm. The 10 mm well was closed on one side with black filter paper held in place by Super Strength Adhesive[1], and on the other by a 22 x 22 mm coverslip held in place by a letter clip. A 10 mm well was chosen as an ideal cell size because it was small enough to facilitate observation and large enough to accommodate large colonies of mites (Figure 3).

The observation cells were placed in two-liter capacity pyrex desiccators over potassium hydroxide solutions designed to give the

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[1] An all-purpose adhesive immune to fungi and water resistant, manufactured by Minnesota Mining and Manufacturing Co.

Figure 3. "Predator-prey cell." It was modified and used throughout the study.

desired relative humidities (Solomon, 1951) and then stored in constant-temperature cabinets. One egg was placed in each cell (four at each treatment in series I and ten at each treatment in series II), and checked at least twice a day until they hatched. Observations were made with an AO Spencer dissecting microscope with the aid of an overhead fluorescent lamp. No microscope lamp was used.

Newly-emerged larvae were fed once a day on larvae and nymphs of Acarus farris (Oud.) and observed at least three times a day, as were the later stages. Observations were made frequently to obtain accurate timing of the appearance and length of the various stages, and of their quiescent and active periods. Emerged females were kept for observation in order to determine fecundity of virgin females reared under the experimental conditions (see section entitled "Fecundity Studies").

In series I and II, one egg, 24 hours old, was transferred to each of four and ten cells respectively at the temperature and humidity combinations given above. Percent egghatch was determined by dividing the number of original eggs that hatched by the total number of eggs (four or ten). Eggs, larvae, and protonymphs that died were replaced by eggs in an effort to obtain an adult mite in each cell. Mites that died during the course of the experiments were replaced by eggs so that enough C. lepidopterorum could be observed to the adult stage to determine accurately rates of development at each temperature-

humidity treatment and to fill in the gaps present in the literature where no detailed studies have been done.

Egg Stage

At 30°C and 80% R. H. the percent egg hatch was 100% in both series I and series II (Figure 4 and Appendix Tables 3 and 4). Egg hatch was poorest at 20°C and 80% R. H. and 25°C, 80% R. H. where 100% of the eggs in series I and 80% of eggs in series II hatched (Figure 4 and Appendix Tables 5, 6, 9, and 10). The percentage of egg hatch of the other temperature-humidity combinations are given in Figure 4 and Appendix Tables 1, 2, 7, and 8. The average percent development of each stage at each temperature-humidity combination is given in Figure 4.

The eggs which did not hatch shriveled and collapsed, a few maintaining their shape for a few days and becoming white opaque before shrivelling--an indication that some embryonic development had taken place.

The duration of the egg stage was shortest at 30°C, 80% R. H., average of 56. 6 hours, and longest at 25°C, 80% R. H. The other durations are given in Appendix Tables 1, 2, 5, 6, 7, and 8.

Larval Stage

The duration of the larval stage was longest at 20°C, 80% R. H.

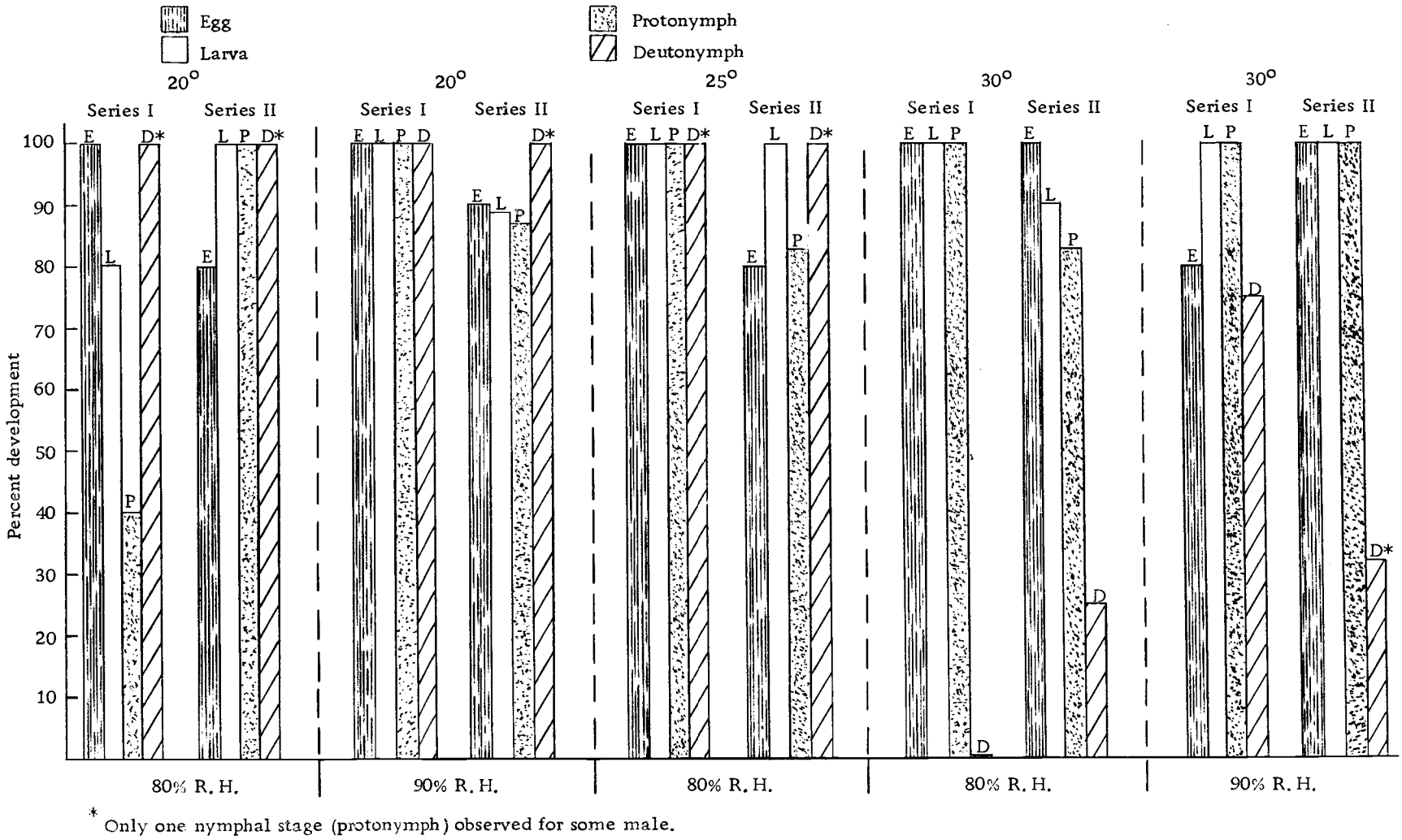

Figure 4. Percent development of Cheletomorpha lepidopterorum (Shaw) at each immature stage of life cycle at three temperatures and two humidities.

(Appendix Tables 7 and 8), an average of 82.2 hours with a range of 60 to 120 hours. The larval stage was shortest at 20°C, 90% R.H. (Appendix Tables 5 and 6) an average of 46 hours. At this temperature-humidity combination (20°C, 90% R.H.) the larval stage ranged from 36 to 60 hours. The duration of the other temperature-humidity combinations is given in Appendix Tables 1, 2, 3, 4, 9 and 10.

The quiescent interval following the larval stage was longest at 20°C, 90% R.H. (Appendix Tables 5 and 6)--21.00 hours and shortest at 30°C, 90% R.H. (Appendix Tables 1 and 2)--18 hours. The length of duration of the quiescent interval at the other temperature-humidity combinations is given in Appendix Tables 3, 4, 7, 8, 9 and 10.

Protonymph Stage

Rate of survival through the quiescent interval following the larval stage was lowest at 30°C, 80% R.H. (76.92%) and highest at 25°C (100% at both series) (Appendix Tables 3, 4, 5, 6, 7 and 8). The rate of survival at the other temperature-humidity combinations is found in Appendix Tables 1, 2, 9 and 10. The percent development of protonymphs at each temperature-humidity combination is given in Figure 4.

The duration of the protonymph stage was shortest at 30°C, 80% R.H. (40.67 hours) and longest at 25°C, 80% R.H. (76.80 hours).

The duration of the protonymph stage at the other temperature-humidity combinations is found in Appendix Tables 1, 2, 5, 6, 7 and 8.

The quiescent period following the protonymph stage was shortest at 30°C--18 hours at both humidities and longest at 25°C, 80% R.H.--31.2 hours (Appendix Tables 1, 2, 3, 4, 9 and 10). The other temperature-humidity combinations are found in Appendix Tables 5, 6, 7 and 8.

I discovered that some adult males emerged from the quiescent stage following the protonymph stage, apparently never becoming deutonymphs. Treat (1965) thought that the deutonymph stage was omitted in male ontogeny of the moth ear mite, Dicrocheles phalaenodectes. In C. lepidopterorum this phenomenon occurred at the following temperature-humidity combinations: 20°C, 90% R.H. in series II (Appendix Table 6); 30°C, 90% R.H. in series II (Appendix Table 2); and 20°C, 80% R.H. in both series (Appendix Tables 7 and 8); and 25°C, 80% R.H. in both series (Appendix Tables 9 and 10). Two possible explanations can be offered: (1) these mites normally have only one nymphal stage, (2) C. lepidopterorum males may go through the deutonymph stage only under environmental conditions which were not determined during the course of this experiment.

Deutonymph Stage

At 30°C, 90% R.H., 53.85% of the mites entering the resting period following the protonymph stage emerged from it (Appendix Tables 1 and 2). All the mites that entered the quiescent period at 20 and 25°C survived it (Appendix Tables 5, 6, 7, 8, 9 and 10). The duration of the deutonymph stage was shortest at 30°C, 90% R.H. (24 hours) with a range of 18 to 36 hours (Appendix Tables 1 and 2), and longest at 20°C, 80% R.H. (60 hours) (Appendix Tables 7 and 8). The duration of the other temperature-humidity combinations is found in Appendix Tables 3, 4, 5, 6, 9 and 10. The percent survival of mites entering the deutonymph stage was 100% at 20 and 25°C (Appendix Tables 5, 6, 7, 8, 9 and 10). At 30°C, 80% R.H. 16.67% (one of six) survived the stage (Appendix Tables 3 and 4). Three mites (50%) survived the deutonymph stage at 30°C, 90% R.H. (Appendix Tables 1 and 2).

All mites that entered the subsequent quiescent period survived it. At 20°C, 90% R.H. and 30°C, 90% R.H., both male and female quiescent forms were present. This quiescent period was longest for the mites at 25°C, 80% R.H. (42 hours) (Appendix Tables 9 and 10) and shortest for a single female at 20°C, 80% R.H. and the single male at 30°C, 80% R.H., both of which spent 18 hours in the quiescent period before emerging as adults (Appendix Tables 4 and 8). The duration of the deutonymph period at the other temperature-

humidity combinations is found in Appendix Tables 1, 2, 3, 5, 6, 7 and 8.

Adult Stage

The number of adult mites obtained in this rate of development experiment was as follows: at 30°C, 90% R.H., three males and one female; at 30°C, 80% R.H., a male; at 20°C, 80% R.H., eight males and one female; at 20°C, 90% R.H., five males and five females; and at 25°C, 80% R.H., six males and four females.

Percentage of survival to adulthood of hatched eggs was as follows: 30°C, 90% R.H. --28.57% (4 of 14 eggs); 30°C, 80% R.H. --7.13% (1 of 14 eggs); 20°C, 80% R.H. --64.29% (9 of 13 eggs); 20°C, 90% R.H. --76.92% (10 of 13 eggs); and 25°C, 80% R.H. --76.92% (10 of 13 eggs).

The interval from egg to adult at 30°C, 90% R.H. for the two males of series I (Table 3) and the one male of series II was 264 hours and 192 hours respectively. The interval from egg to adult for the one female was 408 hours. At 30°C, 80% R.H. the interval from egg to adult was 258 hours in the one mite, a male, which completed its life cycle. The interval from egg to adult at 20°C, 90% R.H. in series I was 333 hours for two females and 420 hours for one male. In series II it was 273 hours for the four males and 296 hours for the three females. The males in series I (20°C, 80% R.H.) averaged 315 hours to develop from egg to adult. In series II the time required

Table 3. Summary of the life cycle of Cheletomorpha lepidopterorum (Shaw) at three temperatures and two humidities in hours.

30°C, 90% R.H.		30°C, 80% R.H.		25°C, 80% R.H.		20°C, 80% R.H.		20°C, 90% R.H.	
Series I	Series II	Series I	Series II	Series I	Series II	Series I	Series II	Series I	Series II
Average life cycle 312 ± 67.88 hrs Female - 408 hrs Male - 264 hrs	Average life cycle 192 hrs Male - 192 hrs	No mites completed their life cycle	Average life cycle 258 hrs Male - 258 hrs	Average life cycle 342 ± 37.56 hrs Female - 314 ± 17.20 hrs Male - 384 ± 12.00 hrs	Average life cycle 334.8 ± 26.12 hrs Female - 384 hr. Male - 322.5 ± 9.84 hrs	Average life cycle 315 ± 39.00 hrs Male - 315 ± 39.00 hrs	Average life cycle 286.18 ± 13.11 hrs Female - 306 hrs Male - 283 ± 11.18 hrs	Average life cycle 362 ± 42.80 hrs Female - 333 ± 15.00 hrs Male - 420 hrs	Average life cycle 282.86 ± 19.62 hrs Female - 296 ± 10.19 hrs Male - 273 ± 19.21 hrs

was 283 hours for the six males and 306 for the single female. At 25°C, 80% R.H. the interval from egg to adult averaged 314 hours for three females and 384 hours for two males in series I. Series II males averaged 322.5 hours from egg to adult; the female required 384 hours.

Discussion

The favorable effect of the preconditioning environment of 20°C, 80% R.H.--the temperature and humidity from which the eggs were taken--was evident in early post-embryonic development; i.e., survival of the immature forms at 30°C was as good as their survival at 20°C and 25°C (Figure 4).

The quiescent period following the protonymph stage demonstrated dramatically the effects of the higher temperature of 30°C. Only 53.84% and 66% of the resting mites at 30°C, 90% R.H. and 30°C, 80% R.H., respectively, survived to enter the deutonymph stage. These figures compared with 100% survival of resting mites at 20°C and 25°C. Only 16.67% of the deutonymphs at 30°C, 80% R.H. and 57% at 30°C, 90% R.H. survived the last nymphal stage, although the duration of the stage was shorter for those mites that did survive than it was for mites at the lower temperatures (Appendix Tables 1, 2, 3, and 4).

The relatively poorer survival of the immature stages at 30°C could have been due to (1) dehdration; (2) general upset of the metabolic balance (Hopf, 1940; Larsen, 1943; Wigglesworth, 1965);

Table 4. Analysis of variance -- two factors (treatment and mated). P = % (four mites per replicate), N = 4.

Source of variation	df	Mean square	F
Treatment (T-H combination)[a]	4	1.279	.781
Mated (M vs UM)	1	4.961	3.027
Interaction	4	5.052	3.083*
Error	20	1.639	--
Total	29		

*P < .05

[a]Temperature-humidity

Table 5. Fecundity of C. lepidopterorum. Mean number of eggs laid by mated and virgin females at three temperatures and two humidities.

20°C		25°C		30°C	
Mated	Virgin	Mated	Virgin	Mated	Virgin
80% R.H.					
115.67*	82.67*	42.33*	19.67*	0	5.00*
90% R.H.					
92.33*	97.67*	-[a]	-[a]	9.00*	13.67*

*All means significant at .05 and .01 levels.

[a]No experiment carried out at this temperature-humidity combination.

were added to each cell. Eggs were removed with a fine needle and counted every 24 hours. Collected data were then subjected to an analysis of variance (see Table 4). Results at each temperature-humidity treatment are given below.

20°C, 80% R.H.

Mated females oviposited an average of 115.67 eggs over an average period of 22 days, while virgin females laid 82.67 eggs over a period of 20.33 days. Mated females lived an average of 29 days, compared to 32.33 days for virgin females. Mated females oviposited their first eggs 2.66 days after their emergence as adults, while unmated females first oviposited at least four days after emergence. Eggs were laid on 16.33 days by virgin females and on 22 days by mated females, constituting an egg-laying rate of 5.06 per day for the former and 5.26 per day for the latter. The difference between the mean number of eggs laid by mated females and virgin females was significant at the .05 and .01 levels (Table 5).

20°C, 90% R.H.

Virgin females laid an average of 97.67 eggs, while mated females averaged only 92.33 eggs in their lifetimes. The length of life averaged 22.33 days and 21.33 days for virgin and mated females, respectively. Mated females laid eggs three days after emergence, and virgin females oviposited 2.66 days after emergence. The rate of egg-laying was 6.23 per day for virgin females and 6.35 per day for mated females. Eggs were laid on 15.66 days by virgins and on

16.00 days by mated females. There was a significant difference in the total number of eggs laid by the two groups at the .05 and .01 levels, an average of 97.67 for each virgin female and 92.33 for each mated female (Table 5).

25°C, 80% R.H.

Virgin females laid an average of 19.67 eggs, while mated females laid 42.33 eggs. This difference was significant at both the .05 and .01 levels (Table 5). Eggs were laid four days after emergence by virgin females, while mated females started ovipositing after only 2.66 days. Rate of egg laying by mated females was 3.97 eggs per day (on 10.66 days) and by virgin females, 3.93 eggs per day (on five days). The mated females lived an average of 17.66 days compared to 11.00 days for virgin females.

30°C, 80% R.H.

Although mated females oviposited no eggs at this temperature-humidity treatment, virgin females laid an average of 5.00 eggs at the rate of 3.00 eggs per day on 1.66 days. First oviposition occurred eight days after emergence. Mated females lived an average of 8.66 days, shorter than the average life span of 11.00 days for virgin females.

30°C, 90% R.H.

Virgin females laid an average of 13.67 eggs on 3.00 days (4.55 per day), while mated females oviposited 9.00 eggs on 3.66 days (2.45 per day). There was a significant difference between the mean total number of eggs laid by the two groups (Table 5). Mated females lived 11.00 days and virgin mites lived 7.00 days. First oviposition for the mated and virgin mites, respectively, occurred 3.66 and 2.33 days after emergence.

Discussion

The temperature range 20 to 25°C with 80 to 90% R.H. seems to be suitable for the reproduction of C. lepidopterorum. This fact is confirmed when the results of the life cycle, fecundity, and longevity experiments are combined to give a broader picture of the mite's biology.

Mated females laid significantly more eggs than did virgin females, when the total numbers of eggs laid by all 30 mites in the experiment are compared. However, if the individual temperature-humidity treatments are viewed separately, virgin females had a significantly higher oviposition rate than did mated females at 20°C, 90% R.H., 30°C, 90% R.H., and 30°C, 80% R.H. The mean number of eggs laid by both mated and unmated mites was greatest at 20°C, 80% R.H., and poorest at 30°C, 80% R.H. (Table 6).

The results of these experiments indicate that both bisexual and parthenogenetic reproduction is common in C. lepidopterorum, with mated females laying more eggs over a longer period of time than virgin females. However, these results also indicate that under environmental conditions of higher temperature, virgin females have a higher oviposition rate.

Table 6. Fecundity of C. lepidopterorum. Mean number of eggs laid by all females at each temperature-humidity combination.

Relative humidity (%)	Temperature (°C)		
	20	25	30
80	99.17*	31.00*	2.50*
90	95.00*	-	11.33*

*All means significant at .05 and .01 level.

Survival Under Starvation Conditions

A series of observations were made to determine the length of time a newly-emerged female or male of C. lepidopterorum could live without food. Three newly-emerged females and one newly-emerged male each were placed in cells (28 x 50 mm) in desiccators at the following temperature-humidity combinations: 20°C, 80% R.H.; 20°C, 90% R.H.; and 25°C, 80% R.H. The cells were checked twice a day (Table 7).

Table 7. Longevity experiments using newly-emerged starved females and males of Cheletomorpha lepidopterorum (Shaw).

	Survival from emergence to death of mite (days)			
	Female #1	Female #2	Female #3	Male
20°C, 80% R.H.	22	20	31	12
20°C, 90% R.H.	37	26	31	2
25°C, 80% R.H.	16	11	8	8

Average longevity

Female: 20°C, 80% R.H. = 23.66 days
20°C, 90% R.H. = 31.33
25°C, 80% R.H. = 11.67

Male: 20°C, 80% R.H. = 12 days
20°C, 90% R.H. = 2
25°C, 80% R.H. = 8

At 20°C, 80% R.H. the females lived an average of 23.66 days, and the single male lived 12 days. At 20°C, 90% R.H. the females lived an average of 31.33 days, the male only two days. Females lived 11.67 days and the male lived eight days at 25°C, 80% R.H. Length of life for the females ranged from 20 to 31 days at 20°C, 80% R.H.; from 26 to 37 days at 20°C, 90% R.H.; and from 9 to 16 days at 25°C, 80% R.H.

Conditions at 20°C, 90% R.H. were conducive to longest life for females; the male at 20°C, 80% R.H. lived the longest. All the mites became less active as the experiment progressed, slowly dried up, and eventually died.

Discussion

The results of this experiment may be compared with the results obtained in the predator-prey study (page 107) to determine if any trend is evident in the survival of the mites at the various temperature-humidity combinations.

The survival of starved newly-emerged mites, especially females, was prodigious. Survival was longest at 20°C, 90% R.H., which supports the findings of the predator-prey and fecundity studies. Because only one male was used at each temperature-humidity combination, no conclusions could be drawn from the longevity of the males in this experiment. See predator-prey study for more accurate

information on survival of male mites.

The survival of predators in the absence of prey species is very important in the overall role of the species as a predator. If, as mentioned by numerous researchers, Cheyletus eruditus (Schrank) is able to feed on Glycyphagus spp. in the absence of its primary prey, A. siro, and resort to cannibalism when no prey mites are present, then it is well adapated to its habitat, in which the number of prey mites may vary seasonally.

C. lepidopterorum survives well without food. This fact, along with data from the section on behavior in mass culture, seems to indicate that C. lepidopterorum is well adapted to its habitat in that it may survive up to 31 days after adult emergence without food. Indeed, adult females have been observed to live for more than four months at 5°C, 80% R.H., feeding very little (see predator-prey study, page 107). C. lepidopterorum feeds on other prey in its habitat in the absence of its primary prey and eventually resorts to cannibalism for the eventual survival of adult females (see section on behavior in mass culture) which then are able to begin egg laying when prey again becomes available.

Sex Ratio of the Progeny of Mated and Unmated Females

Having noticed a large number of males in laboratory cultures,

a finding which was at variance with the observations of Michael (1878) and Hughes (1961)[2], I decided to determine the sex ratio of the progeny of mated and nubile females. The fact that virgin females produce eggs parthenogenetically had been established earlier and is reported in the section entitled "Fecundity of C. lepidopterorum."

Females were removed from cultures as deutonymphs for use in these experiments. Mated females were obtained by placing newly-emerged adult females with males in separate cells which are described in the section on rate of development. The nubile females were introduced into cells, as previously mentioned, and fed on A. farris females as were the mated females. The cells were labeled and placed in desiccators over KOH solutions designed to maintain 80% R.H. and stored in a constant-temperature cabinet at 20°C. Two hundred mated females in 60 cells and 100 nubile females in 50 cells were used. Test animals were allowed to lay eggs for at least one week and then removed to prevent their feeding on their own progeny. Males were removed before eggs were laid because of their predilection toward eggs of their own species, even when prey mites are present.

The emerging larvae and subsequent nymphs were fed every day with larvae and nymphs of A. farris to reduce the incidence of

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[2] Both Michael and Hughes stated that males of C. lepidopterorum are rare and that reproduction usually occurs parthenogenetically.

cannibalism. The cells were examined every 24 hours and all adults were counted and removed from the cells. The experiments were initiated in January 1969 and terminated in July 1970, and repeated from September to November, 1970, using 34 nubile females in 31 cells.

The initial experiments indicated a very high ratio of males to females in the progeny of nubile females--13:1--while mated females produced progeny which had a much lower ratio of males to females--2:1. As the experiment continued there was a reduction in the ratio of males to females in the progeny of virgin females (4.01:1), but the ratio in mated females remained about the same. Cells with virgin females produced 1,685 adults (1,351 males and 334 females), while the mated females produced 2,484 adults (1,730 males and 754 females). The final ratio of males to females among the progeny of nubile females was 4.04:1. The final ratio among the progeny of mated females was 2.29:1 (see Table 8).

The later experiments using only nubile females gave rise to progeny that were almost entirely male, a single female appearing at the end of one test. The male-to-female sex ratio was 291:1 (see Table 9). These results agreed with those of Oliver, Camin and Jackson (1963) who demonstrated arrhenotoky cytologically in the snake mite, Orphionyssus natricis (Gervais), with Cooper (1937) who demonstrated arrhenotoky for the Pyemotidae, with Schrader (1923)

Table 8. Comparison of progeny of mated and virgin females of Cheletomorpha lepidopterorum (Shaw). Series I.

	Mated females	Virgin females
Number of cells	70	50
Number of adults placed in cells	200	100
Total number of progeny	2, 484	1, 685
Number of males	1, 730	1, 351
Number of females	754	334
Ratio of males to females	2.29:1	4.04:1

Table 9. Comparison of progeny of mated and virgin females of Cheletomorpha lepidopterorum (Shaw). Series II.

	Mated females	Virgin females
Number of cells	3	31
Number of adults placed in cells	3	34
Total number of progeny	34	292
Number of males	25	291
Number of females	9	1
Ratio of males to females	2.78:1	291:1

for the Tetranychidae, with Pätau (1937) for the Pyemotidae, with Jary and Stapley (1936) for the Anoetidae, with Filipponi (1955, 1957) for the Macrochelidae, and others.[3]

In a repeat of the experiment, three virgin females were placed in separate cells with young, vigorous males and allowed to mate. The males were then removed from the cells, with females and subsequent eggs being treated as in the earlier experiment. The results (see Table 9) gave a male-to-female ratio of 2.78:1, which is slightly higher than the original sex ratio of the progeny of mated females.

Discussion

In no cells of either set of experiments did all female progeny occur. Males appeared first in all cells, probably due to their shorter development time, since the deutonymphal stage was omitted in male ontogeny, as noted by Treat (1965). If a mated female was allowed to lay eggs for only a few days, the ratio of males to females in the progeny was much higher. It appeared that a greater proportion of the eggs laid early in the female's oviposition period produce males. Females appear later, and bring subseqient reduction of the male to female ratio to 2:1. Males are produced from eggs throughout

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[3]For example, Putman (1939) for the Eriophyidae; Hansell, Millison and Putman (1964) for Phytoseiidae; Helle and Bolland (1967) and Helle, Guierrez and Bolland (1970) for Tetranychidae; and Wysoki and Swirski (1968) for Phytoseiidae.

the oviposition period; no regular or cyclical alternation could be demonstrated. This phenomenon was also observed by Oliver, Camin and Jackson (1963) in Ophionyssus natricis. These findings run counter to those of Hansell, Mollison and Putman (1964), Treat (1965), and Costa (1969), all of whom found that males appeared in cyclical alternation in the female's oviposition period.

The data indicate that a haplo-diploid type of sex-determining mechanism--arrhenotoky--is operative in Cheletomorpha lepidopterorum. This conclusion is based on the rearing data obtained in this study and does not have cytological confirmation. The results of the first series of experiments, where nubile females produced both males and females in the ratio of 4.04:1 may have been the result of (1) the mating of the male progeny and the female parent as reported by Filipponi (1955) for Nothrholaspis fimicola, (2) the inadvertent use of mated females, or (3) a switchover from arrhenotoky to thelytoky as reported by Helle, Gutierrez and Bolland (1970). The first explanation is unlikely, as observations on the mating behavior of this species indicate that females avoid mating after laying eggs. Since the nubile females were isolated as deutonymphs, and mating was never observed in immature stages, the second explanation also is untenable. The third explanation seems most dependable and has precedence. The occurrence of females among parthenogenetically-produced progeny of an arrhenotokous species is not unknown. It has

been observed by Ries (1935) among the progeny of Eurytetranychus buxi (Garman), Boudreaux (1963) in Tetranychus urticae (Koch), and Helland and Bolland (1967) in T. pacificus (McGregor).

The results of the second series of experiments, in which nubile females laid eggs which with the exception of one, developed parthenogenetically into males agrees with the findings of those investigators already mentioned who determined, on the basis of cytological or rearing data, that they were dealing with arrhenotokous species. The genetic basis of arrhenotoky is still obscure, according to Helle, Gutierrez and Bolland (1970). In an inbred population males usually are more numerous than females, even when there is a differential sexual mortality favoring females, a fact that suggests that arrhenotoky usually does not favor the production or maintenance of a 1:1 male/female ratio. Oliver, Camin and Jackson (1963) explained this phenomena on the basis of the fact that when there are numerous males most of the females will be inseminated, while when males are scarce or absent, most of the females will remain nubile and produce parthenogenetic haploid eggs, which develop into males.

The results of the experiments using mated females conform to the pattern of reproduction in arrhenotokous species described in the preceding paragraph, in which the ratio of male to female progeny is greater than 1:1. Both series of experiments using mated females yielded a male-to-female ratio of over two to one (2.29:1 in the first

series and 2.78:1 in the second series).

In an arrhenotokous species such as C. lepidopterorum the sex ratio in a population may be expected to shift from an abundance of males to one of about equal sex ratio and then back to an abundance of males. There may be a drastic differential mortality in the field since females greatly outnumber the males in field-collected samples when the mites are abundant. If, as they do in laboratory cultures, males attack and feed on each other when the number of adults is high, they may greatly reduce their own numbers.

It has been demonstrated that the progeny of fecundated females includes both females and males; however, the mechanism by which they lay both fertilized and unfertilized eggs is not known. Oliver, Camin and Jackson (1963) were of the opinion that the ratio between the sexes would favor females in an arrhenotokous species only if there were a drastic differential mortality between the sexes. White (1954), speaking about arrhenotoky, said

> It is thus characteristic of groups with haploid males that the sex ratio fluctuates rather widely from species to species. . . and also to some extent with various environmental factors, showing no particular tendency to conform to any fixed percentage of males (p. 326).

Thus this experiment indicates that C. lepidopterorum is arrhenotokous with mated females producing both males and females and unmated females producing predominantly male progeny. These results are in agreement with Dzierzon who found that the females of certain species can, without mating, lay fertile eggs (Pellet, 1946).

BEHAVIOR

Mass Culture

This study was undertaken to determine interactions between the various stages of C. lepidopterorum and between C. lepidopterorum and its prey, A. farris (Oud.). Large (37 x 50 mm) and small (28 x 50 mm) bakelite cells of the type described in the section on development (page 29) housed the cultures. The holes drilled in the large cells were 16 mm in diameter, while those in the small cells were 10 mm in diameter. Holes of these diameters proved to be ideal for the two different-sized cells, having adequate room for the mites and for making observations and manipulating the mites. A 24 x 40 mm cover glass was used to cover the large cell, and a 22 x 22 mm cover glass closed the 10 mm cell. All the cultures were started with females alone (five in the small cells and ten in the large cells). The mites used were obtained from hay at the Oregon State University beef barn and were cultured in the acarology laboratory at Oregon State University and fed on A. farris. Observations were made twice a day through a dissecting microscope.

The cells were stored in desiccators over KOH solutions designed to give 80% and 90% R.H. at 20°C, because these temperature and humidity combinations proved optimal in the fecundity and rate of development experiments.

Feeding Behavior

Newly-emerged larvae of C. lepidopterorum were observed feeding on eggs or larvae of A. farris. In the absence of other prey, they fed on eggs or larvae of their own species. Older larvae usually preyed on eggs, larvae, and nymphs of A. farris or, in the absence of these, eggs and other stadia of their own species. Occasionally, larvae were observed feeding on adult A. farris. C. lepidopterorum eggs (although protected by silk) and larvae were the stages most vulnerable to cannibalism by other stages.

Observations indicated that nymphs and adults fed on all stages of A. farris, including hypopi. In the absence of suitable food, they fed on all stages of their own species. At times, two males were observed preying on a single male of the same species. Newly-emerged males were particularly vulnerable to predation by other adults. In a starving colony, however, the immobile and immature stages were eaten before predation shifted to adult males.

Female C. lepidopterorum were the stage least frequently cannibalized. Dead females were never observed with the dehydrated bodies typical of those mites which have fallen prey to other mites. Only once were they observed being successfully attacked by other stages. Although nymphs often seized the legs of females, the female under attack simply withdrew its leg.

All stages of starved C. lepidopterorum contained in observation

cells reacted to the introduction of prey by waving legs I and moving around the cell. Females moved more quickly than other stages Several minutes often elapsed before the predator attacked the prey and began feeding. Larvae and protonymphs usually found the prey and commenced feeding before the deutonymphs and adults. In cultures with starved females, the prey might be seized and devoured as soon as it was introduced into the cell. Females in the process of laying eggs would seize immediately any prey that touched them. Males usually were last to feed in any culture, occupying themselves instead with moving around the cell or guarding female deutonymphs.

The larvae were voracious eaters, attacking and feeding on one or two A. farris in one hour. They searched out their prey by moving about with the anterior pair of legs extended at approximately a 45° angle from the horizontal axis of the idiosoma. Less hungry mites may wait for or search out their prey. Their attacks are most successful on larvae and nymphs of the prey species. Adult prey also were attacked, but seldom successfully, because the adult prey mite was able to pull from the grasp of the larvae. Prey was seized by the leg or gnathosoma with the aid of the raptorial palps, pierced with the chelicerae, and sucked dry. The prey attempted to escape for about one minute, but then became quiescent except for slight leg movements. The sucking motion of the pharyngeal pump was observed as the fluids of the prey passed into the predator. The predator's body

swelled perceptibly as the prey was devoured. The palps were used to clean the cheliceral stylets immediately after feeding was completed. Larvae usually sucked their prey completely dry, but did not manipulate the prey as did other stages in an effort to obtain body fluids. I was able to feed starving larvae by placing a prey larva or nymph directly in front of it, using a fine needle. The predator immediately seized the prey and began to feed. The average time spent feeding by ten starving larvae was 37.5 minutes.

Nymphs were even more voracious than larvae and were larger in size. No attempt was made to distinguish between the superficially similar protonymphs and deutonymphs in observing feeding behavior. Nymphs attacked all stages of A. farris, but they were most successful on larvae and nymphs of the prey. Nymphal specimens were observed preying upon three A. farris in slightly over one hour. Nymphs usually seized their prey by the leg, but prey also was held by the gnathosoma. Attempts by the prey to escape ceased after one or two minutes, with subsequent movement confined to feeble leg movements. The prey usually were lifted from the substrate by the predator and held aloft until struggling ceased. Adult prey sometimes escaped by simply pulling themselves out of the grasp of the predator. The predator might shift its hold on the prey when the prey had been sucked nearly dry. The average time spent feeding by 15 nymphs was 29.5 minutes (range of 15-53 minutes). The shorter feeding period of

the nymphs when compared to that of larvae was probably due to the fact that the nymphal period was a period of accelerated activity and rapid development, and the demands of growth made nymphs particularly edacious. The palps were used to clean the cheliceral stylets after feeding as did the larvae. Immediately after cleaning, the nymph might attack and feed on another prey.

Males did not appear to be as voracious as the other stages, preferring to be in constant motion except when guarding female deutonymphs. Males attacked and fed on all stages of A. farris, but preferred the nymphal stages. Males were never observed, as were nymphs, feeding on two prey mites in quick sequence. The male seized the prey in a manner similar to that of the nymph, and the same struggling was observed on the part of the prey. The male gnathosoma was longer in relation to its total body length than that of the female, and he had no trouble seizing prey by the gnathosoma and feeding on it without endangering his legs by contact with the prey. Males lifted their prey off the substrate when subduing it, so the prey had no solid surface to aid in its escape. Ten males averaged 34.9 minutes feeding, the range being 15 to 90 minutes. Males left partially consumed prey more often than did females.

Females were the most ravenous stage of C. lepidopterorum. They fed on all stages of A. farris, preferring nymphs and adults, and pursued prey a short distance if not successful in their first attack.

Prey usually were seized by the leg, but some were held by the gnathosoma, lifted off the substrate, and subdued in one to two minutes. The female usually manipulated the prey while sucking out its body fluids. The average time spent feeding by 12 females was 37.6 minutes (range of 13-63 minutes). This was the longest feeding time of all C. lepidopterorum stages. The palps were used to clean the cheliceral stylets upon completion of feeding. It is not surprising that the female, being the largest, longest-lived stage and also the egg-laying stage, consumed more prey mites than did any other stage.

During feeding, all stages of C. lepidopterorum had characteristic positions to which their legs I are rotated during feeding to protect these delicate, intricate sensory structures (see Figure 5). Females held their first pair of legs laterally and rearward after attacking and successfully subduing a prey mite. This position apparently was adopted to protect these appendages. The legs were rotated through a 90° angle from the original "rest" position. Females constantly rotated their legs to one of about four positions while feeding.

Males held legs I at one of five positions while resting and feeding, the most common being at a 90° angle to the body wall. Unlike other stages, males typically held legs bent at the articulation between the genu and tibia. Nymphs held legs I either straight out from the sides of the body or at 30 to 45° to the body. Larvae held

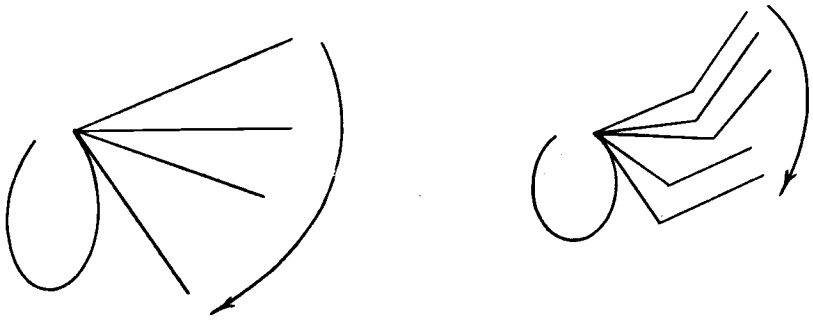

Figure 5. The various positions that Cheletomorpha lepidopterorum (Shaw) hold their legs I while feeding.

them at approximately a 45° angle from horizontal axis of the idiosoma.

The only chance for the prey to escape, other than by pulling out of the grasp of the predator, was by feigning death. This sometimes caused the predator to abort its attack, although C. lepidopterorum consumed immobile as well as active stages of the prey.

If C. lepidopterorum was well fed or was preparing to molt, it moved away from prey at initial contact. Even when active or starving, however, larvae or small nymphs usually would not attempt to attack the much larger adult A. farris.

The abbreviated struggle of A. farris when it was attacked by adult or nymphal C. lepidopterorum indicated that the predator might possess a toxin in its saliva in later stages. Loss of coordination and apparent paralysis occurred in prey specimens which were held for even a short period by the predator.

Silk Production

Female Cheletomorpha lepidopterorum were observed depositing silk over their eggs in laboratory cultures. The female moved back and forth over the egg for five to ten minutes, occasionally touching her palps and rostrum to the substrate. Silk was laid down over the eggs during this operation. Without the aid of a microscope lamp it was difficult to see the fine silk as it was produced from the tip of the

rostrum. The female used the palps for manipulating the silk, as reported by Hughes (1957). While the silk covering protected the eggs to some extent, other stages fed on them when prey was in short supply.

Feeding on Quiescent C. lepidopterorum by Acarus farris

Cultures of C. lepidopterorum fed on A. farris often contained inordinate numbers of dried-up immobile forms of the predator. In speculating about the cause of their death, I surmised that they could have been the prey of a hungry member of their own species or the victims of the "prey" species, A. farris. A possible solution to the problem presented itself one day while immobile female deutonymphs were selected for a mating behavior study.

The immobile deutonymphs were placed in a plastic cell with a charcoal-plaster base. Upon examining the cell after several days, I noticed that A. farris had gained entrance to it from prey mite colonies left unnoticed on my table when colonies of C. lepidopterorum were fed. These mites were feeding on the immobile forms of C. lepidopterorum. The dead deutonymphs were yellowish after the fluids had been drained from them--similar to the dehydrated deutonymphs seen in cultures of C. lepidopterorum fed on A. farris. Whether the acarids or the predators were responsible for these dead nymphs was not ascertained in over a year of close observation.

The other possible explanation for the dried-up immobile forms of the predator is the saprophagic feeding of the prey species on the predator mites that either have been killed in cannibalistic attacks of active forms of the predator on quiescent forms of the predator or have died due to unfavorable substrate conditions. However, this explanation does not appear plausible because the dehydrated forms of the predator were found in cells which had a high prey-to-predator ratio, where there was abundant prey for the predator but food was in short supply for the prey. Because cannibalism was not observed in cultures with a high prey-to-predator ratio, it is unlikely that C. lepidopterorum would attack members of its own species. It is possible, however, that A. farris would prey upon quiescent forms of the predator. The phenomenon of prey species preying upon the quiescent predator was reported by Beer and Dailey (1956), who found that semistarved Tyrophagus sp. mites would attack and feed on molting cheyletids.

Mating Behavior

No attempt to observe mating behavior of C. lepidopterorum has been reported in the literature. However, Beer and Dailey (1956) studied the mating habits of Cheletophyes knowltoni Beer and Dailey, ostensibly a closely related species which was recently placed in synonymy with C. lepidopterorum by Volgin (1969) and Summers and

Price (1970). A comparison of my data with that of Beer and Dailey indicated that these two mites differ in a number of morphological and behavioral characters. Whether these differences are great enough to warrant specific designation has not been determined because no live C. knowltoni were available for breeding experiments.

Although males of C. lepidopterorum have been considered rare or produced only at certain times of the year (Michael, 1878; Hughes, 1961), numerous male specimens were found in cultures throughout the year. Mating observations were begun as soon as the presence of both females and males was determined.

Mating behavior was first observed in mass cultures in large bakelite cells (similar to those described in the section on mass behavior) which were undisturbed except for the adding of prey mites, and later in small bakelite cells (similar to those described in the section on rate of development) where a single vigorous male was placed in a cell with a virgin female. The observations were made at least twice a day through a binocular dissecting microscope using overhead fluorescent lighting. At no time was a microscope lamp used.

Guarding of the inert female deutonymph by an adult male was a common phenomena in both mass culture and individual cells. Mating of the newly-emerged adult female was observed whether or not the female had been guarded by a male before emergence. The presence and absence of mating between female and guard male are described

below as Sequence I and Sequence II, respectively. The reaction of males to females who had escaped mating for a longer period of time is also discussed.

Sequence I

Male guards potential mate while the latter is an immobile deutonymph and later mates with her.

In mass culture, males seemed to be attracted to female deutonymphs shortly before the latter became immobile. Males usually took up a position nearby and waited for the deutonymph to cease movement. When the deutonymph had assumed its characteristic flattened position prior to molting, the male took up a position directly over, or slightly in front or behind it (see Figure 6). Males used their palps to touch, grasp, and move the immobile forms. Legs I usually touched or lay adjacent to the deutonymph, allowing the male to be aware of other mites which might touch or crawl over the "guarded" mite. Males chased away other mites by attacking them with their palps. Mites thus attacked included other males as well as females, nymphs, and larvae of C. lepidopterorum, and all stages of A. farris. A number of unattached males often were seen a short distance from guarded deutonymphs.

The male became more active as the deutonymph's molting time approached. The legs of the deutonymph began to move before actual

Figure 6. Male guarding female deutonymph. Note the flattened position of the quiescent female.

molting, and it responded to being touched by other mites, although it could not crawl. The female emerged from the deutonymph skin by pushing her way out of a split between the idiosoma and gnathosoma; then with legs III and IV freed, she pulled legs I and II and the gnathosoma free from the remnants of the old skin. The posterior portion of the cast skin was usually left fastened down to the substrate while the female shed the anterior portion of the skin. The male might or might not assist the female to emerge from the deutonymphal skin. When assistance occurred, the male pulled on that part of the deutonymphal skin which covered the gnathosoma, a small part of the propodosoma, and legs I and II. The female pulled to extract her legs from the old skin which the male held. It required about half the time for the female to emerge with the aid of the male than was necessary without assistance.

With the emergence of the female, the critical time was at hand for the guard male because the other males, which might be a short distance away, pressed closer. The guard male seized the newly-emerged female by the palps, pulled her a short distance across the cell and, with a firm hold on her palps, slid under her and inserted the aedeagus into her genital opening for 15-25 seconds. The female bent her venter downward to make contact with the male intromittent organ.

During mating the female's legs I were held upward and to the

side, and she remained passive. Following insemination, the male released his hold on the female's palps so that they might separate. They faced each other for a few seconds, and then the female swiftly backed away from the male. She avoided subsequent contact with all males in the cell. Mating behavior is shown in detail in Figures 7 through 13 and Figure 14.

Beer and Dailey (1956) found that the male of C. knowltoni ran rapidly around the newly-emerged female, tapping her body. He then pinched the palp of the passive female and seized her by one palp, leading her forward, sideways, and backward for some time in a rapid sort of dance. Then the male slid under the female and actual mating took place. Beer and Dailey reported that intermittent courtship and mating continued for ten minutes. These observations were strikingly different from observations on the mating behavior of C. lepidopterorum reported above.

Rarely, a situation occurred in which the emerging female was not disposed to mating and escaped from the male. Here the subsequent events were identical to those in Sequence II.

Sequence II

Female deutonymph does not mate with a guard male.

All males and females were removed from selected mass culture cells (see section on behavior in mass culture), leaving only immobile

Figure 7. Male and female C. lepidopterorum facing each other.

Figure 8. Male taking hold of palps of female.

Figure 9. Male C. lepidopterorum pulling female across cell.

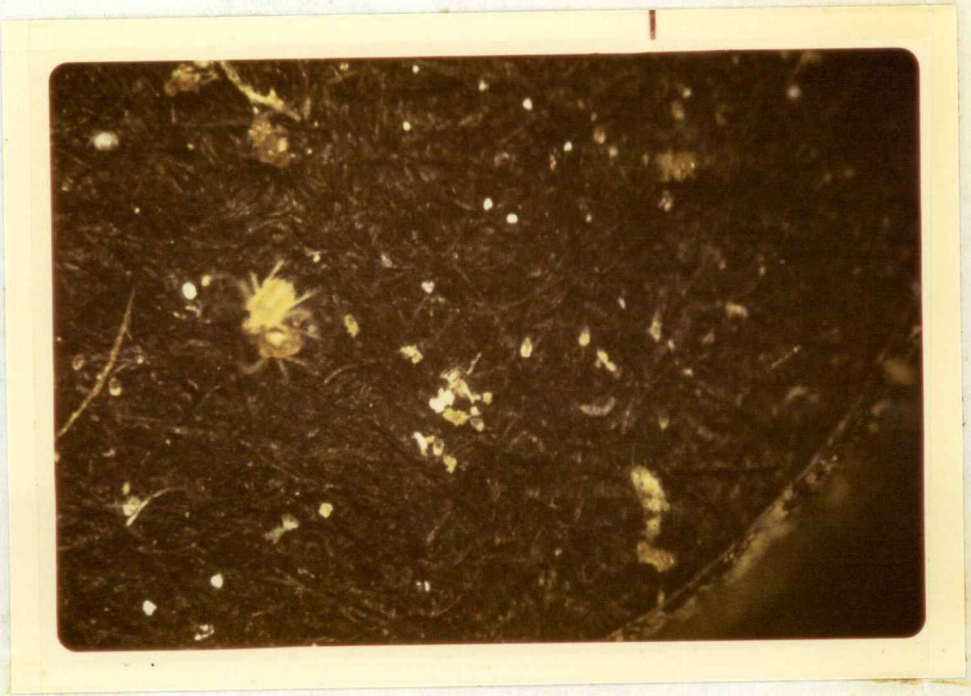

Figure 10. Male sliding under female.

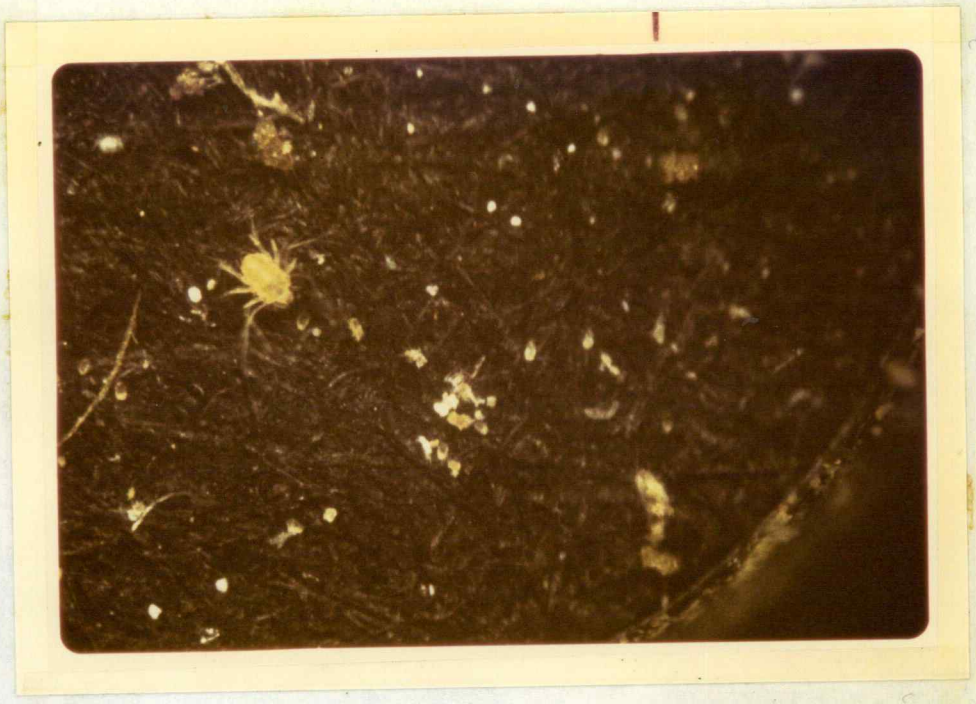

Figure 11. Actual mating of C. lepidopterorum.

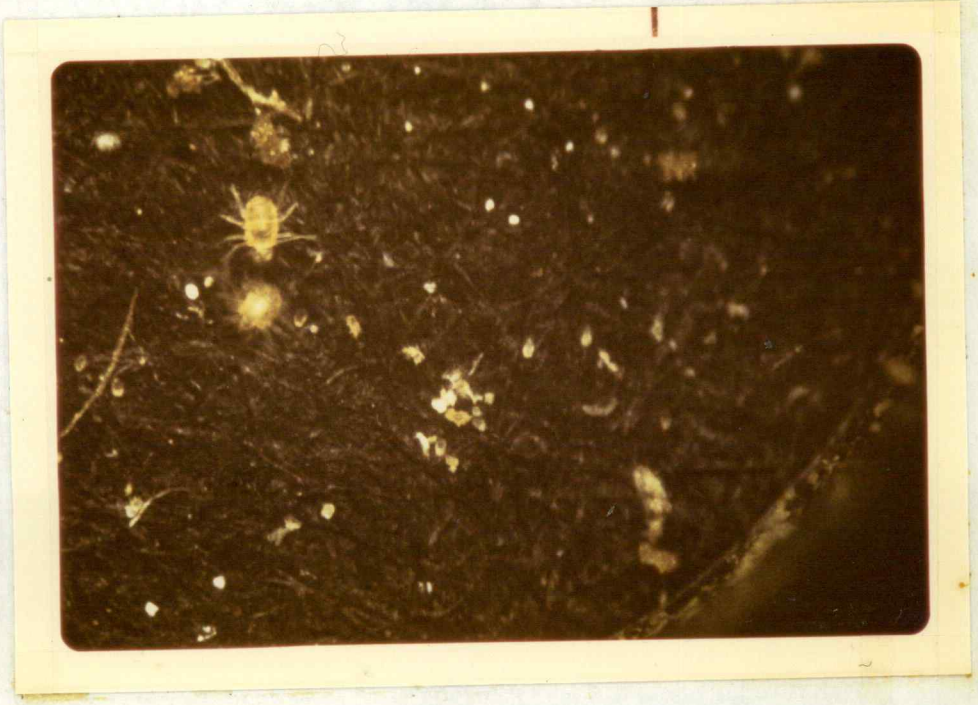

Figure 12. Male emerging from under female.

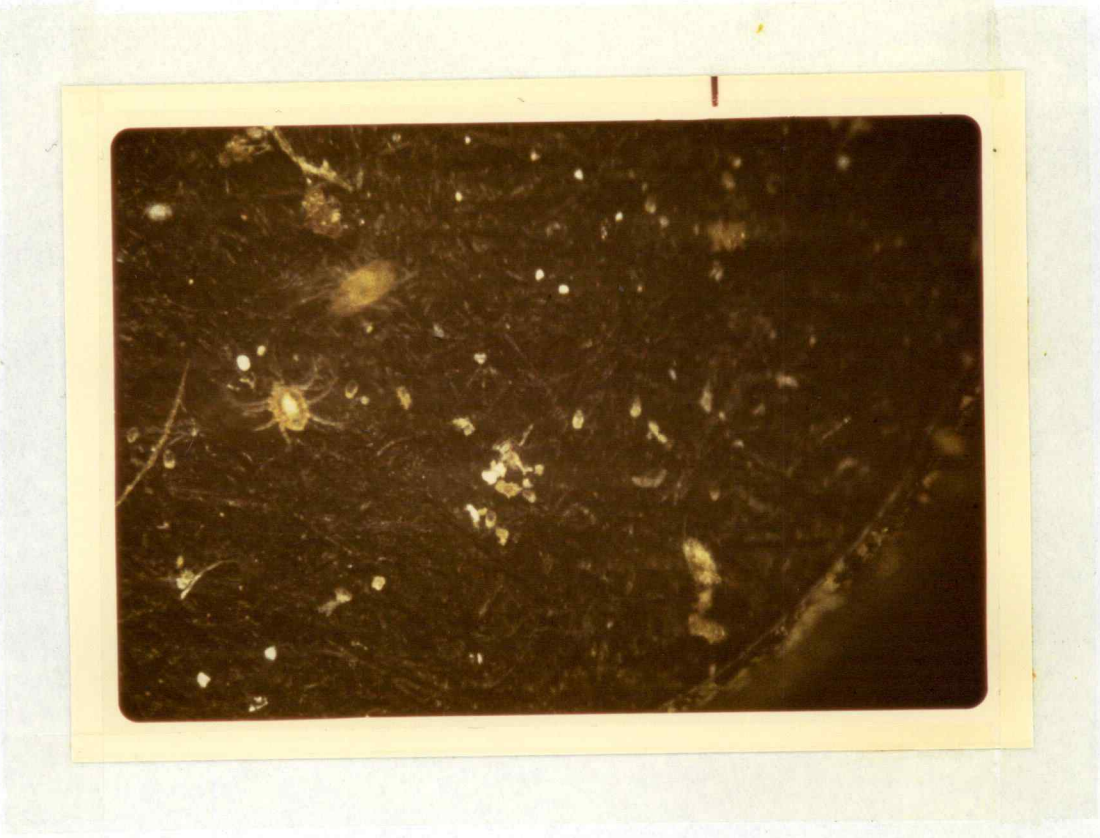

Figure 13. Female C. lepidopterorum moving away from male.

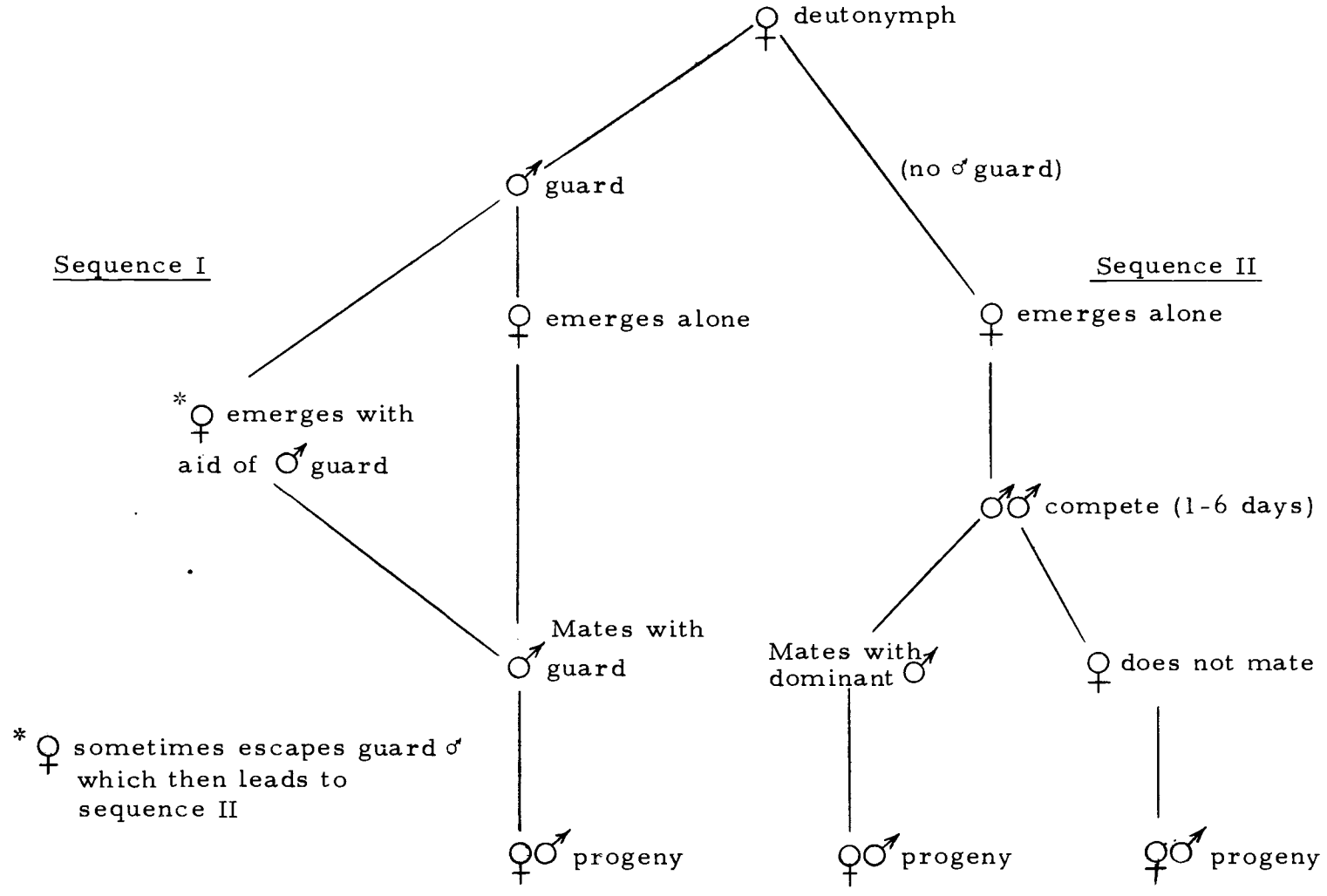

Figure 14. Sequence of encounters between male and female C. lepidopterorum from initial contact of male with female deutonymph.

nymphs, active nymphs, and larvae. Since males develop to the adult stage before females, the removal of all adult mites usually left the culture cells with a larger number of immobile female deutonymphs than the subsequently emerging males could guard. At times, the males guarded up to three female deutonymphs if there was a dearth of males. Virgin females which had emerged from deutonymphs not guarded by males or had escaped from original "guard" males moved about the cells and even fed before being discovered by one or more males. They would descend on her, grabbing her palps and legs. The female usually held legs I over her body which is characteristic of virgin females receptive to males. Up to 10 males have been observed around one female, all attempting to mate with her. She was usually pulled from several directions and carried around the cell but at no time did she struggle or attempt to free herself. The pulling can be so forceful that one or more legs may be pulled off. As the female was being dragged around the cell, the number of males actually pulling on her usually dropped to two or three. One male usually held her by the palps while the others grasped the legs. The male which held the palps of the female usually succeeded in mating with her but sometimes failed if dislodged by another male. Occasionally the female would succeed in escaping from the male in the mating position. A fight between males then ensued and continued until one male succeeded in mating with her. The female then behaved as did the females in Sequence I.

Observations over one hour in duration were made on the attempts by up to ten males to mate with the same female. In the pulling and dragging that occurred among males, the female lost portions of legs I and IV. Injured and severely handicapped by the loss of these leg parts, she was attacked by several other mites and eventually killed. Sequence II is described in Figure 14.

Reaction of Males to Females Who Have Escaped Mating for One to Eleven Days

These observations were undertaken to determine the length of time a newly-emerged female would attract males and mate with them. In artificial situations such as those found in laboratory cultures, mites may behave in a manner which may not be characteristic of their behavior under natural conditions. Sequences I and II were the only mating behavior procedures observed in mass cultures, but the response of males to older, unmated, egg-laying females in individual cells also was noted, as described below.

Immobile female deutonymphs were selected from large cultures and isolated in individual cells at 20°C, 80% R.H. A clue to the sex of a deutonymph was afforded by the fact that male deutonymphs were smaller and that only female deutonymphs were guarded by males. These phenomena greatly facilitated isolating only females.

One newly-emerged female was placed in a standard bakelite

observation cell along with a male chosen from the mass culture cells. Only active vigorous males were utilized in these tests. Three females were observed for mating behavior up to seven days; then two females were used from day 7 through day 11 because of the lengthy observations required after the seventh day. The results of these observations are summarized in Table 10.

Female One Day Old. A one-day-old female and one male were placed in each of three cells. In Cell #1 the mites wandered for two minutes before the male approached the female and made leg contact with her. He advanced, seized her by the palps, and pulled her. Subsequent mating took about 25 seconds, after which the female moved rapidly away from the male. Length of time elapsed prior to mating was two minutes.

In Cell #2, the male made immediate leg contact with the female. This activity of male reconnaisance and female quiescence amounted to a "pre-contact phase" and shall be so referred to in the rest of this section. He seized her by the palps and pulled her, activity best identified as "pre-mating contact," but then released her. He reverted to the pre-contact phase for 20 minutes more, then seized her again and mated for 18 seconds. The pair then separated, with the female showing the usual avoidance reaction to the male (see Sequence I). Length of time elapsed prior to mating was 20 minutes.

In Cell #3, the male crawled around for approximately 1.5

Table 10. Reaction of virgin female C. lepidopterorum of various ages to males.

Age of nubile ♀ (days)	Day	Matings	Eggs laid	Behavior of female
1	I	Yes (3/3)[a]	No	Passivism
2	II	Yes (3/3)	No	Passivism
3	III	Yes (3/3)	No	Passivism
4	IV	Yes (2/3)	No	Avoidance
5	V	Yes (1/3)	Yes	Antagonism and avoidance
6	VI	Yes (1/3)	Yes	Antagonism and avoidance
7	VII	No	Yes	Antagonism and avoidance
8	VIII	No	Yes	Antagonism and avoidance
9	IX	No	Yes	Antagonism and avoidance
10	X	No	Yes	Antagonism and avoidance
11	XI	No	Yes	Antagonism

[a]Successful matings

minutes before pre-contact activity began. Pre-mating contact was made and the subsequent mating took about 30 seconds, followed by post-mating avoidance on the part of the female. The length of time elapsing prior to mating was two minutes.

Female Two Days Old. One two-day-old female and one male were placed in each of three cells. In Cell #1, the male moved around for two minutes, while the female remained motionless. Pre-contact activity, pre-mating contact, and a mating period of about 40 seconds followed. The male attempted pre-contact activity again, but the female retreated from every advance. Time prior to mating: two minutes.

In Cell #2, pre-contact activity ensued for five minutes. Both mites then crawled around actively for an additional four minutes, during which time the male thoroughly examined the cast skin of the female. Following this, pre-mating contact was made and the subsequent mating took 20 seconds. No further mating behavior occurred. Time elapsed to mating: 10 minutes.

Initial leg contact between male and female in Cell #3 occurred over a period of 15 minutes. The female was then seized by the palps and pulled up the cell wall. Following the usual mating procedure, the pair mated for 2.5 minutes, falling from the wall to the floor of the cell without separating. Three times during copulation, the male appeared ready to release the female, but did not release his hold on

her palps. They separated and moved rapidly around the cell. No further mating behavior was observed. Length of time to mating: 19 minutes.

Female Three Days Old. Both male and female remained motionless for five minutes following introduction into Cell #1. The male then began to crawl around. Initial pre-contact activity prompted the female to move around. After ten more minutes, the female began to exhibit a retreat during pre-contact activity, then she became motionless, exhibiting the usual quiescence. Ten minutes after cessation of female movement, the male seized the passive female by the palps and pulled her. Mating lasted 20 seconds, followed by female avoidance of the male. Length of time elapsed prior to mating was 25 minutes.

In Cell #2, both mites were crawling actively after introduction. After seven minutes of female retreat, pre-contact activity began. Pre-mating contact led to an unsuccessful attempt at mating. A second attempt succeeded, and they mated for 20 seconds. Pre-copulatory activity took ten minutes.

Pre-contact activity began immediately and lasted for five minutes in Cell #3. Mating took 25 seconds.

Female Four Days Old. Five minutes of pre-contact activity preceded one minute of pre-mating contact in Cell #1. After attempting to mate several times, the male succeeded, and they mated for

135 seconds. After separating, the male made pre-mating contact again. This time mating lasted 20 seconds. Female avoidance was pronounced after the second separation. Length of time prior to first mating was six minutes.

In Cell #2, the pre-contact phase lasted 25 minutes and was interspersed with short periods of apparent disinterest on the part of both mites as they passed each other or made leg contact with no reaction. Pre-mating contact was unsuccessful two times before he was able to grab her palps, pull her across the cell, and mate with her for 1 minute, 40 seconds. Length of time which elapsed prior to mating was 25 minutes.

Pre-contact activity lasted for three minutes in Cell #3 before the male attempted pre-mating contact, failed, and reverted to pre-contact activity for 22 minutes. He attempted pre-mating contact many times in the next 19 minutes, after which he reverted to making leg contact with the female. These mites were observed for 138 minutes, with only the seizing of the female palp suggestive of mating.

Female Five Days Old. In Cell #1, 15 minutes elapsed before leg contact was made. After the female retreated from this attempt, this pair of mites spent the remaining observation period either crawling or at rest. No further leg contact was noted.

The female reacted to pre-contact activity by retreating for the first ten minutes in Cell #2. Then leg contact and seizure of the

female palp by the male led to mating, which took 25 seconds. The female avoided any further advances by the male.

In Cell #3, the female had already laid four eggs. She retreated every time leg contact was attempted by the male. His passage in front of her caused her to move legs I, but no other reaction was noted. No mating occurred during the 130 minutes of the test.

Female Six Days Old. The six-day-old female in Cell #1 had laid four eggs. When the male attampted pre-contact activity the female appeared ready to attack, with open palps and forward movement. Her antagonism was pronounced at each incident of leg contact with the male. During the 48 minutes of the test, the only behavior resembling pre-contact activity was the leg contact, which did not make the female passive.

In Cell #2 the male made contact with the female's body but she did not respond. He continued to crawl around until the female assumed the "attack position," extending her legs I at a 45^{o} angle from the body wall and spreading her palps widely. When he resumed moving about again, they met, the male attempted pre-mating contact, but she retreated. The test lasted 70 minutes and ended with both mites assuming stationary positions, having made no further contact.

In Cell #3, after ten minutes of alternating moving and remaining stationary, the male made leg contact with the female, advanced, and grabbed at her palps. This pre-mating attempt was unsuccessful.

Pre-mating contact was successful the second time, and they mated for 15 seconds. The female avoided leg contact after mating. Length of time to mating was ten minutes.

Female Seven Days Old. Reactions in both cells were similar. Both females had laid several eggs. The mites spent most of the time crawling around. The females avoided leg contact with the males. Often they would pass with no response from either mite. After approximately 30 minutes, the female in both cells became aggressive, attempting to seize the male's leg. The male countered and forced the female to abandon her attack. The male in Cell #1 fed on an egg laid by the female. At the end of 100 minutes, no mating had taken place in either cell.

Female Eight Days Old. Cells 1 and 2 had similar interactions between the mites. The mites spent the major portion of the time crawling around the cell. When they made leg contact, they squared off as if to attack. If the male advanced, the female retreated. No indications of mating were evident during the 120 minutes of the test except the advancing of the male following leg contact.

Female Nine Days Old. In both cells, the male advanced when he met the female, causing her to retreat. Pre-contact activity would cause the female to attempt an attack. The experiment was terminated after 120 minutes, with no mating having taken place. The only response which resembled the pre-mating behavior of the earlier days

was the advancing of the male after leg contact with the female.

Female Ten Days Old. Both females in this test had laid up to ten eggs. Reactions of the mites in both cells were similar. In the course of their movement, the mites frequently crawled past one another with no response. When the male made contact with the female, she either failed to respond or she retreated from him. The males fed on the eggs laid by the female. Several times the female assumed the "attack" position. Observations continued for 120 minutes with no mating or pre-mating behavior being observed, except for the male's establishing leg contact.

Female Eleven Days Old. In both cells the females had laid up to ten eggs. The female appeared ready to attack the male if he made leg contact with her. She would, however, retreat if he advanced. The experiment was terminated after 120 minutes with no mating having occurred. The male's advancing was the only pre-mating behavior observed.

Discussion

Mating behavior of C. lepidopterorum is unique, although it resembles the mating behavior of C. knowltoni in the aspects of (1) male guarding of female deutonymph, (2) male's seizure of the female by the palps, and (3) male's reversal so that he is under the female during mating. The male of C. lepidopterorum performs no mating

dance and will guard the female deutonymph against the advances of other males for as long as 48 hours. Mating is usually accomplished only once, with the mites separating afterwards and avoiding further contact.

Three pre-mating sequences were observed: (1) the male guards the female while she is in the deutonymph stage and subsequently mates with her; (2) an unguarded female deutonymph, or one that has escaped male protection, attracts a number of males at the time of molting, all of which attempt to mate with her, (3) a single male mates with a virgin female who has escaped detection for a number of days. The actual act of mating is essentially the same, regardless of pre-mating activities.

The guarding of female deutonymphs may be significant for reasons which are discussed under the section entitled "Conclusions." Escape of the newly-emerged female occurs frequently in culture, and is probably not uncommon in nature, since I found many females in hay samples which doubtless were virgins since they produced only male progeny (see section entitled "Sex Ratio of Progeny of Mated and Unmated Females").

Sequence II placed a vigorous male in a cell with a virgin female to determine the length of time the female would attract the male for the purpose of mating. All virgin females from one to three days of age were passive in their behavior toward the male. The courtship

consisted of leg contact, male seizure of female palp, and mating. Two of the three four-day-old females remained passive during courtship. The remaining female did not respond to leg contact; that is, she did not raise legs I over the body. Only one of the five-day-old females mated. The other two showed an avoidance reaction to the male during the leg contact interlude. One of three six-day-old females mated, and an antagonistic attitude on the part of the female toward the male was observed for the first time. No females mated after six days, although the males attempted pre-mating behavior. The antagonistic behavior on the part of the female became more pronounced with increasing age of the females until in experiments involving six-day-old females, the latter showed no avoidance reaction, but attacked the male on contact.

Thus, there appears to be several behavioral patterns based primarily on the age of the female. Duration of pre-mating and mating behavior is presented in Figures 15 and 16, respectively.

Duration of the pre-mating period increased from 8.33 minutes for females one day old to 15.5 minutes for females four days old. The females that mated at five and six days indulged in ten minutes of pre-mating behavior. There appears to be no correlation between the age of the female and the length of the pre-mating period to the duration of actual mating. There is a correlation between the age of the female and the frequency of mating.

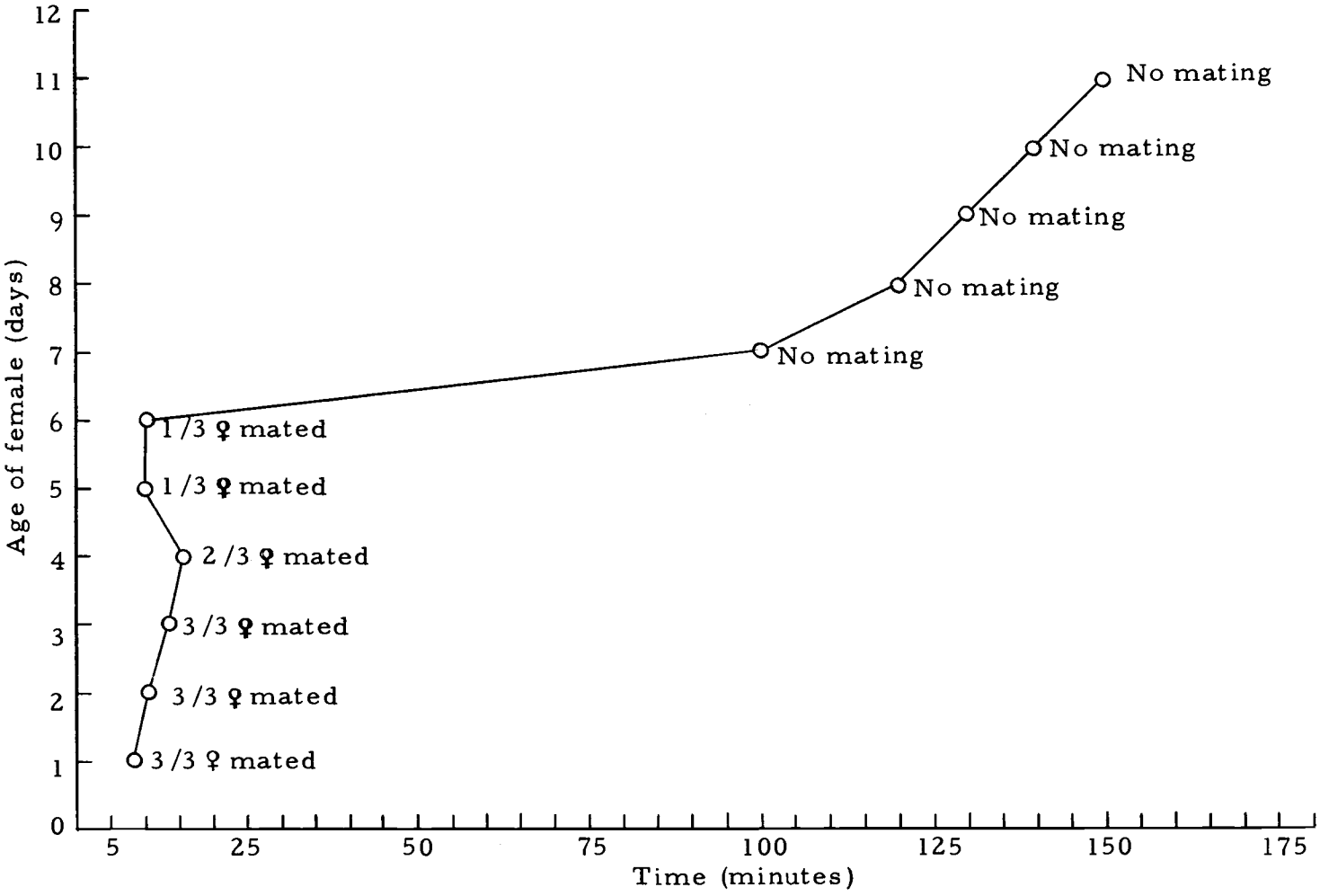

Figure 15. The effect of age of female on duration of pre-mating behavior behavior in Cheletomorpha lepidopterorum (Shaw).

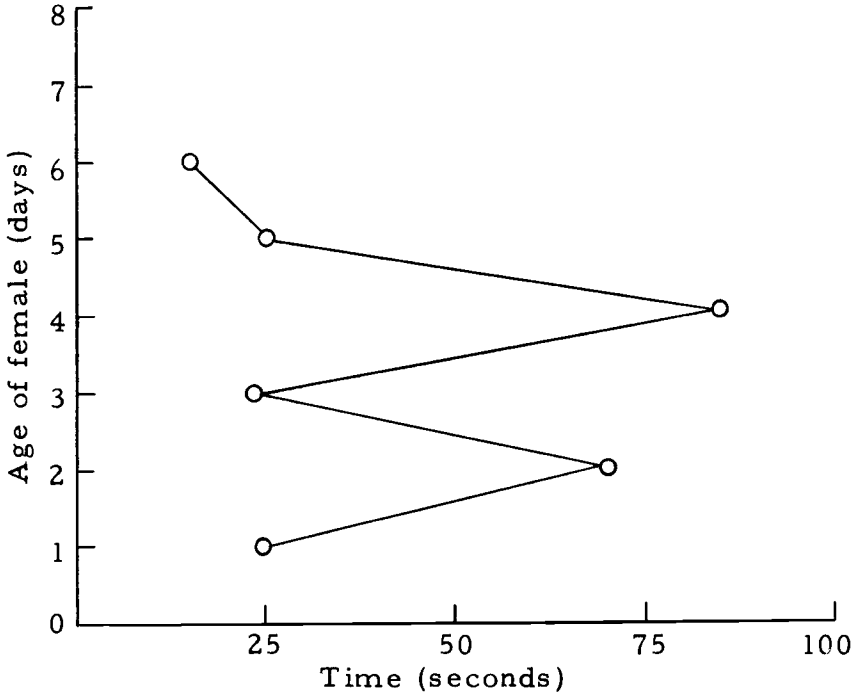

Figure 16. Effect of age of female on duration of mating in Cheletomorpha lepidopterorum (Shaw).

Attractant Studies

The purpose of these experiments was to determine if females would attract males when they were separated from males by a 155 mesh/inch screen.

Experiment I

Two plastic tubes (16 mm high, 12 mm inside diameter) were embedded in the centers of the charcoal-plaster bases of two plastic zipper vials (Figure 17). Two immobile female deutonymphs were placed in each of the tubes, the tops of which were covered by mesh-155/inch-held in place by Elmer's Glue. This brand of glue had earlier been found to be nontoxic to the mites.

Seven males were selected and placed on the floor of each of the zipper vials after the glue had dried for 24 hours. Observations were made four to five times a day, using a binocular dissecting microscope and overhead fluorescent lighting to determine if emergence of the females affected the behavior of the males. The cells were kept in a constant temperature cabinet at 20°C. Results are shown in Figure 18.

By the fourth day, there were four males on the mesh screen in Cell #1 and two on the screen in Cell #2. The females had emerged on the first day in both cells. At the end of the fifth day, five males

Figure 17. Attraction study cell used in Experiments I, II, and III.

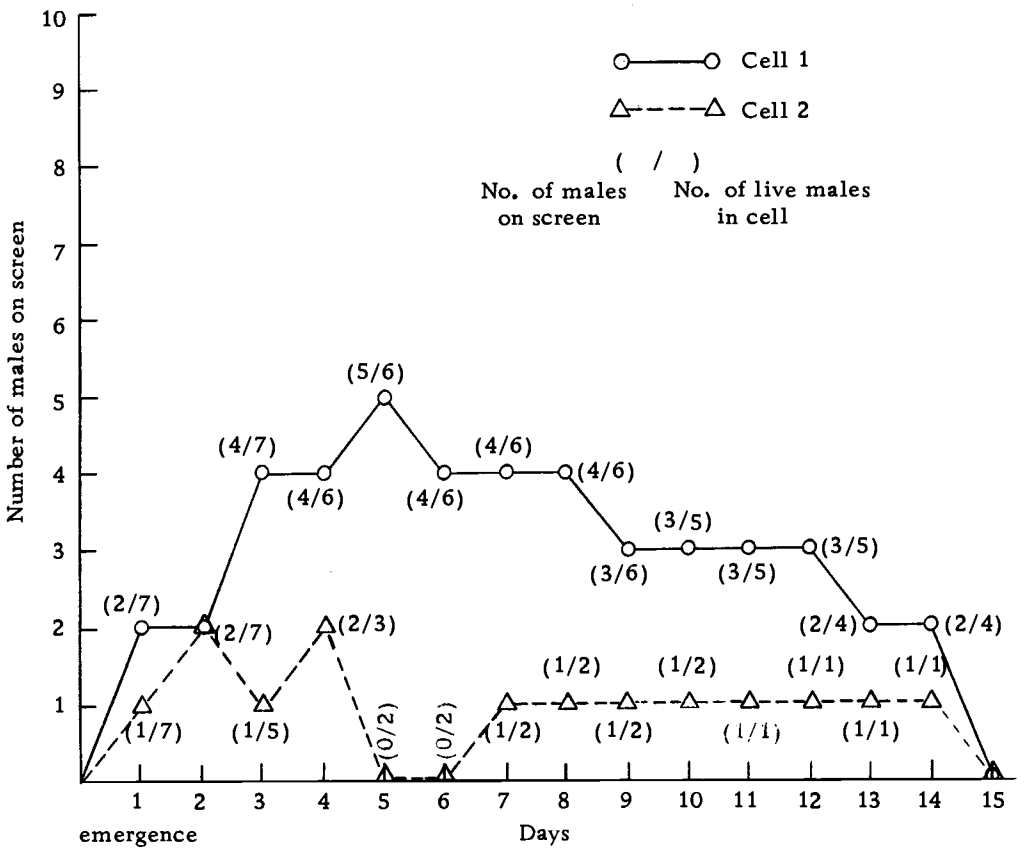

Figure 18. Attraction experiment using two immobile female deutonymphs and seven males of Cheletomorpha lepidopterorum (Shaw).

were observed on the screen in Cell #1. There were no males on the screen in the other cell; cannibalism had reduced the number of males in this cell to two. On the sixth day, four males remained on the screen; on the ninth day, three; and on the thirteenth, two. On the seventh day, a male in Cell #2 returned to the screen, and one male remained on the screen until day 14. When the experiment was terminated at the end of the fifteenth day, there were no mites on the screen in either cell, although the females were alive and active.

Experiment II

This experiment was similar to Experiment I except that, in addition to the cells containing female deutonymphs (Cells 3 and 4), there were two check cells (Cells 1 and 2) which did not have immobile female deutonymphs in the mesh-covered center cell. Results are shown in Table 11. There appeared to be slight attraction on the part of the males to the females for the first eight days of observations. Despite attrition due to cannibalism, it was evident that the presence of the female had little effect on males during this period.

The females emerged on the first day of the experiment. On the tenth day, five males crowded around on the screen in Cell #3 just above two females (see Figure 19). The males were all dead in Cell #4. Cell #1 males were on the zipper vial substrate, while Cell #2 had two widely-separated males on the screen. Four males

Table 11. Attraction experiment using two immobile female deutonymphs and seven males of Cheletomorpha lepidopterorum (Shaw). Experiment II.

Day	Cell #1 (check) Males on screen	Cell #2 (check) Males on screen	Cell #3 Males on screen	Cell #4 Males on screen
1	0/7**	0/7	0/7*	0/7*
2	0/7	0/7	0/7	0/7
3	0/6	0/6	1/7	0/5
4	1/6	1/6	2/6	0/3
5	0/5	0/6	2/6	0/2
6	0/5	0/5	1/5	2/2
7	0/4	0/5	2/5	0/2
8	0/4	1/4	2/5	0/2
9	1/4	1/4	2/5	0/1
10	0/4	2/4	5/5	-
11	0/4	2/4	3/4	-
12	0/4	1/4	4/4	-
13	2/4	-	0/4	-
14	-	-	2/4	-
15	-	-	2/4	-
16	-	-	2/4	-
17	-	-	0/4	-
18	-	-	0/4	-

*Females emerged on day 1

**The figure to the right of the line indicates the number of live males in the cell.

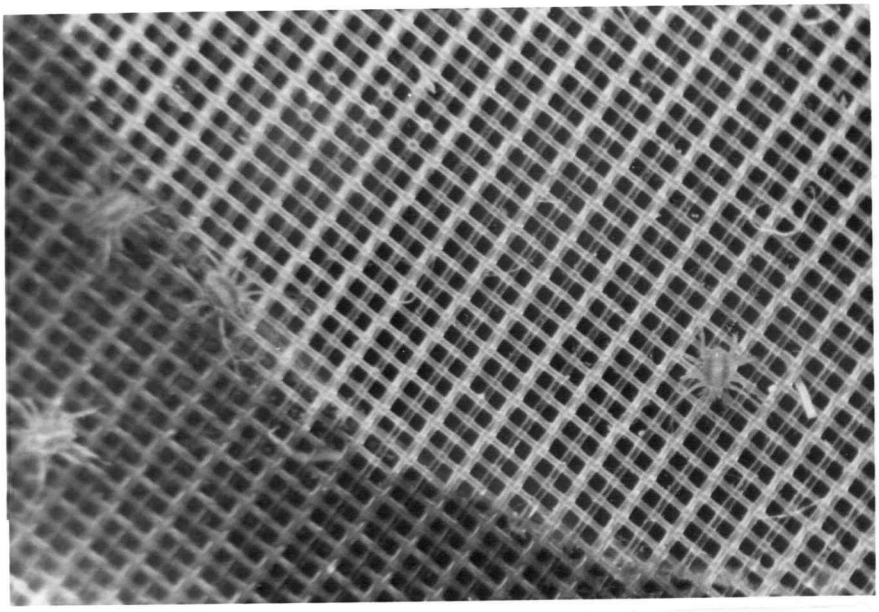

Figure 19. Four males of C. lepidopterorum "attracted" to virgin females in mesh-covered cell below them. A fifth male was out of range of the camera.

persisted on the screen in Cell #3 12 days after the start of the experiment, and all the males were dead in Cell #4. Two males had moved onto the screen in check Cell #1 on the thirteenth day, and all males were dead in the other control cell. The experiment was terminated 18 days after introduction of the males to the cell, because the four living males had not been on the screen for several days.

Experiment III

This experiment was conducted in the same manner as the previous two, except that there were three cells containing no female deutonymphs, and three check cells containing two females--check Cells #1, #2, and #3, and Cells #4, #5, and #6, respectively. Results are shown in Table 12. No more than two males were found on the screen in a cell, and this was three days after inception of the experiment, one day following the emergence of the females on the second day, in Cell #5. Cannibalism so reduced the number of mites in the cells that the experiment was terminated in seven days. At that time some of the cells had only one or no males remaining.

Experiment IV

A specially-designed cell consisting of a lower plastic cylinder lined with charcoal-plaster and an upper plastic cylinder with a removable bottom lined with fine mesh (155/inch) and a plastic cover

Table 12. Attraction experiments using immobile female deutonymphs and males of Cheletomorpha lepidopterorum (Shaw). Experiment III.

Day	Cell #1 (check) Males on screen	Cell #2 (check) Males on screen	Cell #3 (check) Males on screen	Cell #4 Males on screen	Cell #5 Males on screen	Cell #6 Males on screen
1	0/7**	0/7	0/7	1/7	1/7	1/7
2	0/6	0/5	0/4	0/6*	0/6*	0/5*
3	0/4	0/4	0/2	0/5	2/5	0/5
4	0/2	0/3	0/0	0/4	0/3	0/3
5	0/2	0/2	-	0/4	1/3	1/2
6	0/1	0/1	-	0/4	0/0	0/1
7	0/0	0/0	-	0/4	0/0	1/1

*Females emerged on day 2.

**The figure to the right of the line indicates the number of live males in the cell.

with a cotton plug was used in this experiment (Figures 20, 21). Five immobile female deutonymphs were placed in the lower section, while seven males were placed in the upper section. Observations were made two or three times a day. Results are shown in Table 13.

Five males were on the screen on the third day, and two females had emerged. None of the other females emerged; the moldy deutonymphs were discarded after the sixth day. By the sixth day both living males were on the screen. Only two males were still alive on the seventh day, and they did not congregate on the screen. The experiment was terminated after nine days, with one male and two females alive. Some eggs had been laid by the females.

Discussion

Results of Experiments I, II, and IV indicated that virgin females produce some substance that attracts males. On the fifth day in Experiment I, five of the six males were gathered above the females. Only three males escaped cannibalism in the second cell, but of these three, two were on the screen on the day after the females emerged. All five of the living males were attracted to the ten-day-old female in Experiment II. The companion cell had had its number of males reduced to two by cannibalism, but both of these were on the screen on the sixth day. Experiment IV also demonstrated the attraction of the females to the males; on day three, five males were on the screen.

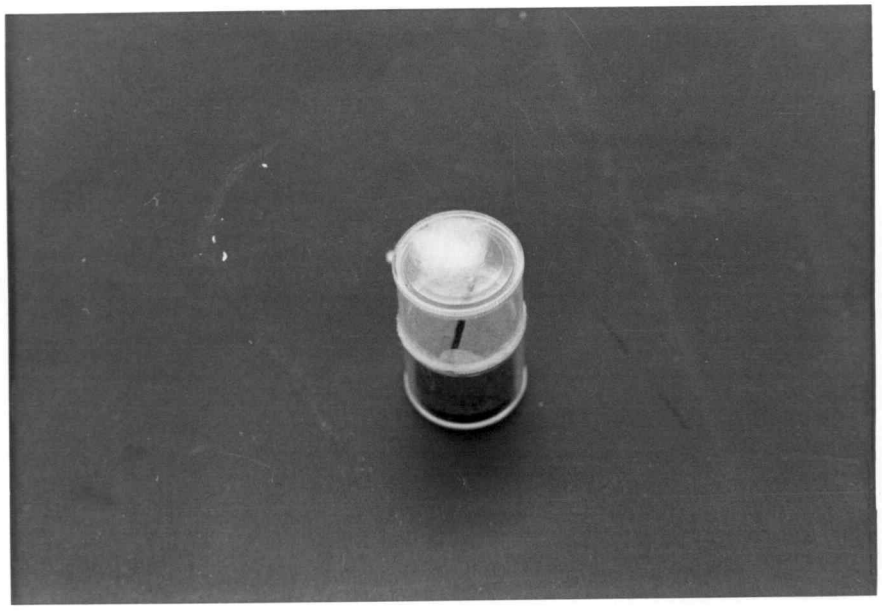

Figure 20. Attraction study cell type used in Experiment IV.

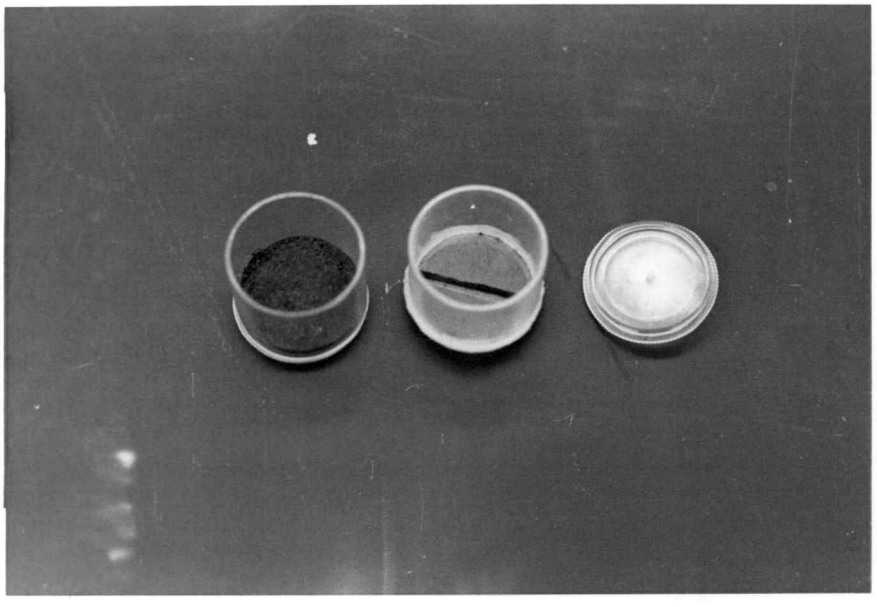

Figure 21. Attraction study cell used in Experiment IV, disassembled.

Table 13. Attraction experiments using five immobile deutonymphs and seven males of Cheletomorpha lepidopterorum (Shaw).

Day	Males on screen
1*	2/7**
2	4/7
3*	5/6
4	1/2
5	1/2
6	2/2
7	1/2
8	0/1
9	0/1

*Female emerged on day 1 and day 3.

**The figure to the right of the line indicates the number of live mites in the cell.

Experiment III did not confirm or refute the results of the other experiments, because cannibalism so reduced the number of mites that not more than two males were found on a given screen at a given time.

Lack of interest of males to the control cells in Experiment II and III further substantiates the female's attractiveness to the males. In Experiment III, at no time was a male found on the screen above the empty cell. The largest number of mites reported on the screen above the empty cells used as checks in Experiment II was two. This is in contrast to five, three, and four found on the tenth, eleventh and twelfth days in Cell #3 with females.

The attraction to the females by the males was clearly evident (i.e., there were at least two males hovering over the female) for days after emergence in Experiment I, from 7-12 days after emergence in one cell in Experiment II, and until three days after emergence in Experiment IV (all but two males died on the following day). These long periods of attraction to the female on the part of the male agree with the observations made in the mating behavior experiments in which the male attempted mating up to 11 days, even though avoided and attacked by the female.

These experiments seemed to indicate that the quiescent female deutonymphs, under the conditions of these experiments, did not attract males, even though mass culture observations showed males

guarding quiescent female deutonymphs. However, upon emergence the females in these experiments attracted males, and the attraction lasted for up to 14 days.

ROLE AS A PREDATOR OF ACARUS FARRIS (OUD.)

Predator-Prey Study at Three Temperatures and Two Humidities

The objectives of the predator-prey study were (1) to determine some of the interactions between graminivorous and predaceous mites in stored grain and grain products by observing their behavior under various conditions of temperature and humidity; and (2) to conduct experiments involving selected predaceous mites which might provide guidelines for later investigators in the selection of biological control agents.

Feed and seed samples were collected from the grain bin at the Oregon State University Entomology Farm and Beef Barns in order to determine natural associations between graminivorous and predaceous mite species in this area. The most common predators were Cheyletus eruditus (Schrank) in cattle feed and Cheletomorpha lepidopterorum (Shaw), Androlaelaps casalis (Berlese), and Blattisocius tarsalis (Berlese) in stored grain (wheat).[4] The four predators

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[4] C. lepidopterorum was found in such large numbers in the grain bin that the Berlese samples appeared orange in color. A. casalis was abundant and possibly was the prey of C. lepidopterorum, although little feeding was observed on A. casalis. The large populations of Tyrophagus putrescentiae (Schrank) and Glycyphagus sp. originally present in the sampled bin may have been exterminated by the predators because no graminivorous mites were found in later samples.

were then evaluated according to the following criteria: (1) searching ability, (2) ease of rearing, (3) ease of observation, (4) effectiveness as a predator of the chosen prey species, Acarus farris (Oud.), and (5) suitability for dispersal experiments. The biology and behavior of C. eruditus, A. casalis, and B. tarsalis in culture, as well as their role as predators of stored grain pests, have been studied in the past (see Literature Review). Only C. lepidopterorum had not been studied from the standpoint of its being a major predator of stored grain mites. It is briefly mentioned by Champ (1966) as being a predator of Tyrophagus putrescentiae (Schrank) along with C. eruditus and C. malaccensis.

C. eruditus was the first of the four mites to be investigated. It was easily reared in the zipper vials previously described, but was light sensitive and tended to hide under the wheat germ provided as food for the acarid mites. Many secreted themselves in pits made in the charcoal-plaster cell floors where they waited for A. farris, seizing the prey as it crawled over the depression and retreating with it to obscure positions. Observations often were erratic because the opening of the cell cover affected the behavior of the mites. For these reasons it was decided not to use C. eruditus in the predator-prey study. Other factors affecting this decision are presented in the section entitled "Dispersal Studies."

Blattisocius tarsalis (Berlese) was not numerous in the sampled bins so there were few specimens to use for experimentation. B. tarsalis is a fast-moving mesostigmatid mite with a well-developed capacity to search for prey, as reported by Barker (1967) for B. keegani (Fox). Because of its speed and incessant activity, it is difficult to follow in culture. When placed in a cell with A. farris, B. tarsalis was never observed to feed on any stage of the prey species. This may have been due to influence of cell conditions on their normal behavior. The inability to make close and accurate observations of the biology and behavior of B. tarsalis, its apparent reluctance to feed on A. farris, and its low population in the grain bin and laboratory cultures, along with other disadvantages discussed in the section on dispersal, led to the decision not to use it in the predator-prey studies.

Androlaelaps casalis (Berlese) is a fast-moving predaceous mesostigmatid mite with a well-developed searching capacity (Barker, 1968). It has been known to feed on farinaceous material, dried blood, eggs of other mites, and species of Hypoaspis and Haemogamasus (Evans et al., 1961). A. casalis was difficult to observe in culture because it rarely remained in one place when the cell was placed under the microscope for observations. The lids could not be removed from the zipper vials for close observation because the mites rapidly escaped. This escape also occurred when prey was introduced or when

debris was removed from the cell. Other disadvantages which played a part in this species' failure to be chosen as the predator for this study are listed under the section entitled Dispersal Studies.

Cheletomorpha lepidopterorum was a fairly slow-moving mite with extremely long legs I and orange pigmentation. It had good searching ability, but in small-cell situations it tended to remain in a "ready" position until it detected prey.

C. lepidopterorum was easily reared, requiring the feeding of live prey every few days if the culture contained primarily adults, or every day if many eggs were present and one wished to reduce cannibalism to a minimum. Its slow movements made observations accurate and relatively simple. Bright lights, even in the absence of heat, tended to attract this species, so all observations were made without the use of microscope lamps. Mating, emergence from eggs, molting, feeding, and intraspecific and interspecific interactions could be readily observed. A. farris proved to be a highly suitable prey for C. lepidopterorum, with adults and nymphs of the predator feeding on all stages of the prey, and larvae feeding primarily on the eggs and larvae of the prey. The predator did not thrive if too many prey were present in the cell. Under this condition, C. lepidopterorum was constantly in motion, fed little, and laid few eggs. Of the three mite species tested in preliminary dispersal experiments using a flour substrate, C. lepidopterorum, C. eruditus, and A. casalis,

the first was the only one that made distinct trails in the flour (see Dispersal Study). Consequently, because of ease of observation and rearing, searching ability, effective predation on A. farris, and its suitability for dispersal experimentation, C. lepidopterorum was selected as the predator to use in the predator-prey studies.

C. lepidopterorum females were selected from vigorous cultures which were maintained in bakelite cells (37 x 50 mm and 28 x 50 mm) and placed, one to a cell, in four cells (37 x 50 mm) at the following temperature and humidity combinations: 5°C, 80% R.H.; 20°C, 80% R.H.; 20°C, 90% R.H.; and 25°C, 80% R.H. Five female A. farris were added to each cell along with a few flakes of wheat germ to serve as food for them.

The cells were examined each day, the number of live prey was recorded, and new prey was added to bring the number of prey in each cell to five. Eggs and larvae of both predator and prey were removed when they appeared. Predators were replaced when they died, preferably by young females (which could be identified from old females by their paler orange color and smaller size). These experiments were conducted over a period of four months (see Table 14).

The mean number of prey consumed per day at the different temperature and humidity combinations was as follows: 5°C, 80% R.H. --.471; 20°C, 80% R.H. --3.844; 20°C, 90% R.H. --3.265; and

Table 14. Summary of predator-prey study using Cheletomorpha lepidopterorum (Shaw).

	Temperature-humidity combination			
	5°C, 80% R.H.	20°C, 80% R.H.	20°C, 90% R.H.	25°C, 80% R.H.
Females fed on adult A. farris				
Average no. mites eaten/day	0.47**	3.84**	3.26**	3.50**
Average length of life (days)	71.80	32.08	28.12	19.74
Eggs laid	No	Yes	Yes	Yes
Males fed on A. farris tritonymphs				
Average no. mites eaten/day		2.26	1.71	3.33
Average length of life (days)		25.86	18.00	40.00
Males fed on adult A. farris				
Average no. mites eaten/day			1.06	3.55
Average length of life (days)			8.75	17.00

**Significant at .01 and .05 level.

25°C, 80% R.H.--3.507. These results were significant at the .05 and .01 levels.

5°C, 80% R.H.

C. lepidopterorum lived for a long period (71.80 days), but was not very active. It stayed in one place most of the time and fed very little, eating less than .5 mites per day. In contrast, A. farris was much more active. It fed, laid eggs, and increased in number at this temperature and humidity.

20°C, 80% R.H.

C. lepidopterorum lived an average of 32.08 days. It was very active and voracious, eating an average of 3.84 mites per day. It was often hungry enough to seize the prey mites as they were being introduced into the cell. Eggs were laid by both predator and prey. The predator thrived best at this temperature-humidity combination.

20°C, 90% R.H.

C. lepidopterorum lived an average of 28.12 days, eating an average of 3.26 mites per day. Its feeding reactions were similar to those of the mites in the 20°C, 80% R.H. experiment, except for a slower consumption of prey. Eggs were laid by both predator and prey. Mold growth was a problem at this higher humidity so food for

the prey mites had to be changed frequently.

25°C, 80% R.H.

C. lepidopterorum lived an average of 19.74 days and devoured an average of 3.51 mites per day. The higher temperature and lower humidity combination reduced the longevity of the individual mites.

The temperature range from 20 to 25°C and a humidity range from 80 to 90% seems to be ideal for C. lepidopterorum.

Since only females were used in the preceding experiments, males were studied in companion experiments to determine if the predation rate of males differed from that of females. However, these males were fed on tritonymphs of A. farris which they seemed to prefer (see section entitled "Behavior in Mass Culture"), and the females were fed on adult A. farris. Later, six males at 20°C, 90% R.H. and 25°C, 80% R.H. were fed on adults of A. farris to compare their predation rate more accurately with that of females (see Table 14).

These experiments were conducted in cells of the type described in "Rate of Development." Six males, one in each of six cells, were observed at 20°C, 80% R.H., and four males were observed at 20°C, 90% R.H. and 25°C, 80% R.H. The males consumed tritonymphs at the rate of 2.26/day at 20°C, 80% R.H.; 1.71/day at 20°C, 90% R.H.; and 3.33/day at 25°C, 80% R.H. Adult A. farris were consumed at

the rate of 3.55/day at 25°C, 80% R.H. and 1.06/day at 20°C, 90% R.H.

The number of larvae and nymphs consumed by each developing C. lepidopterorum in the section on rate of development was recorded (Figure 22). The observations to determine the prey consumption of immature stages of C. lepidopterorum yielded the following results. The largest number of prey larvae and nymphs consumed by any immature state was 70, consumed by a developing female at 30°C, 90% R.H. The males at this temperature-humidity combination consumed an average of 11.4 larvae and 16.0 nymphs from the larvae through the deutonymph stage. Mites were most voracious at 25°C, 80% R.H., at which females consumed an average of 19.2 larvae and 18.2 nymphs, and the males consumed 15.0 larvae and 17.4 nymphs. Females at 20°C, 90% R.H. consumed more nymphs than those females at 20°C, 80% R.H., but fewer larvae. The smallest number of larvae and nymphs consumed by C. lepidopterorum was at the conditions of 30°C, 80% R.H. at which an average of 9.0 larvae and 10.0 nymphs were consumed.

The preceding observations from the rate of development study, along with survival percentages and the predator-prey study indicate that the range of temperatures and humidities over which C. lepidopterorum is most successful as a predator is 20-25°C with a relative humidity of 80-90%.

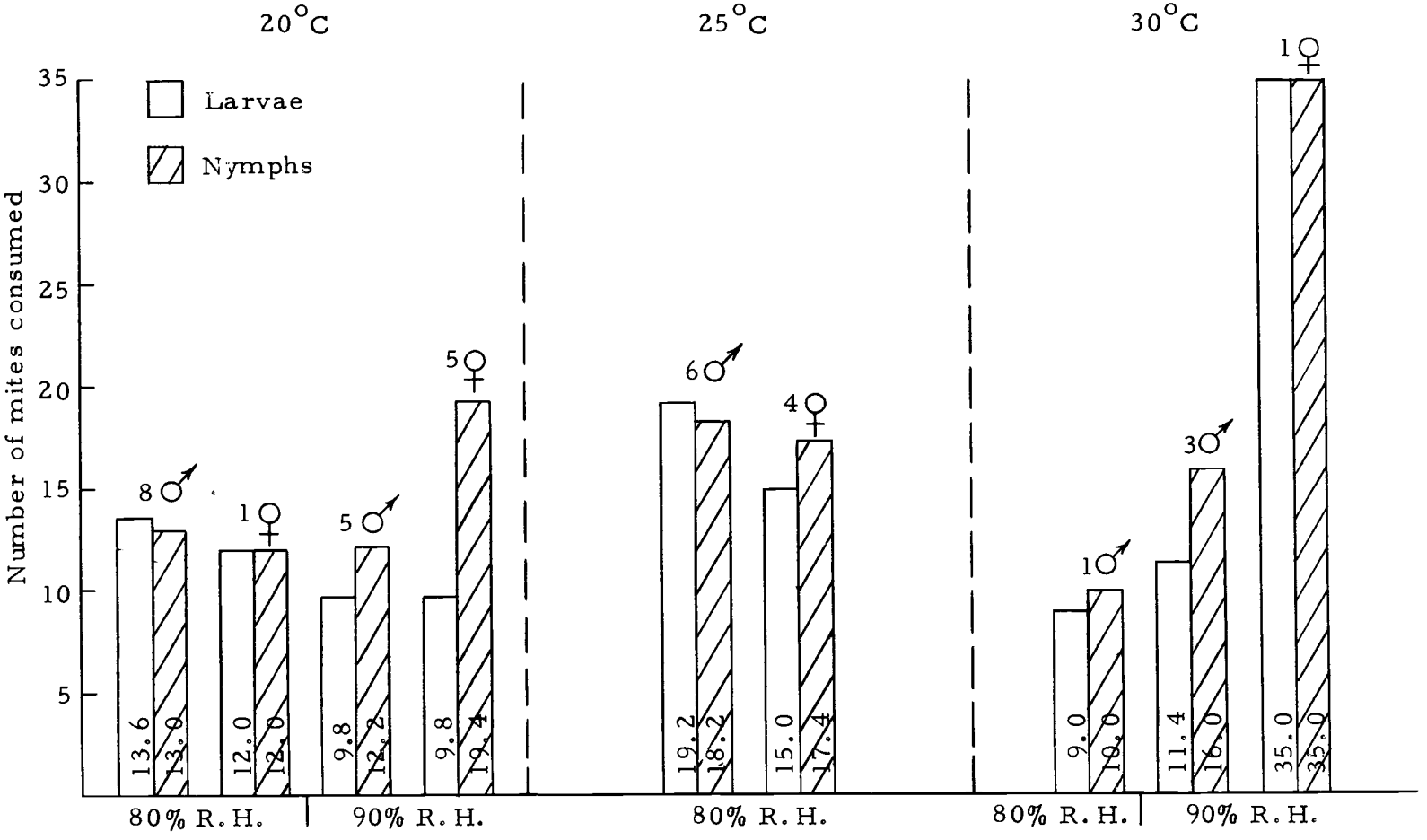

Figure 22. Average number of larvae and nymphs of Acarus farris consumed by Cheletomorpha lepidopterorum (Shaw) males and females in their development from egg to adult at three temperatures and two humidities.

Discussion

These studies confirm the earlier suppositions put forth concerning C. lepidopterorum as a predator of the grain mite A. farris (see section entitled "Behavior in Mass Culture"). The adults of C. lepidopterorum are effective predators on the adult and nymphal stages of the prey. Females consume the most prey at 20°C, 80% R.H., while males consume the most prey at 25°C, 80% R.H., so the temperature range 20-25°C and a humidity from 80-90% seems to be ideally suited to predation. C. lepidopterorum is a very inefficient predator at 5°C, 80% R.H., consuming less than one mite per day even though the prey develops and feeds normally. C. lepidopterorum survival is poor at 30°C, but their rate of predation is as good as at 20°C.

When fed on tritonymphs of A. farris, C. lepidopterorum males lived an average of 40 days at 25°C, 80% R.H., while those fed on adult A. farris lived only 17 days at the same temperature and humidity. The reason for this differential is unclear. Observations reported in the section entitled "Behavior in Mass Culture" indicated that males prefer to prey on the immature stages of A. farris. Males devour fewer mites and live a much shorter period of time at 20°C, than at 25°C. Thus it is seen that the combination of longer-lived voracious females and somewhat shorter-lived males, both with definite prey preferences,

in addition to larvae and nymphs, which prefer to prey on eggs, larvae and nymphs of the prey, would enable C. lepidopterorum to provide effective predation on A. farris.

Dispersal Studies

Dispersal is the movement of individuals away from an aggregation or a population (Kendeigh, 1961; Southwood, 1966). According to Odum (1962) it is the movement into or out of the population or population area. Odum (1961) states that it supplements natality and mortality in shaping population growth forms and density. Population pressure and failure of food supplies are two of the factors which are reported to induce dispersal (Kendeigh, 1961; Solomon, 1962). For example, Acarus siro L. tended to leave very damp grain because of food shortage and overcrowding.

In studying the role of Cheletomorpha lepidopterorum as a predator of grain mites, specifically Acarus farris, it was decided that too little consideration has been given to the dispersal and interaction of graminivorous mites and the predaceous mites which feed on them; therefore, some studies were undertaken to determine the effect of population density, sex, and predators on the dispersal of A. farris. It was decided that these studies should be made under more natural conditions than the small cells in which predator-prey studies were

carried out. In the small cells, the prey had little chance to survive, nor was any degree of dispersal possible.

The interaction and dispersal experiments were carried out, therefore, in a series of large plexiglass universes (see Figure 23) 30 x 30 x 4 inches with a 25 x 25 inch elevated glass floor and a 32 x 32 inch glass top. The glass top had a 2 inch hole in the center of it which was covered by a 6 x 6 inch square of glass. Originally the floor and top also were plexiglass but problems with static electricity necessitated a switch to a glass floor and top, at the suggestion of OSU physicists. A substrate of white flour passed through a 150 mesh sieve provided a background on which the trails left by the mites could be seen. This flour was conditioned for several days in a desiccator over a KOH solution designed to maintain 80% R.H. The universes were kept at 80% R.H. by the use of KOH solutions. The room was kept dark except when the experiments were started and at the end of 24 hours. The temperature was maintained at 72°F.

Predaceous mites were collected from the Butler bin at the Entomology Farm OSU, and from the OSU beef barn (see predator-prey study). Graminivorous mites, A. farris and A. siro, were obtained from cultures in the acarology laboratory at OSU. The predators collected were Cheletomorpha lepidopterorum, Androlaelaps casalis (Berl.), Blattisocius tarsalis (Berl.) and Cheyletus eruditus (Schrank).

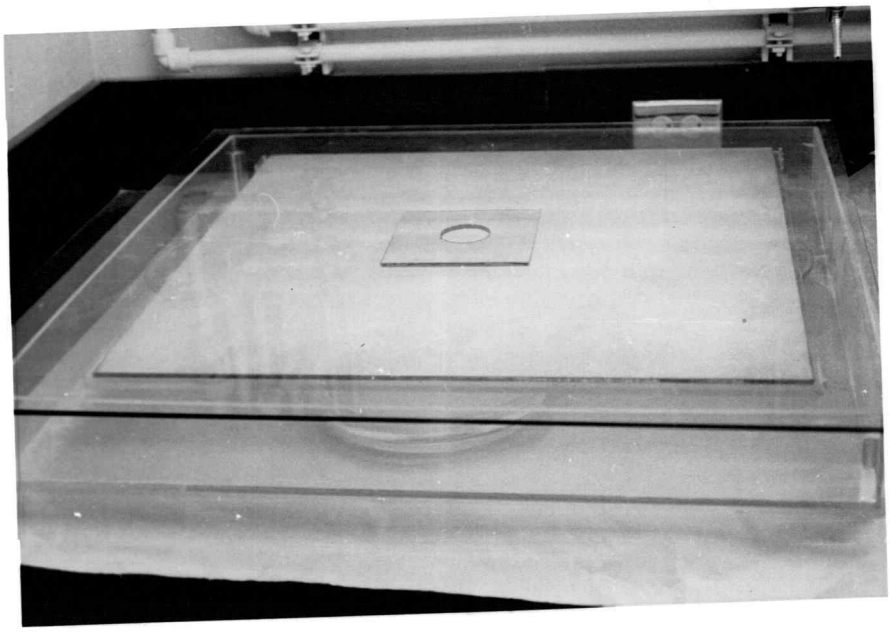

Figure 23. Plexiglass universe used in dispersal experiments.

In earlier experiments it was discovered that A. farris, A. siro, Glycyphagus destructor, and C. eruditus leave characteristic trails on sieved flour substrates. A series of observations was made of the trail-making patterns of these species in a plexiglass universe in order to determine if individual mite species could be traced on the white flour substrate by this means. Active mites were removed from cultures using a moistened paint brush and gently placed in the center of the universe. The cover was then placed over the universe. Observations were made at 12 and 24 hours. Drawings and photographs were made during these observation periods.

The results of these experiments showed that A. farris (male and female), A. siro (female), and C. eruditus (female) all leave characteristic trails which easily can be distinguished from one another. Males of A. farris leave short darkened irregular trails in the flour, while females leave long serpentine trails which are easy to see and follow (Figure 24). Females of A. siro leave winding, twisting trails which double back on themselves, making them difficult to trace (Figure 25). The trail of C. eruditus is very irregular due to its indiscriminant searching habits. It appears as a darkened disturbed area in the flour which often extends beyond the edge of the universe (Figure 26). When C. eruditus is placed in the universe with A. farris or A. siro the characteristic trails of the latter two species are virtually obliterated because the searching behavior of C. eruditus

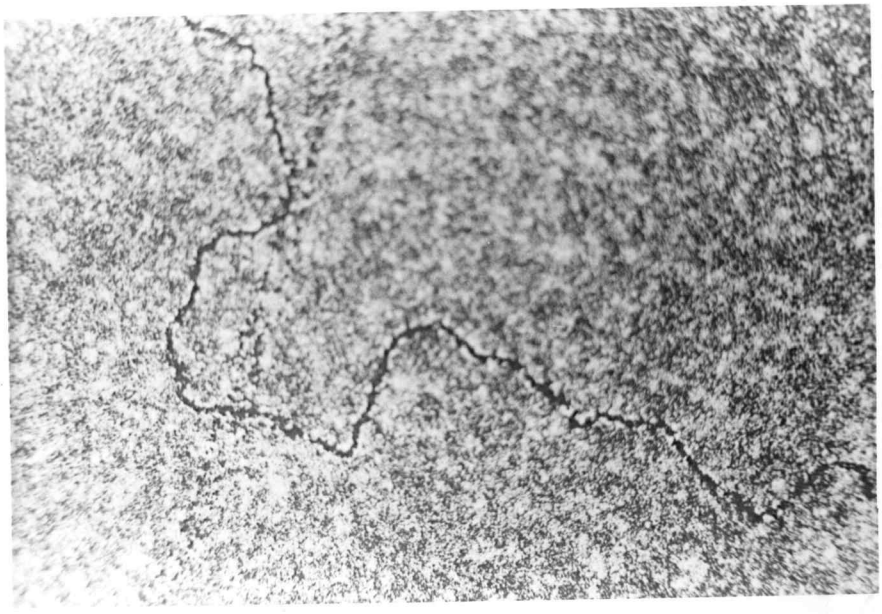

Figure 24. Trail of A. farris female in flour. Note the lack of twists and turns.

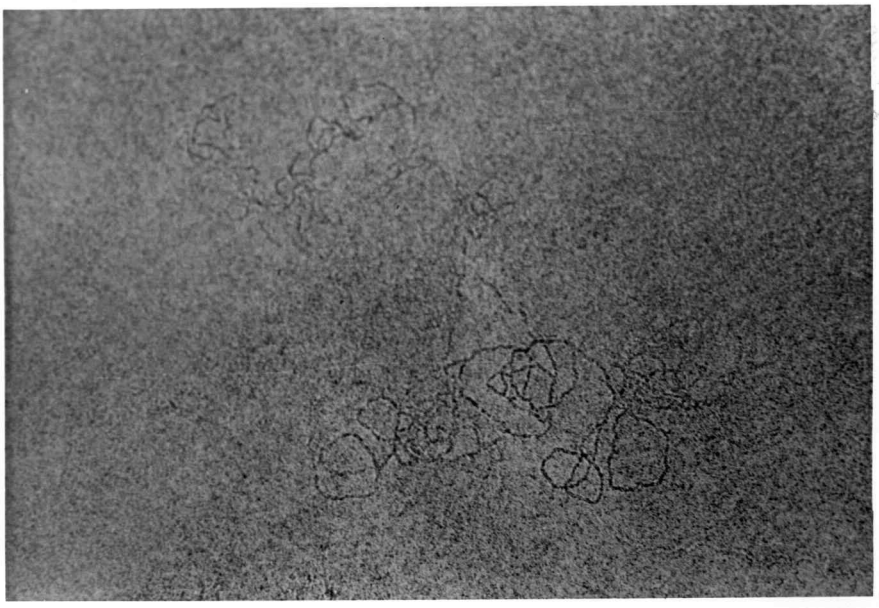

Figure 25. Trail of A. siro females. Note the twists and turns.

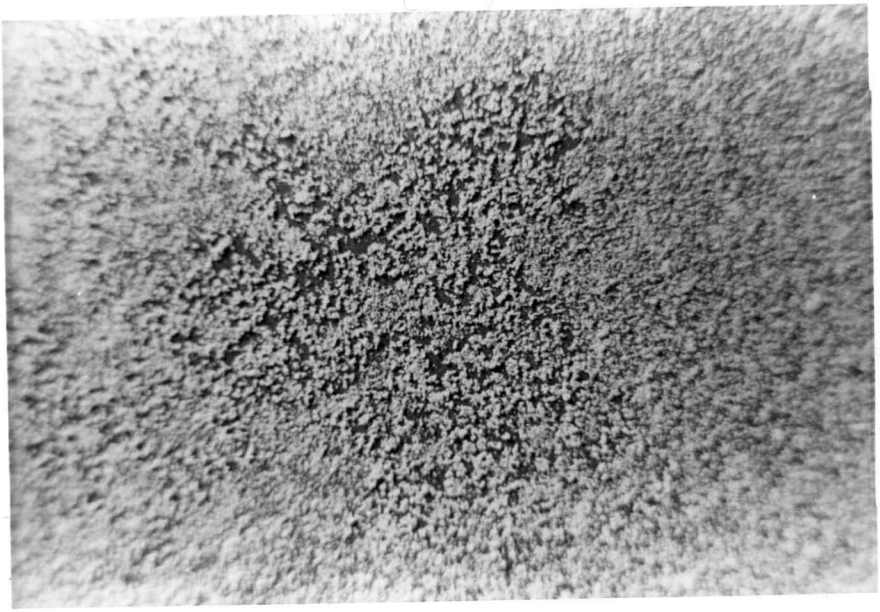

Figure 26. Trail of Cheyletus eruditus (Schrank).

obscures them. G. destructor puts down a trail somewhat like that of C. eruditus, probably because of its jerky gait and long lateral and posterior setae. The setae tend to brush the trail, resulting in masking or obliteration.

In addition to information on trail variations, preliminary experiments gave an indication that (1) males of A. farris inhibit the dispersal of females, and (2) females of A. farris disperse much more than males.

Later experiments dealt with the interaction and dispersal of A. farris, C. eruditus, and C. lepidopterorum within a prescribed universe. Special emphasis was placed on the study of the influence of overcrowding and predation on the degree and pattern of mite dispersal. The mites used in these experiments were gently removed from cultures with a paint brush and placed in a small plastic cell with a fine mesh bottom. They were then introduced into the universe through the 2 inch hole in the cover by tapping the bottom of the plastic container.

Observations on mite dispersal were made at the end of a 24-hour period. A red wax pencil was used to trace the dispersal pattern on the glass top of the universe. A piece of tracing paper was placed over the wax tracing, and the pattern was traced on the paper with India ink. The following experiments were carried out: (1) Determination of the characteristic type of trail made by C. lepidopterorum,

A. casalis, and B. tarsalis; and (2) Interaction and dispersal experiments using C. lepidopterorum and A. farris to determine whether degree and pattern of mite dispersal differs from that of C. eruditus and A. farris.

The following results were obtained: (1) C. lepidopterorum makes a long twisting trail which is easy to follow and trace, while A. casalis and B. tarsalis either do not leave clear trails or make trails which are only partially traceable. While C. lepidopterorum has a tendency to stop and assume the typical cheyletid "attack" position, it moves around more than C. eruditus and is seldom found in the center of the universe after 24 hours; (2) The dispersal of A. farris in the presence of the predator C. lepidopterorum at a ratio of 10:1 does not differ markedly from that which occurs in the presence of C. eruditus. The difference in the overall pattern is in the degree and direction of movement by C. lepidopterorum as compared to C. eruditus. C. lepidopterorum can travel across most of the universe in 24 hours, but usually closely follows the trails of A. farris. Cheyletus, however, seems to wander indiscriminantly (C. eruditus has no eyes, while Cheletomorpha possesses propodosomal ocelli) around the universe, ending up in "attack" position in the center or edge of the universe center.

A final set of experiments was conducted on interaction and dispersal of A. farris and C. lepidopterorum within the previously

described universes. These experiments were set up to determine if an increase in number of A. farris alone or in the presence of a constant number of predators (C. lepidopterorum) would increase the degree of their dispersal. Special attention was given to the effect of overcrowding, sex of the mites, and predator-to-prey ratio on the degree and pattern of mite dispersal.

The flour substrate was conditioned and sieved as described for previous experiments. Flour was conditioned at 80% R.H. for several days and dusted on the glass floor, after which the system was allowed to come to equilibrium overnight. The numbers of A. farris used in individual tests were 10, 20, 30, and 40. The following combinations were utilized for each number: females alone, males plus females, and males plue females plus predators. The number of predators used in each of the latter combinations was five. The ratio between predator and prey population, therefore, was 2:1, 4:1, 6:1, and 8:1. Within these ratios, the sex combination classes which had females plus males had the two sexes on a 1:1 basis. All predator-to-prey ratios each with their three combination classes were replicated six times. For a summary of classes and ratios see Table 15. For actual dispersal trails see Plates 5-11.

The mites were allowed to remain in darkness for 24 hours after they were introduced into the universe in order to eliminate the effect of light on dispersal. At the end of the 24-hour period a desk light was

Plate 5. Dispersal trails of 10 Acarus farris (Oud.) of both sexes and five Cheletomorpha lepidopterorum (Shaw). Total dispersal - 585 mm. Plate increased 12%.

Plate 6. Dispersal trails of 20 Acarus farris (Oud.) of both sexes and five Cheletomorpha lepidopterorum (Shaw). Total dispersal - 1066 mm. Plate reduced 13%.

Plate 7. Dispersal trails of 26 Acarus farris (Oud.) males and females. Total dispersal - 1880 mm. Plate reduced 46%.

Plate 8. Dispersal trails of 30 Acarus farris (Oud.) of both sexes and five Cheletomorpha lepidopterorum (Shaw). Total dispersal - 2913 mm. Plate reduced 38%.

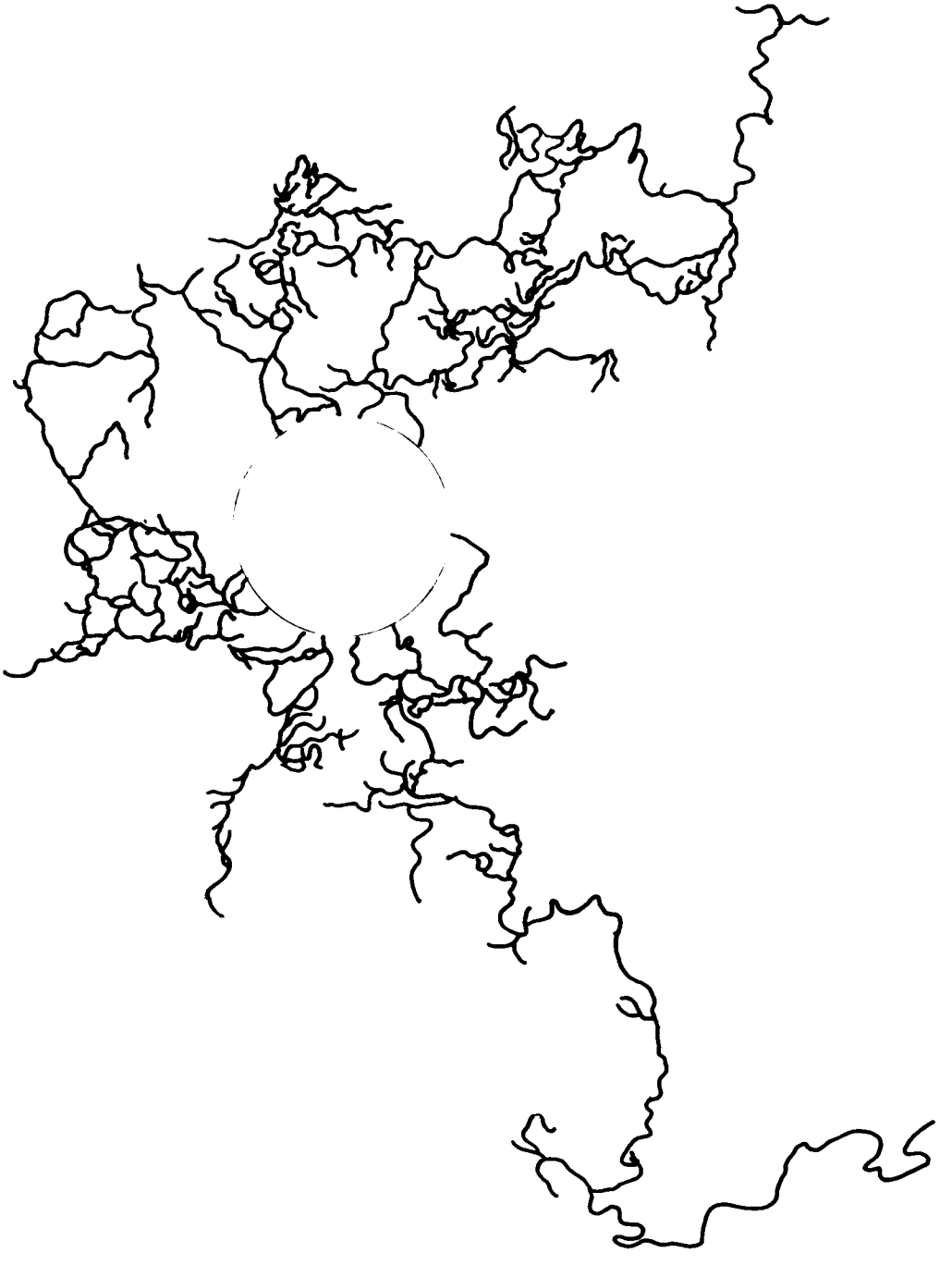

Plate 9. Dispersal trails of 36 Acarus farris (Oud.) males and females. Total dispersal - 2749 mm. Plate reduced 62%.

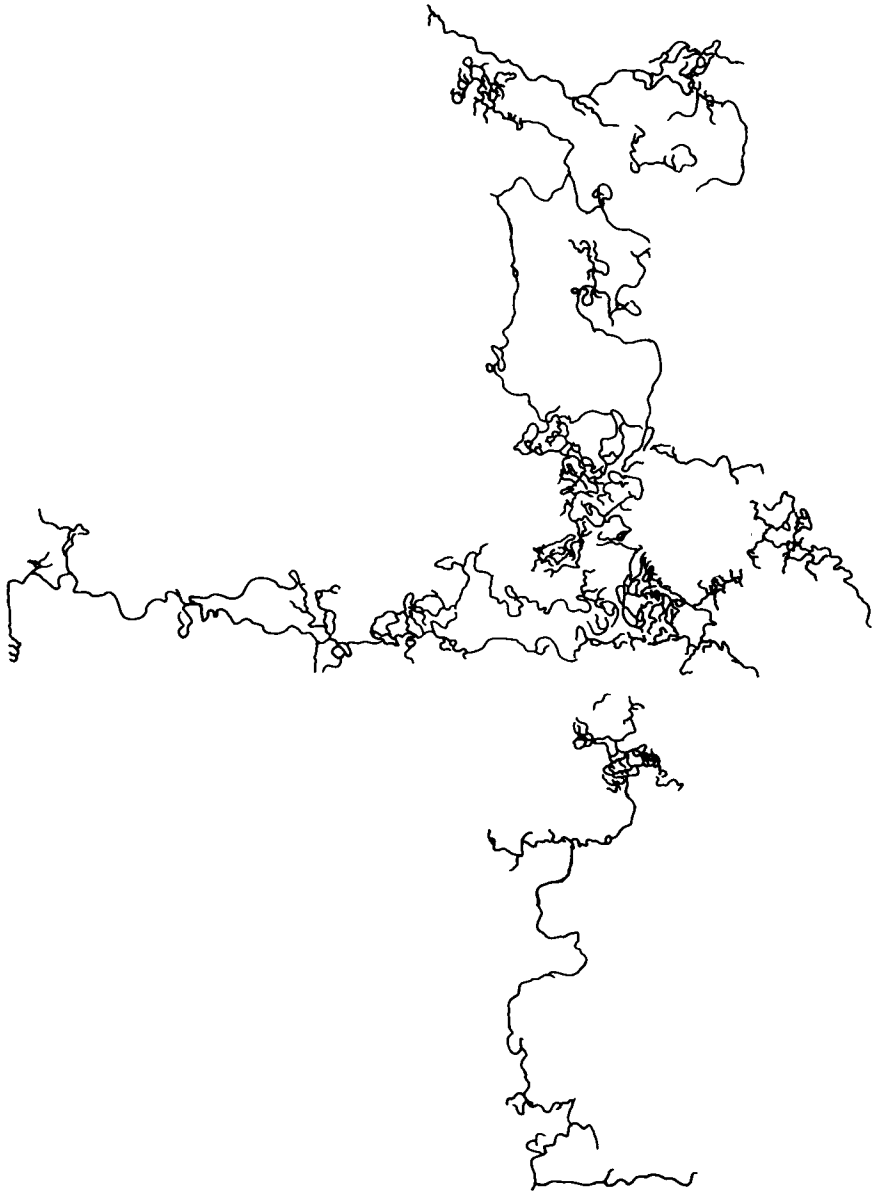

Plate 10. Dispersal trails of 40 Acarus farris (Oud.) and five Cheletomorpha lepidopterorum (Shaw). Total dispersal - 2204 mm. Plate reduced 37%.

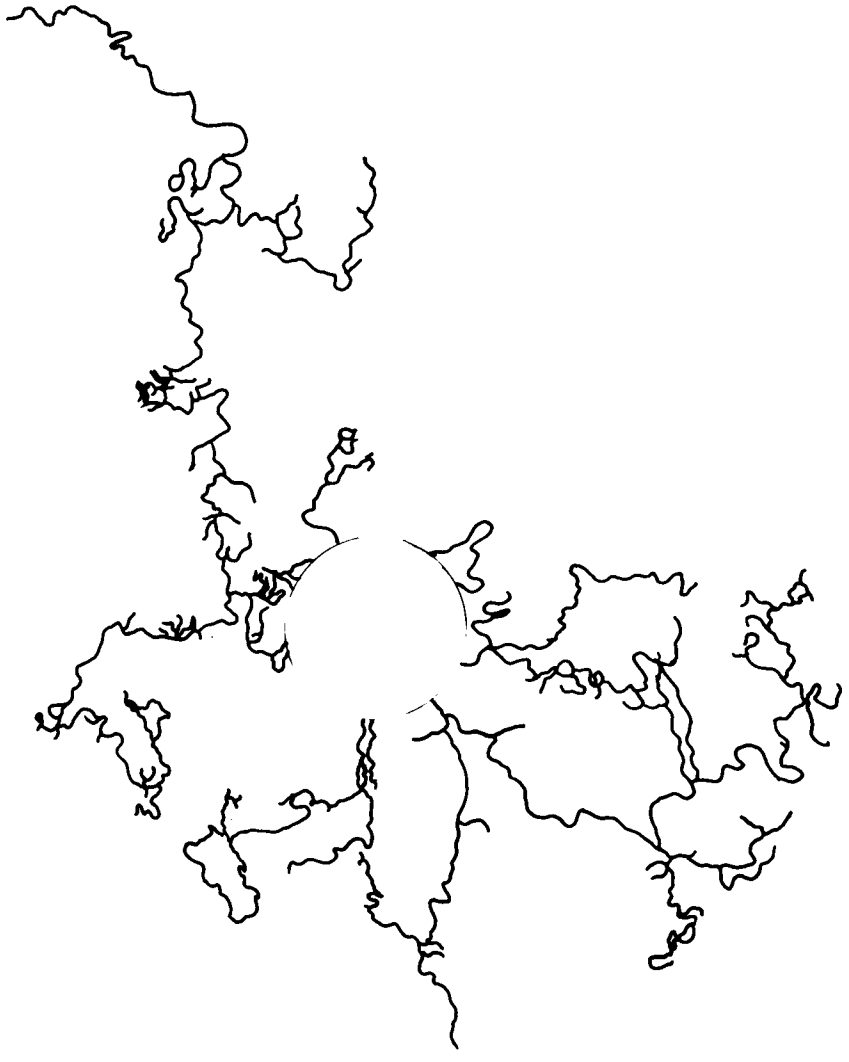

Plate 11. Dispersal trails of 45 female Acarus farris (Oud.). Total dispersal - 6876 mm. Plate reduced 55%.

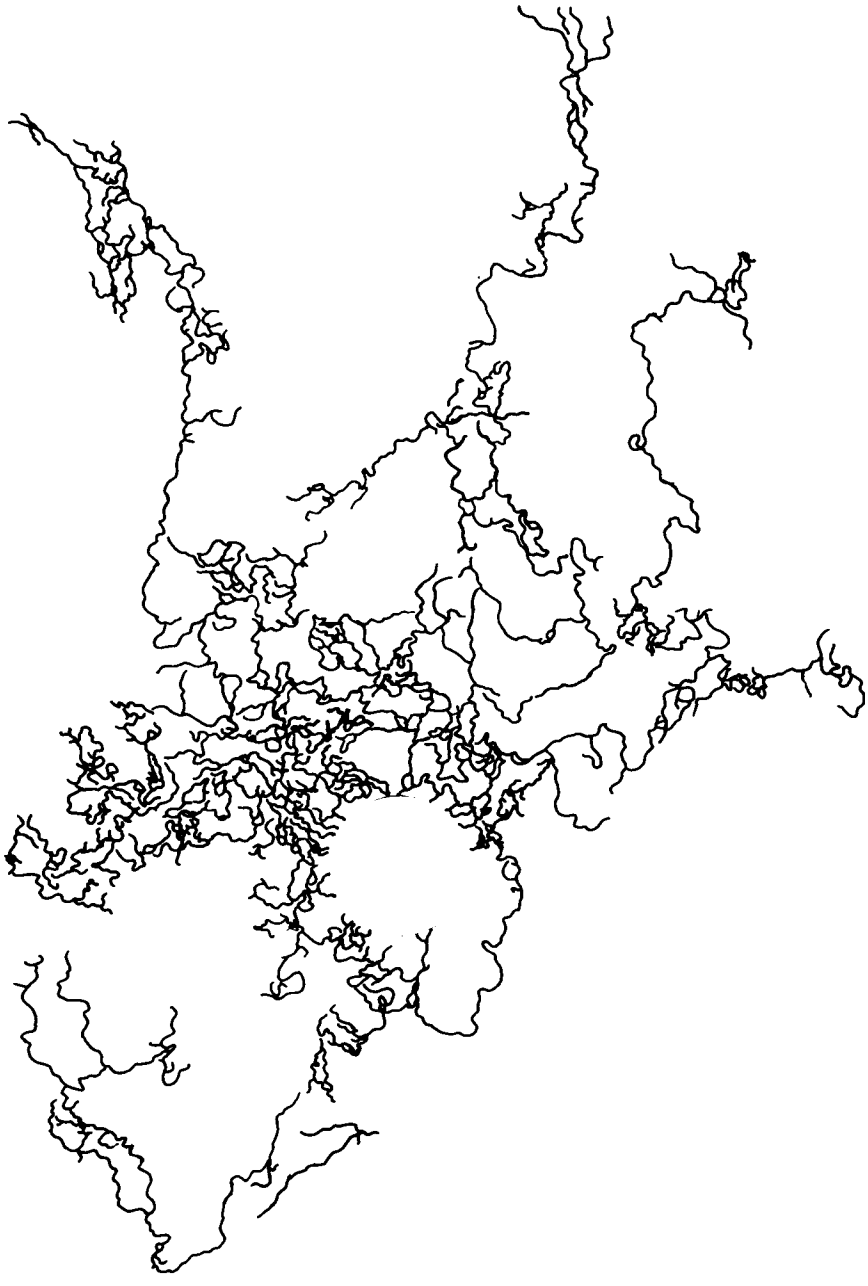

Table 15. Ratios and classes in dispersal experiments using Acarus farris (Oud.) and Cheletomorpha lepidopterorum (Shaw).

Ratios	Classes		
	Female	Female + male*	Female + male + predator*
8:1	45	46	40 + 5
6:1	35	36	30 + 5
4:1	25	26	20 + 5
2:1	15	16	10 + 5

*Equal numbers of females and males.

used to provide the illumination for the drawing of trails on the glass cover with a wax pencil. The trails were then traced onto a piece of tracing paper and set aside for measurements. Original measurements were done with a ruler, which gave only the linear distance covered in 24 hours. The curving, looping, and coalescence of the trails rendered the linear measurement inaccurate. A piece of graph paper with mm squares was then used to measure the actual length of the trails. A map reader, reported useful by Barker (1968), was tried, but the many turns and loops greatly reduced its accuracy and necessitated a return to counting of mm squares. The total amount of dispersal was determined for each pattern measured. The data was analyzed using an analysis of variance (Table 16).

There was a significant difference in the means of total dispersal of the ratios 2:1, 6:1, and 8:1 at the .05 level. The ratio 4:1 differed significantly from the 8:1 ratio at the .05 level, while the ratio 2:1 was significantly different from the ratio 8:1 at the .01 level.

There was no significant difference between the means of total dispersal in the classes (male + female, male + female + predator, and female alone) at the .05 or .01 level. The means of total dispersal within all the possible combinations of predator-prey ratios (2:1, 4:1, 6:1, 8:1) x sex combination classes (females, males + females, males + females + predators) are shown in Table 17. There was a significant difference at the .05 and .01 levels between 2:1 and 6:1 and at the

Table 16. Dispersal of Acarus farris (Oud.).
Analysis of variance: Three-factor (ratio; class; and run).

Source of variation	df	Mean square	F
Ratio	3	49927202.09	18.06*
Class	2	31047230.59	11.23*
Run	5	5436925.19	1.97 NS
Ratio x class	6	6246128.08	2.26 NS
Ratio x run	15	2271433.05	0.82 NS
Class x run	10	3708643.31	1.34 NS
Ratio x class x run	30	2763768.69	--
Error	0	2.00	--
Total	71		

*$P < 0.01$.

Table 17. Mean dispersal of Acarus farris (Oud.) in mm.

Class[a]	Ratio[b]			
	2:1	4:1	6:1	8:1
1	421.17	2165.67	3296.50	3374.33
2[c]	679.00	1211.50	3072.67	3079.33
3	1138.17	3764.00	4002.00	7555.33

[a] 1 = male + female
2 = male + female + predator
3 = female

[b] Number of A. farris to number of C. lepidopterorum.

[c] The predator was C. lepidopterorum.

.05 level between 2:1 and 8:1. Females alone had significant differences at the .05 level between 2:1 and the three other ratios, and between 4:1, 6:1 and 8:1. At the .01 level there were significant differences between 4:1 and 8:1 and between 6:1 and 8:1.

In comparing the means of total dispersal between the different predator-prey ratios and sex combination classes, no significant difference was found between the means of the classes at the 2:1 ratio. At the 4:1 level a significant difference was noted between the mean of male plus female plus predator and the mean of the all female class at the .05 level. There were no significant differences between the means of the classes in the 6:1 ratio. At the 8:1 ratio, a significant difference was found between the means of the all-female class and the means of the male plus female and male plus female plus predator class at both the .05 and .01 levels. The class females alone had the greatest amount of variation between the means of all the ratios, while the class male plus female had the second greatest amount. The class male plus female plus predators has the least degree of variation.

Discussion

Table 17 shows the results for dispersal in A. farris. The figures in the table are the mean distances traveled by the mites in a 24-hour period. A three-factor analysis of variance was used to

determine the effect of ratio of prey to predator, class, and run on the variances of the means shown in the table (Table 16).

The analysis of variance showed that ratio and class were highly significant in contributing to the variance. Females were found to be significantly more mobile than the mixed-sex class and mixed-sex plus predators. No significant difference between mixed-sex class and mixed-sex plus predators class could be demonstrated, although mites in the males plus females plus predators class are consistently the least mobile.

Females of A. farris are much more active in the dispersal universe than males (see predator-prey study). Mixed-sex classes are generally less mobile than females, but more mobile than males plus females plus predators, while males are the least mobile sex in the dispersal universe.

Each increasing ratio of prey to predator showed an increase in dispersal, but these differences were not all significant. There was a significant difference between the 2:1 ratio and the 6:1 and 8:1 ratios, while the 4:1 ratio was significantly different from the 8:1 ratio. I noticed that when mites were placed in the small plastic container for transferral to the universe, the rate of dispersal, or attempts at escape, increased as the number of mites in the container increased. The simple contact between individual A. farris and the frequency of this contact seems to trigger their dispersal from a population center.

Observations on the two species in mass culture indicate that A. farris responds to predators only when unsuccessfully attacked, after which they move with increased speed around the cells. In a large universe this increased movement would no doubt take the form of movement away from "danger" and across the universe, as was observed in this study.

C. lepidopterorum searching trails could be seen in the flour where they covered the area of the A. farris trails. The fate of all A. farris placed in the universe was not determined because the coalescence of their trails made individual trails impossible to follow and because the experimental procedure did not allow observations during the 24 hours after placement in the universe.

The results of this experiment indicate that dispersal in A. farris depends on both density and sex. An increase in the density of mites causes an increase in dispersal, but the amount of increase depends on whether the population consists of males, males and females, or females. Dispersal in A. farris is not dependent on the presence of C. lepidopterorum in ratios as high as 8:1 of predator to prey.

SUMMARY

1. Cheletomorpha lepidopterorum was studied to determine its effectiveness as a possible biological control agent of A. farris, a mite that infests stored grains and grain products.

2. C. lepidopterorum and Cheletophyes knowltoni can be differentiated on the basis of statistical data obtained from the four populations along with the morphological, behavioral, and biological data.

3. The temperature range 20 to 25°C and a relative humidity from 80 to 90% is ideally suited to the rearing of C. lepidopterorum, such conditions yielding a percent survival of eggs of up to 77%.

4. Mated females lay more eggs than unmated females at optimum environmental conditions.

5. C. lepidopterorum starved females survived for the longest period of time at a temperature/humidity combination of 20°C, 90% R.H.--31.33 days. Starved males lived 12 days at 20°C, 80% R.H.

6. C. lepidopterorum females will live for over four months at 5°C.

7. C. lepidopterorum reproduces both sexually and parthenogenetically. Parthenogenesis produces a higher proportion of males than does bisexual reproduction. These observations refute earlier published observations on C. lepidopterorum.

8. All stages of C. lepidopterorum are voracious predators and will revert to cannibalism to survive if prey is in short supply.

9. Immobile female deutonymphs of C. lepidopterorum are guarded by males for the purpose of mating after they emerge.

10. Female deutonymphs and emerging females of C. lepidopterorum may secrete a substance which attracts males.

11. There is evidence that A. farris, normally the prey of C. lepidopterorum, may feed on the immobile forms of the predator or may feed saprophytically on the predator.

12. C. lepidopterorum females consume from .471 A. farris per day at 5°C, 80% R.H. to 3.844 A. farris per day at 20°C, 80% R.H., and males consume slightly fewer.

13. The greatest dispersal is shown by A. farris females alone in the universe. Mixed-sex classes are usually less mobile than females, but more mobile than males plus females plus predator, while males are the least mobile sex in the dispersal universe.

14. The presence of C. lepidopterorum does not influence dispersal of A. farris.

CONCLUSIONS

Cheletomorpha lepidopterorum has many of the attributes necessary for being an effective predator of Acarus farris--a prey preference by stage, lack of effect on dispersal of prey population, prodigious potential for survival under adverse conditions, ability to search out and pursue prey mites, and voracious appetite.

All stages of C. lepidopterorum feed on A. farris. Females prefer nymphs and adults while males, along with the nymphal and larval stages, feed mainly on the immature stadia of A. farris. Predator larvae also feed on eggs of the prey, as do the other stages when post-embryonic prey is scarce. Even hypopi of A. farris, which are rejected by most predators, are eaten by nymphs and adults of C. lepidopterorum.

A. farris displays avoidance only when the predator is not successful in an attack. Indifference of the prey to the presence of the predator would help to explain why the presence of the predator failed to bring about a significant increase in the dispersal of A. farris in plexiglass universe experiments. It could be surmised that the presence of C. lepidopterorum would not cause grain mite infestations to spread into adjacent uninfested grain.

C. lepidopterorum has great potential for survival under adverse conditions of low relative humidity, cold, and starvation. By having a greater resistance to desiccation than the graminivorous mites, C.

lepidopterorum can survive when A. farris cannot, and then increase again when food is available. In addition to this advantage, because it prefers a somewhat lower relative humidity than Acarus farris, it may be found around the edges of infestations as well as in them. Consequently, when food shortages, overcrowding, and toxic waste products produced in the moist rotting grain or grain products force the migration of the graminivorous species into the drier, peripheral areas, C. lepidopterorum is present to attack them.

Even though C. lepidopterorum is a poor predator at low temperatures, moving and feeding very little, it may live for long periods under such conditions, recover when it becomes warmer, and begin to feed and reproduce. This ability to live for extended periods without food is an indication of the adaptation of C. lepidopterorum to its environment, in which the number of prey mites may vary seasonally.

The survival of predators in the absence of prey is very important in the overall role of the species as a predator. Not only can C. lepidopterorum survive without food, but it also will feed on species other than its preferred prey and resort to cannibalism for survival. When prey numbers are low, adult females feed on all stages of its own kind, males feed on all but adult females, and nymphs and larvae prey on other nymphs, larvae, and eggs. This "pecking order" enhances the survival potential of the females.

In addition to feeding on all stages of A. farris, eliciting little or no escape response from the prey, and high survival potential, C. lepidopterorum has another characteristic which makes it an effective predator of A. farris: the ability to search out, pursue, and immobilize its prey. Prey is captured when it comes into contact with the predator or when it passes near the predator's outstretched legs I. If the initial attack is unsuccessful, C. lepidopterorum often pursues the potential prey for a short distance. Attacked mites are quickly immobilized and do not recover, even if released. This immobilization may be the result of a toxic secretion as reported for C. knowltoni by Beer and Dailey (1956).

On the basis of the number or prey mites consumed in predator-prey experiments, it may be surmised that the voracious appetite of C. lepidopterorum marks it as a predator that greatly reduces the number of prey mites in a population if conditions are suitable.

Being an arrhenotokous species, C. lepidopterorum usually requires fertilization to produce female progeny. Mating is accomplished under a variety of circumstances, one of which involves the guarding of a quiescent female deutonymph by a male. Guarding is significant for three reasons: (1) it ensures the protection of the female until the time of emergence; (2) it ensures that most females will be inseminated, which provides for the production of some females in the next generation; and (3) guarding ensures that, through natural selection,

only the most successful combatants or defenders of their territories mate with females.

C. lepidopterorum has several disadvantages which should be considered in an evaluation of its potential as a predator of grain mites: (1) a large prey-to-predator ratio tends to reduce its effectiveness because constant interaction with the prey causes ceaseless motion, poor feeding, and low fecundity; (2) it is inactive and feeds little at temperatures of 5°C and below, a temperature at which Acarus farris can live and reproduce; (3) its effectiveness in the presence of other cheyletid predators such as Cheyletus eruditus is not known, but Hughes (1961) observed C. eruditus preying upon C. lepidopterorum; (4) its resistance to pesticides is not known but, on the basis of observations on other cheyletid mites, it is probably more sensitive to insecticides than are the grain mites on which it feeds.

This study of the biology and behavior of C. lepidopterorum has obtained basic information on (1) the rate of development; (2) fecundity; (3) progeny of mated and unmated females; (4) mating behavior; (5) behavior in mass culture; (6) attraction of males to immobile female deutonymphs and newly-emerged females; (7) predator-prey relationships; (8) dispersal of A. farris in the presence and absence of C. lepidopterorum. All the experiments were conducted in the laboratory. The results of these experiments indicated that C. lepidopterorum has shown enough potential to justify testing under field conditions.

Predator-prey experiments in grain bins and feed storage areas should further show its effectiveness as a predator of graminivorous mites.

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Appendix Table 1. Life cycle of Cheletomorpha lepidopterorum (Shaw) at 30°C, 90% R.H. in hours. Series I.

Mite no.	Egg	Larva	Rest	Protonymph	Rest	Deutonymph	Rest	Adult
1	48	60	18	36	18	a		
2	48	36	18	108	18	18	18	♂
3	72	84	18	36	18	18	18	♂
4	48	144	18	108	18	36	36	♀
5	b							
Average and standard deviation	54± 10.39	81± 40.14	18	72± 36.00	18	24± 8.48	24± 8.48	

[a] Lived 96 hours, then died.

[b] Egg did not hatch. It was accidentally introduced into a cell with another egg.

Appendix Table 2. Life cycle of Cheletomorpha lepidopterorum (Shaw) at 30°C, 90% R.H. in hours. Series II.

Mite no.	Egg	Larva	Rest	Protonymph	Rest	Deutonymph	Rest	Adult
1	60	36	18	36	a			
2	60	36	18	36	a			
3	60	60	18	36	18	a		
4	60	132	18	96	18	a		
5	60	60	18	36	a			
6	60	60	a					
7	60	84	18	36	a			
8	60	60	18	60	a			
9	60	60	18	36	18			♂ [b]
10	60	60	18	36	a			
Average and standard deviation	60	64.8± 25.85	18	45.7± 19.41				

[a] Lived 24 hours, then died.

[b] Only one nymphal stage observed.

Appendix Table 3. Life cycle of Cheletomorpha lepidopterorum (Shaw) at 30°C, 80% R.H. in hours. Series I.

Mite no.	Egg	Larva	Rest	Protonymph	Rest	Deutonymph	Rest	Adult
1	48	84	18	60	18	a		
2	60	60	18	84	b			
3	60	84	36	36	b			
4	48	84	18	60	18	c		
5	d							
6	d							
Average and standard deviation	54.0± 6.00	78.0± 10.39	22.5± 7.79	60.0± 16.97	18			

[a] Lived 60 hours, then died.

[b] Died while in resting stage.

[c] Lived 84 hours, then died.

[d] Eggs did not hatch.

Appendix Table 4. Life cycle of Cheletomorpha lepidopterorum (Shaw) at 30°C, 80% R.H. in hours. Series II.

Mite no.	Egg	Larva	Rest	Protonymph	Rest	Deutonymph	Rest	Adult
1	48	60	36	36	a			
2	96	60	a					
3	84	36	a					
4	60	60	18	18	18	b		
5	48	108	18	18	18	c		
6	48	c						
7	48	84	18	d				
8	48	108	18	18	18	b		
9	48	108	a					
10	48	84	18	36	18	36	18	♂
11	e							
12	e							
13	e							
Average and standard deviation	57.6± 16.8	78.67± 24.73	21.0± 6.71	25.2± 8.82	18	36	18	

[a]Died while in quiescent interval.
[b]Lived 60 hours, then died.
[c]Lived 36 hours, then died.
[d]Lived 48 hours, then died.
[e]Eggs did not hatch.

Appendix Table 5. Life cycle of Cheletomorpha lepidopterorum (Shaw) at 20°C, 90% R.H. in hours. Series I.

Mite no.	Egg	Larva	Rest	Protonymph	Rest	Deutonymph	Rest	Adult
1	96	84	36	36	18	60	18	♀
2	96	36	36	60	18	36	36	♀
3	216	36	36	60	36	18	18	♂[a]
4	72	60	b					
5	c							
6	c							
Average and Standard deviation	120± 56.28	54± 19.89	36	52± 11.31	24± 8.48	38± 17.20	24± 8.48	

[a] Observed two nymphal stages.

[b] Died while in resting stage.

[c] Eggs did not hatch.

Appendix Table 6. Life cycle of Cheletomorpha lepidopterorum (Shaw) at 20°C, 90% R.H. in hours. Series II.

Mite no.	Egg	Larva	Rest	Protonymph	Rest	Deutonymph	Rest	Adult
1	96	60	18	a				
2	120	60	18	60	36			♂[b]
3	96	c						
4	96	36	18	36	18	60	18	♀
5	120	36	18	18	36	60	18	♀
6	d							
7	96	36	36	60	36			♂[b]
8	96	36	18	36	18	60	36	♀
9	96	36	18	60	36			♂[b]
10	108	36	36	36	18	18	36	♂[e]
11	d							
12	d							
Average and standard deviation	102.7± 9.98	42± 10.39	22.5± 7.79	43.7± 15.28	28.3± 8.91	49.5± 18.19	27± 9.00	

[a] Lived 36 hours, then got smashed under cover glass.
[b] Only one nymphal stage observed.
[c] Lived 24 hours, then died.
[d] Eggs did not hatch.
[e] Observed two nymphal stages.

Appendix Table 7. Life cycle of Cheletomorpha lepidopterorum (Shaw) at 20°C, 80% R.H. in hours. Series I.

Mite no.	Egg	Larva	Rest	Protonymph	Rest	Deutonymph	Rest	Adult
1	72	96	18	a				
2	96	96	18	b				
3	120	120	18	60	36			♂ c
4	72	72	36	60	36			♂ c
5	48	d						
6	e							
7	168	84	18	a				
8	e							
9	e							
10	e							
11	e							
12	e							
13	e							
Average and Standard deviation	96± 39.19	93.6± 15.92	21.6± 7.20	60	36			

[a] Lived 36 hours, then died.
[b] Lived 48 hours, then died.
[c] Only one nymphal stage observed.
[d] Lived 48 hours, then was smashed under cover glass.
[e] Eggs did not hatch.

Appendix Table 8. Life cycle of Cheletomorpha lepidopterorum (Shaw) at 20°C, 80% R.H. in hours. Series II.

Mite no.	Egg	Larva	Rest	Protonymph	Rest	Deutonymph	Rest	Adult
1	[a]							
2	96	84	18	60	36			♂[b]
3	96	84	18	60	36			♂[b]
4	96	60	36	18	18	60	18	♀
5	96	84	18	36	36			♂[b]
6	96	84	18	60	36			♂[b]
7	96	60	36	60	18			♂[b]
8	96	84	18	60	18			♂[b]
9	120	60	[c]					
10	[a]							
11	[a]							
12	[a]							
Average and standard deviation	99± 7.94	75± 11.62	23.1± 8.13	50.6± 15.66	28.3± 8.91	60	18	

[a] Eggs did not hatch.

[b] Only one nymphal stage observed.

[c] Died while in resting stage.

Appendix Table 9. Life cycle of Cheletomorpha lepidopterorum (Shaw) at 25°C, 80% R.H. in hours. Series I.

Mite no.	Egg	Larva	Rest	Protonymph	Rest	Deutonymph	Rest	Adult
1	132	36	18	36	18	36	36	♀
2	132	60	36	108	60			♂[a]
3	108	60	18	36	18	60	36	♀
4[b]	84	108	36	108	36			♂[a]
5[b]	84	36	18	84	18	18	36	♀
6	c							
Average and standard deviation	108.0± 21.47	60± 26.29	25.2± 8.82	74.4± 32.55	30± 16.54	38± 17.20	36	

[a] Only one nymphal stage observed.

[b] Accidently placed two eggs in one cell and obtained two adult mites.

[c] Egg did not hatch.

Appendix Table 10. Life cycle of Cheletomorpha lepidopterorum (Shaw) at 25°C, 80% R.H. in hours. Series II.

Mite no.	Egg	Larva	Rest	Protonymph	Rest	Deutonymph	Rest	Adult
1	108	60	18	84	36			♂[a]
2	[b]							
3	168	[c]						
4	108	[c]						
5	108	84	18	84	36			♂[a]
6	132	60	18	84	36			♂[a]
7	132	60	18	60	18	36	60	♀
8	108	60	36	84	36			♂[a]
9	108	60	36	[d]				
10	[b]							
Average and standard deviation	121.5± 20.29	64± 8.94	24± 8.48	79.2± 9.60	32.4± 7.20	36	60	

[a] Only one nymphal stage observed.

[b] Eggs did not hatch.

[c] Lived 24 hours, then escaped through broken cover glass.

[d] Lived 96 hours, then died.