HILGARDIA

A JOURNAL OF AGRICULTURAL SCIENCE PUBLISHED BY THE CALIFORNIA AGRICULTURAL EXPERIMENT STATION

Volume 52 • Number 9 • December 1984

Biology and Temperature Responses of *Chelonus kellieae* and *Chelonus phthorimaeae* (Hymenoptera: Braconidae) and Their Host, the Potato Tuberworm, *Phthorimaea operculella* (Lepidoptera: Gelechiidae)

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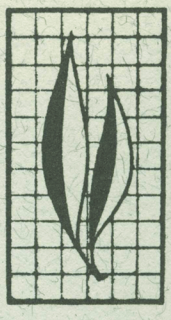
UNIVERSITY OF CALIFORNIA DIVISION OF AGRICULTURE AND NATURAL RESOURCES



Comparative studies were conducted on the biologies and population growth potentials of *Chelonus phthorimaeae* Gahan, an indigenous North American parasite, and *C. kellieae* Marsh, an imported parasite from Costa Rica. Both species are primary, solitary, egg-larval endoparasites of the potato tuberworm, *Phthorimaea operculella* (Zeller).

Eggs of both species are hymenopteriform. In the laboratory, superparasitization was noted within the host egg; however, a single parasite larva develops within the haemocoel of the host larva. The parasite larva emerges before host pupation and constructs a silken-white cocoon within that of the host. There are three larval instars, the first being caudate-mandibulate, later becoming vesiculate-mandibulate. The second and third are mandibulate, with the third possessing spines and setae. The pupae are exarate. Developmental time from egg to adult female emergence is 22 days and 26 days for *C. phthorimaeae* and *C. kellieae,* respectively, at 26.7±1°C, 50% RH. Morphology of the immature stages and host relationships are presented. Parasitization of *P. operculella* by each species resulted in reduction of the size of the fourth instar host larvae. Optimum number and age of host eggs for maximum production of parasite progeny was 150 host eggs, 0-24 hours old, for *C. phthorimaeae,* and 50 host eggs, 0-24 hours old, for *C. kellieae.* Neither species host feeds nor are a carbohydrate source and free water prerequisites for progeny production. Females of both species require a carbohydrate source and free water for greatest longevity. Observations of the mating behavior disclosed males are polygamous and females monogamous. The mating ritual, searching, and ovipositional behavior are described. Both species are arrhenotokous with virgin and mated female *C. kellieae* producing approximately equal numbers of progeny, while mated female *C. phthorimaeae* produced a greater number of progeny than did virgin female *C. phthorimaeae. Chelonus phthorimaeae* and *C. kellieae* exhibited a preovipositional period of 2 hours and 4 hours, respectively, prior to production of female progeny.

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Biology and Temperature Responses of *Chelonus kellieae* and *Chelonus phthorimaeae* (Hymenoptera: Braconidae) and Their Host, the Potato Tuberworm, *Phthorimaea operculella* (Lepidoptera: Gelechiidae)[1]

INTRODUCTION

IN SOUTHERN CALIFORNIA the potato tuberworm, *Phthorimaea operculella* (Zeller), supports a parasite complex that consists of at least 12 species (Graf 1917; Oatman and Platner 1974). Of these, *Chelonus phthorimaeae* Gahan is the only egg-larval parasite. *Chelonus phthorimaeae* occurs throughout North America on hosts such as *Kieferia glochinella* (Zeller) and *Ancylis comptana fragariae* (Walsh and Riley), in addition to *P. operculella* and the tomato pinworm, *Kieferia lycopersicella* (Walsingham) (Muesebeck, Krombein, and Townes 1951; Thompson 1953). Little has been published on *C. phthorimaeae* subsequent to the original description by Gahan (1917) and the brief report by Graf (1917) who listed it as *C. shoshoneanorum* Viereck.

In April 1973, an undescribed species of *Chelonus* was received at the Division of Biological Control, University of California, Riverside. The host material had been collected by E. R. Oatman from potato foliage near Cartago, Costa Rica. After the release from quarantine on 8 June, 1973, the species was cultured for biological studies and subsequent colonization in southern California. Marsh (1979) described the species as *Chelonus kellieae.*

Acquisition of *C. kellieae* provided an opportunity to study its biology and morphology and the influence of temperature on development, reproduction, and survival, to compare it with that of its ecological homologue, *C. phthorimaeae.*

[1]Accepted for publication October 18, 1984.

MATERIALS AND METHODS

Environmental Conditions

Stock cultures of the host and parasite were maintained in an insectary room at 26.7±1°C and 50% RH. Light was supplied by eight 40-watt, cool, fluorescent tubes, and was regulated by an automatic time switch set for alternating periods of 12 hours of light and 12 hours of darkness. A fan circulated air in the room to prevent stratification of air.

Cultures of host

Cultures of *P. operculella* were maintained in the insectary on White Rose and Russett potato tubers, using techniques developed by Platner and Oatman (1968). Adult *P. operculella* were placed in cages which held muslin cloth that had been soaked in potato juice to stimulate oviposition thereon. These "egg cloths" were removed daily and the eggs used to establish subcultures of the parasites or for various experiments.

Cultures of parasite

Chelonus kellieae and *C. phthorimaeae* were handled identically throughout these studies. Studies of both species were conducted concurrently in separate spaces with identical conditions and repeated for replication. A culture of *C. kellieae* has been maintained in the insectary since its release from quarantine in June 1973. The culture of *C. phthorimaeae* was obtained in 1977 from host material collected from potato plants grown on the University of California's field station at Moreno.

The parasite colonies were maintained in wooden cage "emergence units" (41.9 × 41.9 × 35.6 cm) with glass tops, lateral panels of organdy cloth for ventilation, and a detachable section on one side to facilitate manipulation of the material inside the emergence unit without letting the insects escape. White sand was distributed evenly over the bottom of the emergence units for pupation of the larvae. To maintain the culture, female parasites, newly emerged from hosts, were removed daily and placed in a wooden cage "sting unit" (30.5 × 35.6 × 27.9 cm). The sting unit was similar in construction to the emergence unit, except that its top was covered with black cloth to eliminate light. The back organdy panel also was covered with black cloth, except for a 10.2 × 10.2 cm area which permitted light to penetrate. An egg cloth (ca. 10 × 10 cm) with newly oviposited host eggs was fastened to the inside of this lighted area of the sting unit. Female parasites were attracted to this lighted area and, upon contact with the egg cloth, oviposited in the host egg. After a 24-hour exposure, the host egg cloth was removed and placed on punctured tubers on an inverted galvanized wire tray (12 × 12 cm) within the emergence unit. These procedures were repeated periodically, using one emergence unit and one sting unit for each species.

When needed, virgin female or male parasites were obtained by isolating cocoons in clear gelatin capsules (size 000) and holding them until the parasite emerged.

Experimental Rearing Unit

White Rose potato tubers (7 × 8 cm long) were punctured with a tack-studded board (Finney, Flanders, and Smith 1947) to ensure adequate larval infestation. Afterwards, an egg cloth containing parasitized eggs was pinned to the tuber. The tuber with the egg cloth was then placed within a clear, polystyrene container, the "holding unit." This unit measured 7.9 cm in diameter at the bottom, 8.9 cm in diameter at the top, and was 9.5 cm high. The bottom opening of the container was covered with organdy to provide ventilation. The holding unit was inverted to fit tightly inside the rim of a Petri dish cover. The inside of the Petri dish was paper-lined and covered with fine white sand to facilitate pupation of the host larvae. After pupation, the polystyrene container was removed and replaced with the bottom of a Petri dish. This unit was stored in the insectary until host or parasites emerged and died. The adult parasites were then counted and sexed.

Manipulating host eggs and adult parasites

Host eggs, recently oviposited (0-24 hours) on muslin cloth, were utilized in various experiments. After oviposition, host eggs were held in the insectary until they reached the required age for a given experiment. A white card (4 × 2.5 cm) was glued (Wilhold , Chicago, Illinois) to the back of an egg cloth, trimmed to fit the card. Host eggs were counted with the aid of a binocular dissecting microscope until the desired experimental number was achieved and excess eggs were then removed with a camel hair brush. The egg card then was placed within a parasite "ovipositional unit." This unit was a clear, polystyrene vial (44.4 cc) with a snap-on cap. The vial was vented by cutting a hole in the cap and covering the hole with a 100-mesh, brass screen. Honey was forced through the screen to provide food. A hole (9 mm in diameter) at the bottom of the vial was used to introduce the parasites through. Afterwards, a glass, shell vial (0.92 cc) was filled with distilled water, plugged with cotton, and inserted in the hole to provide a water wick. After parasitization, the egg card was removed and placed on a potato tuber within a holding unit.

Parasite adults were manipulated with the aid of a mouth aspirator. To immobilize them for examination, they were placed on an ice pack. No anesthesia was used at any time.

Parasites' immature morphology and relationship with host

This study was conducted at 26.7±1°C, 50% RH, and a 12-hour photoperiod. Immature stages of both species and their relationship with the host was followed by dissecting host eggs and larvae every 6 and 24 hours, respectively, in a 0.9 percent saline salution. Eggs, larvae, and head capsules and mandibles of larvae were measured, using a compound microscope fitted with an ocular micrometer.

Host larvae were extracted from tubers by heat (Platner, Greany, and Oatman 1969). The host larvae were fixed in Bouins solution for 4 to 8 hours, washed in 70 percent EtOH, and stored in 90 percent EtOH until dissection. A sodium hypochlorite solution was used to extract host pupae from the sand substrate. Host cocoons were opened longitudinally to study final instars and pupae of the parasite species. The terminology of Finlayson and Hagen (1977) was used to describe the parasite head structures.

Effect of food, water on adult parasite longevity

To determine the effects of food (not specific dietary requirements) on adult longevity, three treatments were used that included: (1) neither honey nor water, (2) honey but no water, and (3) both honey and water. Newly emerged males and females were observed separately in an ovipositional unit by subjecting 25 of each species and sex to a given treatment. Counts of mortality and survivors were made every 24 hours.

Optimum host age and number for parasitization

To determine optimum host egg number and age for parasitization, an egg card with one of four host egg-ages (0-24, 24-48, 48-72, and 72-96 hours old) at one of four host egg-numbers (25, 50, 100, and 150 eggs) was placed in an ovipositional unit with a mated 4-day-old female parasite for 24 hours. After exposure, the host egg card was placed on a potato tuber in a holding unit in the insectary. This experiment was replicated 15 times at each of the above host age-number combinations for a total of 240 observations. The number and sex of the emerging progeny were recorded.

In previous studies of potato tuberworm parasites (Leong and Oatman 1968; Oatman, Platner, and Greany 1969; Odebiyi and Oatman 1972, 1977; Oatman and Platner 1974; Cardona and Oatman 1975), optimum host age and numbers for parasitization were determined as noninterreacting factors. In the present study a factorial design was employed to determine interacting effects of age and numbers of host eggs on progeny production for each species of parasite. Statistical analysis of this experiment was done using a 4×4 factorial analysis design (Sokal and Rohlf 1969). Duncan's Multiple Range Test (1955) was applied for separation of mean values of resulting parasite progeny for each combination of age and numbers of host eggs. The means were ranked and homogeneous subgroups were generated at the 5 percent level. Effects of combinations of host age and numbers on the percentage of female parasite emergence were tested by the analysis of variance, using an arc sine transformation (Sokal and Rohlf 1969). The means were ranked using Duncan's Multiple Range Test at the 5 percent level.

Effect of food, water on adult parasite fecundity

To determine whether a food source was necessary for progeny production, two treatments were used that included: (1) neither honey or water or (2) honey and water. Newly emerged mated females were observed separately in an ovipositional unit by subjecting 10 of each species to a given treatment. Females observed to copulate with males within 30 minutes of emergence were deemed mated. Every 24 hours host egg cards containing optimum egg number and age combination as previously defined were replaced with identical egg cards in this ovipositional unit. Exposed eggs were held in a holding unit until progeny emergence was complete. This procedure was repeated until all female parasites given access to treatment number one had died; the study was then terminated.

Progeny resulting from mated and unmated adult parasites

To determine the number of progeny resulting from mated and unmated (virgin) females for each species, each of 10 mated females and 10 virgin females was placed in an ovipositional unit containing an egg card with the optimal egg number and age combination. Virgin females were obtained from cocoons previously isolated in gelatin capsules. Every 24 hours, each egg card was replaced with an identical card. Exposed host eggs were held in holding units until progeny emergence was complete and numbers and sex were recorded. This procedure was repeated daily until the last female died.

Determining Preoviposition Period

To determine the occurrence and duration of a preoviposition period for each parasite species, parasite cocoons were isolated in gelatin capsules. Upon emergence, 10 virgin females and 10 mated females were selected for study. At the initiation of the photophase, each female was placed in an ovipositional unit with an egg card containing the optimum combination of host egg numbers and age. Every hour during the 12-hour photoperiod host eggs were replaced with identical egg cards. In this way were determined the age of each female when progeny were first produced and the duration of her production.

Constructing life tables at various temperatures

This study was concerned with the effects of temperature on the potential for population growth of *C. kellieae* and *C. phthorimaeae* compared with that of their host, *P. operculella.* Thus, life tables were calculated for each parasite species to compare population growth rates at each of the various temperatures, and, therefore, performances in a particular environment.

Development of *C. kellieae* and *C. phthorimaeae* was investigated at 21.1±1, 23.9±1, 26.7±1, 29.4±1, and 32.2±1°C, 50% RH, and a 12-hour photoperiod. These studies were conducted in "constant" temperature cabinets and monitored every 24 hours with a hygrothermograph. Life tables were also developed for both species at each of the temperatures.

To follow development of the parasites, two groups of potato tuberworm egg (0-24 hours old) were separately exposed for 2 hours to numerous female parasites of *C. kellieae* and *C. phthorimaeae.* These host eggs were then placed in the temperature cabinets at the previously mentioned temperatures. Every 6 hours thereafter, a few host eggs were dissected and examined for the presence of parasite eggs. This procedure was repeated until the presence of first instar parasite larvae was noted. Several potatoes were then infested with first instar parasitized potato tuberworm larvae. Every 24 hours thereafter, one potato was removed from each of the temperature cabinets and the host larvae were recovered from the potato by heat extraction (Platner, Greany, and Oatman 1969). The host larvae were dissected and the instar stage and duration of development of both host and parasite at each of the respective temperatures were recorded. This procedure was repeated until host larval development was completed. Some tubers were left undisturbed in each temperature cabinet until adult parasite emergence.

Life tables for both species of parasites were constructed at 21.1±1, 23.9±1, 26.7±1, 29.4±1, and 32.2±1°C, 50% RH, and 12-hour photoperiod. Immature parasite survivorship was determined by subjecting host eggs (0-24 hours old) to a series of ovipositing female parasites of each species. Host eggs were on a grid pattern in an arena and observations were made of parasitization. This procedure took approximately 6 hours and was replicated 10 times for each respective temperature. Eggs which were parasitized, nonparasitized, and superparasitized were noted. Those nonparasitized or superparasitized to a great extent were discarded. The first 50 host eggs of this sample observed to be parasitized were placed with a potato in a holding unit that was then placed in the respective temperature cabinets. The parasite cocoons were isolated in gelatin capsules and the resulting number of parasite progeny emerging from the 50 eggs yielded the immature survivorship.

To determine daily progeny production, sex ratio, and adult longevity of each parasite species at the five various temperatures, parasite cocoons were isolated in gelatin capsules (000) at each of the temperature regimes as previously described and 10 adult pairs (male and female) were selected at emergence. Every 24 hours, each pair was transferred to an identical ovipositional unit with the optimal number and age of host eggs in each of the respective temperature cabinets. This procedure was done for each species. After parasite exposure, host eggs were held with potato tubers in a holding unit in each of the respective temperature cabinets until progeny emergence was complete. This procedure was repeated daily until all ovipositing female parasites died.

Data on development, survivorship, fecundity, and progeny sex ratio for each species of parasites at each temperature were used to construct life tables. Statistics were calculated from formulae as given by Krebs (1978) and performed by Cardona and Oatman (1975) and Odebiyi and Oatman (1977).

Cardona and Oatman (1975) constructed life tables for *P. operculella* at various temperatures and relative humidities except at 21.1±1°C and 50% RH. To complete this study a life table was constructed at this temperature and relative humidity.

RESULTS AND DISCUSSION

Describing Adult Parasites

Marsh (1979) described both sexes of *C. kellieae* in detail. In general appearance adults (fig. 1) are black with honey-yellow basitarsus, tibia, and femur. Wings are hyaline. Both males and females are approximately 3 mm long. The female's antennae are 14 segmented and average 1.64 mm in length; those of the male are 16 segmented and average 2.64 mm long.

Gahan (1917) described both sexes of *C. phthorimaeae.* Adults (fig. 2) are black with blackish or dark brown legs, except the tibia which are testaceous and have a narrow testaceous band on the femur. Wings are hyaline. Body length of both sexes ranges from 2.6 to 3.3 mm. Female antennae are 16 segmented and average 2.6 mm in length, extending back at least to the middle carapace. McComb (1968) also described *C. phthorimaeae,* comparing it with *Chelonus empherus* McComb.

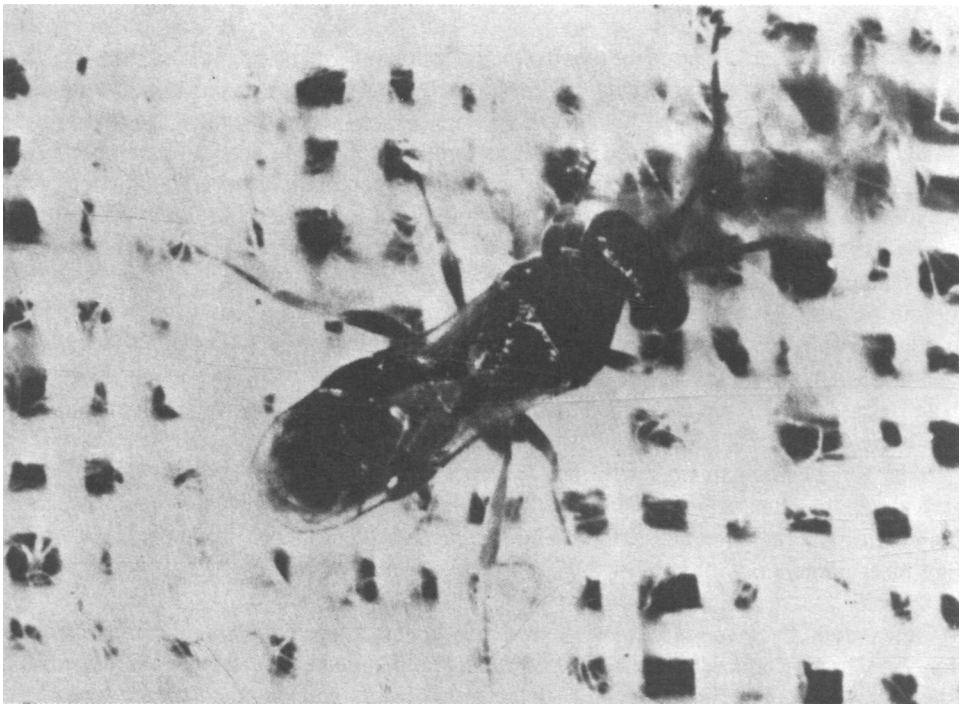

Fig. 1. Adult female *Chelonus kellieae.*

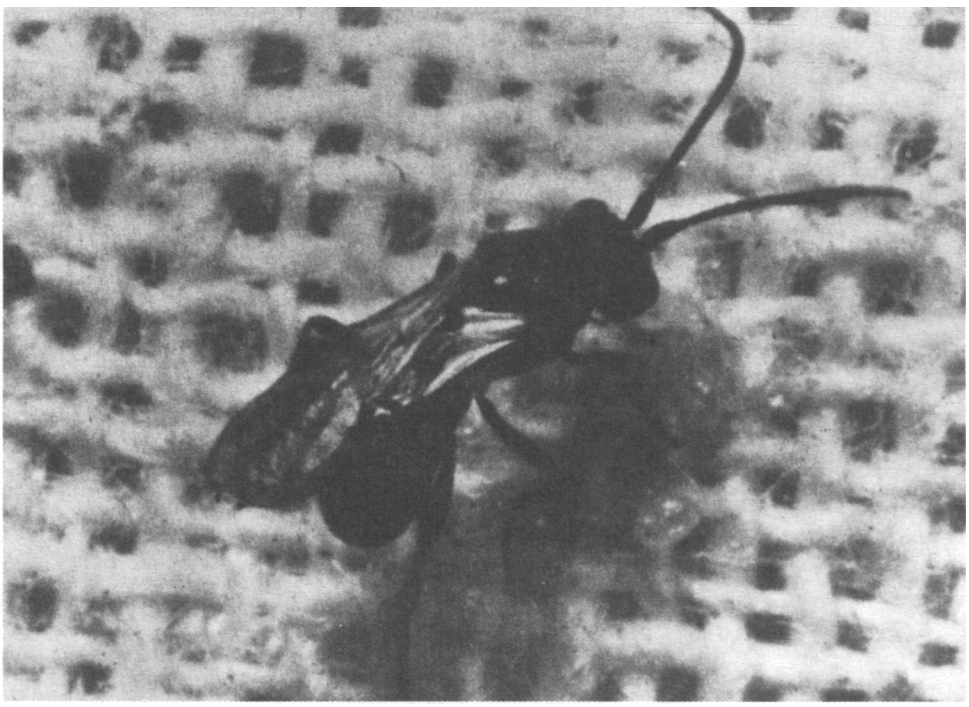

Fig. 2. Adult female *Chelonus phthorimaeae.*

Immature morphology, parasite relationships with the host

Chelonus kellieae. Mean duration from oviposition to adult emergence was 26 days (range, 24-30 days). Males emerged 2 days before females. Mean duration of the developmental stages: egg, 28 hours; first instar, 11 days; second instar, 3 days; third (last) instar, 2 days; and pupa, 9 days. This parasite is an egg-larval parasite, with only one egg being laid with each ovipositional thrust. Superparasitization occurred; however, it did not prevent eclosion of parasite eggs, and several first instars were found in a host egg. These supernumerary parasite larvae occurred only in the host egg, as only one larva developed per host larva.

The parasite larva was found floating free in all areas of the body cavity of the host, but later instars were present, primarily in the host's posterior part. The parasite larva did not feed on vital organs of the host until the parasite was ready to pupate. When the host larva started to spin its cocoon before pupation, it was killed by the endoparasite. The host's integument and head capsule were attached to the parasite cocoon.

Egg: The egg is hymenopteriform (Clausen 1940), translucent, cylindrical, and round at both ends. The surface is smooth, nonsculptured, and the cephalic region is larger than the caudal region at oviposition. The difference becomes more pronounced with time. Egg measurements: width, $\overline{X} = 0.074 \pm 0.007$ mm; length, $\overline{X} = 0.179 \pm 0.019$ mm ($n = 100$).

First instar: Early stages are caudate-mandibulate, later becoming vesiculate-mandibulate. The head is twice as long as wide. The sclerotized mandibles are laterally hinged and inwardly curved. The first instar initially consists of six segments and a caudal appendage. After several days, the body segments differentiate to form a definite head, thorax, and abdomen. The head capsule retains its size, although the rest of the body enlarges. There is a thoracic segment and three abdominal segments in addition to a segment bearing the anal vesical (fig. 3). The mandibles and labial processes are discernible in the first instar. The labium is curved inward from the regions near the base of the mandible. The anteriorly rounded labium extends beyond the curve of the mandible and has two separate processes on its outer margin. The head is free of setae or spines. Head capsule measurements: length, $\overline{X} = 0.033 \pm 0.001$ mm; width, $\overline{X} = 0.069 \pm 0.001$ mm ($n = 109$). Mandible measurements: length, $\overline{X} = 0.029 \pm 0.001$ mm ($n = 109$).

First instars were found in the host's haemolymph between the first and eighth abdominal segments. No visible damage to the host was noted. The first larval molt occurred just as the host entered its fourth and final instar.

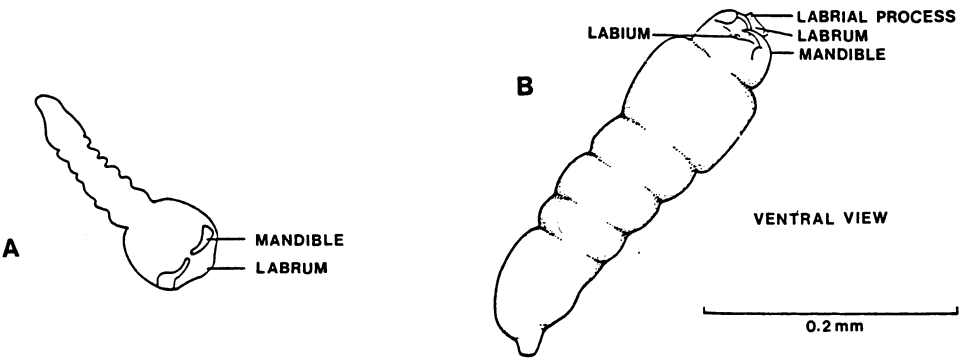

Fig. 3. First instar of *Chelonus kellieae:* A = early first instar; B = late first instar.

Second instar: This stage is characterized by a relatively straight, rounded body which lacks spines or setae (fig. 4). The body is white, and consists of a head and three thoracic and 10 abdominal segments, including an anal vesicle. Mandibles are weakly sclerotized. Head capsule measurements: length, $\overline{X} = 0.028 \pm 0.005$ mm; width, $\overline{X} = 0.260 \pm 0.002$ mm (n = 46). Mandible measurements: length, $\overline{X} = 0.097 \pm 0.002$ mm (n = 46).

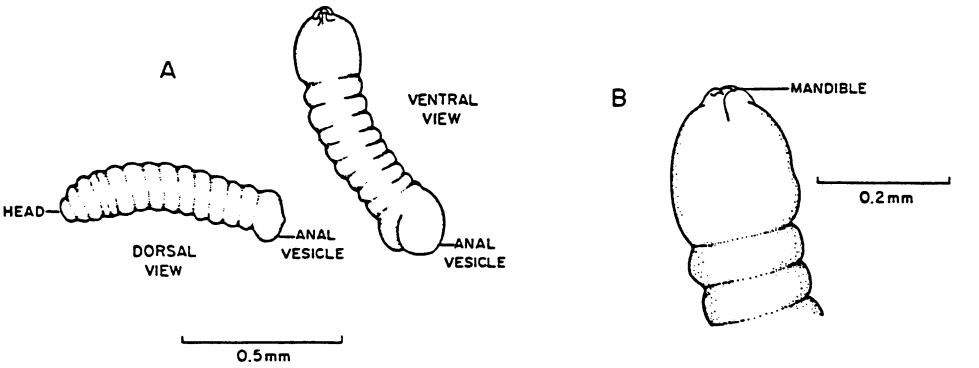

Fig. 4. Second instar of *Chelonus kellieae:* A = dorsal and ventral views; B = head region.

Third instar: This final instar consists of both an internal and external phase in relation to the host. The second instar larval molt occurred about 2 days after the host larva left the potato tuber to construct its cocoon. Within the host, the third instar is white and has heavily sclerotized and toothed mouthparts, this being typical of parasitic Hymenoptera. The internal phase of the third instar was found within the first two to three abdominal segments of the host, its head being oriented anteriorly with respect to the host. It later exits and feeds externally, devouring all but the head capsule of the host. The parasite then spins its cocoon within the host's cocoon. During this external phase, the third instar changes from white to pink. The body prior to pupation is cylindrical, increasing in diameter from head to the abdomen, then tapering posteriorly. The body consists of a head and three thoracic and nine abdominal segments, followed by the anal segment (fig. 5). After feeding for 24 hours, the larva spins a white, silken cocoon anchored to the substrate of the host cocoon. The head capsule of the third instar bears spines and setae that are absent in previous instars.

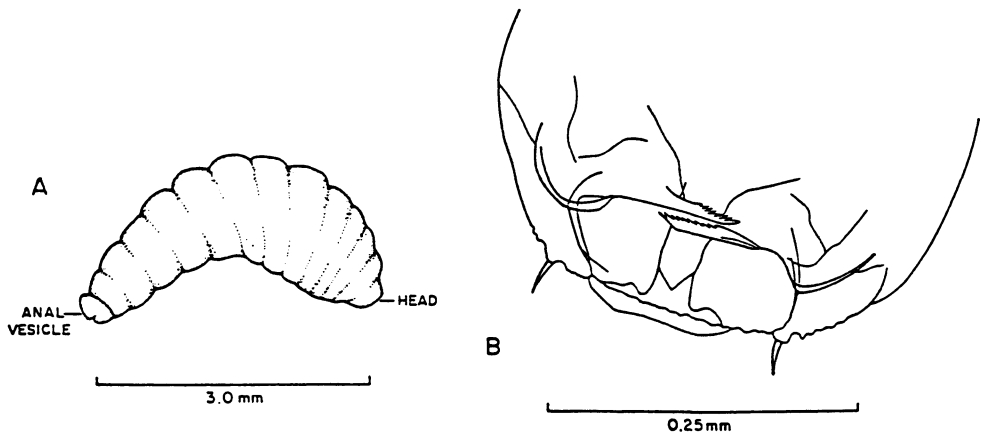

Fig. 5. Third instar of *Chelonus kellieae:* A = lateral view; B = head region bearing mandibles.

Head capsule measurements: length, $\overline{X} = 0.029 \pm 0.001$ mm; width, $\overline{X} = 0.490 \pm 0.002$ mm (n = 48). Mandible measurements: length, $\overline{X} = 0.120 \pm 0.001$ mm (n = 48).

Pupa: This stage is exarate. Early in the pupal stage, it is pale yellow, gradually darkening as development progresses. The pupa lies motionless within the cocoon (3.0 × 7.0 mm), which is parchmentlike in appearance. The cocoon, cylindrical to ovoid, is constructed of glistening white threads. The meconium is located at the caudal extremity of the cocoon. Pupation occurs 16 days after oviposition. Pupa measurements: length, $\overline{X} = 3.00$ mm (n = 40).

Chelonus phthorimaeae. Mean duration from oviposition to adult emergence was 22 days (range 20-26 days). Males emerged 2 days before females. Mean duration of the developmental stages: egg, 25 hours; first instar, 11 days; second instar, 2 days; third (last) instar, 2 days; pupa, 6 days. This parasite is also an egg-larval parasite, one egg being laid with each ovipositional thrust. Superparasitization occurred with several first instars found in the host egg; however, only one parasite larva developed per host larva. The relationship of the parasite larva to its host is the same as for *C. kellieae.*

Egg: The egg is indistinguishable from that of *C. kellieae.* Egg measurements: width, $\overline{X} = 0.050 \pm 0.002$ mm; length, $\overline{X} = 0.200 \pm 0.001$ mm (n = 100).

First instar: Morphology is indistinguishable from the first instar of *C. kellieae.* Head capsule measurements: length, $\overline{X} = 0.059 \pm 0.005$ mm; width, $\overline{X} = 0.072 \pm 0.003$ mm (n = 143). Mandible measurements: length, $\overline{X} = 0.034 \pm 0.001$ mm (n = 143). The relationship of the first instar to the host is similar to that for *C. kellieae.* The first instar larval molt occurs just as the host enters its fourth and final instar.

Second instar: Morphology is indistinguishable from the second instar of *C. kellieae.* Measurements of the head capsule: length, $\overline{X} = 0.230 \pm 0.003$ mm; width, $\overline{X} = 0.380 \pm 0.026$ mm (n = 25). Mandible measurements: length, $\overline{X} = 0.097 \pm 0.027$ mm (n = 25).

Third instar: This stage is composed of an internal and external phase in relation to the host. Morphology is indistinguishable from that of *C. kellieae.* Head capsule measurements: length, $\overline{X} = 0.235 \pm 0.004$ mm; width, $\overline{X} = 0.740 \pm 0.120$ mm (n = 19). Mandible measurements: length, $\overline{X} = 0.155 \pm 0.001$ mm (n = 19).

Pupa: This stage is exarate and its morphology is indistinguishable from that of *C. kellieae.* Pupation occurs 16 days after oviposition. Pupa measurements: length, $\overline{X} = 3.00$ mm (n = 20).

Effect of parasitization on host

In reviewing the biologies of other species of *Chelonus,* Graf (1917), Narayan, Subba Roa, and Thakere (1961), Rechav and Orion (1975), and Jackson, Delph and Neeman (1978) noted adverse effects of these species on the growth and development of their hosts. Therefore, effects of both species of parasites on the growth of *P. operculella* larvae were investigated. Head capsules for each instar of parasitized and nonparasitized host larvae were measured as previously described. A 2-sample t-test was used to detect significant differences in head capsule size and body length to determine differences in growth.

Chelonus kellieae and *C. phthorimaeae.* Results of parasitization on the host are shown in table 1. Parasitization by each species resulted in reduced head capsule width and body size, reflecting a significant effect on the size of the fourth instar host larvae. Dissecting parasitized and nonparasitized host larvae revealed that parasitized fourth instar host larvae have smaller fat bodies. Direct internal physical damage in the host was never apparent.

TABLE 1. EFFECT OF PARASITIZATION BY *CHELONUS PHTHORIMAEAE* AND *CHELONUS KELLIEAE* ON POTATO TUBERWORM GROWTH

Host instar	*Chelonus phthorimaeae*						*Chelonus kellieae*					
	Parasitized			Nonparasitized			Parasitized			Nonparasitized		
	$\bar{x}$ (mm)	± sd	n	$\bar{x}$ (mm)	± sd	n	$\bar{x}$ (mm)	± sd	n	$\bar{x}$ (mm)	± sd	n
						Head capsule widths						
1st	0.206	0.004	40	0.198	0.005	40	0.198	0.003	40	0.195	0.005	40
2nd	0.340	0.011	35	0.330	0.004	35	0.353	0.008	35	0.332	0.004	35
3rd	0.485	0.012	24	0.559	0.010	24	0.498	0.053	24	0.557	0.010	24
4th	0.773*	0.010	36	0.912	0.014	36	0.745*	0.018	36	0.908	0.018	36
						Body lengths						
1st	1.700	0.003	40	1.629	0.004	40	1.705	0.002	40	1.710	0.004	40
2nd	2.315	0.012	35	2.272	0.005	35	2.480	0.014	35	2.500	0.013	35
3rd	4.055	0.015	24	3.772	0.009	24	3.683	0.014	24	3.790	0.013	24
4th	6.197*	0.040	36	7.812	0.014	36	5.268*	0.038	36	6.198	0.027	36

*Values significantly different at the 5% level.

Mating, ovipositional behavior of adult parasites

Chelonus kellieae and *C. phthorimaeae.* Adults of both species of parasites emerged from the cocoon during the light phase of the photoperiod, with males emerging approximately 2 days before females. Soon after emergence, both sexes moved about and fed. During courtship, the male actively pursued the female while rapidly vibrating his wings. This wing-fanning consisted of short periods of rapid wing vibration with the wings extended slightly above the body. The behavior was probably in response to the female sex pheromone (Askew 1968; Matthews 1975).

In both species, once contact occurred, the male mounted the female's dorsum. If the female was not receptive, she rejected such advances by kicking the male away. If she was receptive, the male curved the posterior segments of his abdomen down under hers. During copulation the female remained motionless. Mating was terminated by either the male or female walking away. No postcopulatory behavior was observed. Females are monogamous, even when avidly courted by sexually aggressive males; mated females do not permit the male to mount and copulate. Males are polygamous and occasionally mount dead females.

Female adults of each species exposed to host eggs did not oviposit immediately; however, once oviposition began, female activity increased. The female lowered her antennae until the tips were flattened against the substrate. She then walked, moving her antennae forward until they encountered the host egg, at which time she began probing the host egg with them. The antennae were then extended straight forward while the abdomen assumed a 90 percent angle to the rest of the body, the wings being in a straight line with the thorax and head. Upon acceptance of the host egg, the female positioned herself with her abdomen above the egg and lowered her prothoracic legs. The ovipositor was extended and penetrated the host egg. After completion of oviposition, the ovipositor was withdrawn and the abdomen straightened. The female then resumed her search for more host eggs. This behavior is similar for other species of *Chelonus* as observed by Pierce and Holloway (1912), Loginbill (1928), and Vance (1932).

Effect of food, water, on adult parasite longevity

This study showed for both species that carbohydrates and free water are necessary for maximum longevity.

Chelonus kellieae. Males and females that were starved had a mean longevity of 2.3 days (range, 1-3) and 2.0 days (range, 1-3), respectively. Those males and females given access to honey alone had a mean longevity of 8.2 days (range, 4-19) and 15.0 days (range, 4-21), respectively. Males and females given access to both honey and water had a mean longevity of 17.1 days (range, 5-21) and 37.2 days (range, 14-52), respectively. Access to water in combination with honey resulted in increased longevity for both sexes compared with those with access to honey alone. Mean longevity for females was greater than that for males when given access to either honey or to a combination of honey and water.

Chelonus phthorimaeae. Starved males and females had a mean longevity of 1.8 days (range, 1-3) and 2.6 days (range, 1-4), respectively; males and females given access to honey alone had a mean longevity of 28.1 days (range, 15-45) and 30.9 days (range, 15-47), respectively. Males given access to honey and water had a mean longevity of 24.4 days (range, 4-35); females subjected to the same treatment had a mean longevity of 39.6 days (range, 25-49).

Optimum host egg age and number for parasitization

Significant differences ($P < 0.05$) were found for both species in the total mean numbers of parasite progeny and in mean percentage of female parasite progeny resulting from various combinations of host egg numbers and ages.

Chelonus kellieae—total parasite progeny

Duncan's Multiple Range Test to determine significance of ranking of mean numbers of parasite progeny shows that 50 and 100 host eggs, both 0-24 hours old, were within the same homogeneous subgroup. These combinations produced the greatest mean number of parasite progeny, 29.0 and 24.8, respectively (table 2). The greatest mean number (29.0) of parasite progeny resulted from 50 host eggs, 0-24 hours old. This was used as the optimal number and age of host eggs to be used in other studies.

As host numbers (at all host ages) increased from 25 to 50, total parasite emergence increased. A further increase from 50 to 100 and to 150 host eggs resulted in no further increase in parasite progeny and in some cases a decrease in progeny resulted. Also, within each group of host egg numbers, the resulting parasite progeny decreased with older host eggs (table 2).

Chelonus kellieae—total female parasite progeny

Duncan's Multiple Range Test shows ranking in homogeneous subgroups resulting in the maximum mean percentage (51.0 percent) of female progeny resulted from 50 host eggs, 24-48 hours old, and the minimum mean percentage (7.0) from 100 host eggs, 72-96 hours old (table 2).

TABLE 2. MEAN NUMBER OF PARASITE PROGENY AND PERCENTAGE OF FEMALE PROGENY PRODUCED BY MATED *CHELONUS KELLIEAE* FEMALES EXPOSED TO VARIOUS HOST EGG NUMBERS AND AGES*

Host egg		Mean number	Mean percentage
Number	Age (hrs)	progeny/female†	female progeny/female‡
25	0 - 24	15.6 cd	34 bc
25	24 - 48	10.0 cdef	35 bc
25	48 - 72	2.0 f	29 bc
25	72 - 96	4.4 c f	36 bc
50	0 - 24	29.0a	43 bc
50	24 - 48	15.8 cd	51 c
50	48 - 72	10.6 cdef	33 bc
50	72 - 96	7.8 def	27abc
100	0 - 24	24.8ab	39 bc
100	24 - 48	18.4 bc	35 bc
100	48 - 72	11.7 cdef	33 bc
100	72 - 96	4.4 c	7a
150	0 - 24	18.4 bc	38 bc
150	24 - 48	14.2 cd	36 bc
150	48 - 72	11.0 cdef	33 bc
150	72 - 96	9.7 cdef	37 bc

*Based on 15 replications per number/age cohort.
†Means followed by the same letter are not significantly different at the 5% level.
‡Means followed by the same letter are not significantly different at the 5% level. Mean separation on transformed data (arc sine).

TABLE 3. MEAN NUMBER OF PARASITE PROGENY AND PERCENTAGE OF FEMALE PROGENY PRODUCED BY MATED *CHELONUS PHTHORIMAEAE* FEMALES EXPOSED TO VARIOUS HOST EGG NUMBERS AND AGES*

Host egg		Mean number	Mean percentage
Number	Age (hrs)	progeny/female†	female progeny/female‡
25	0 - 24	11.7 efg	34 b
25	24 - 48	13.3 defg	29ab
25	48 - 72	6.0 g	9a
25	72 - 96	5.8 g	16ab
50	0 - 24	16.9 cdefg	30ab
50	24 - 48	12.2 defg	28ab
50	48 - 72	16.0 cdefg	25ab
50	72 - 96	8.6 fg	20ab
100	0 - 24	30.0 b	30ab
100	24 - 48	23.3 bcde	12a
100	48 - 72	26.5 bc	19ab
100	72 - 96	10.4 fg	10a
150	0 - 24	42.2a	36 b
150	24 - 48	41.6a	35 b
150	48 - 72	23.8 bcd	27ab
150	72 - 96	18.6 cdef	10a

*Based on 15 replications per number/age cohort.
†Means followed by the same letter are not significantly different at the 5% level.
‡Means followed by the same letter are not significantly different at the 5% level. Mean separation on transformed data (arc sine).

Chelonus phthorimaeae—total parasite progeny

Duncan's Multiple Range Test shows that 150 host eggs, 0-24 and 24-48 hours old, were in the same homogeneous subgroup and resulted in the greatest mean number of parasites, 42.2 and 41.6, respectively (table 3). Thus, the optimal host number and age were 150 host eggs, 0-24 hours old.

As host numbers (at all ages) increased from 25 to 150 host eggs, total parasite emergence also increased and, as with *C. kellieae* parasite progeny, decreased in number with older host eggs (table 3).

Chelonus phthorimaeae—total female parasite progeny

Duncan's Multiple Range Test showed a significance in ranking. The maximum mean percentage of female progeny (36.0) resulted from 150 host eggs, 0-24 hours old, and the minimum mean percentage (9.0) resulted from 25 host eggs, 48-72 hours old (table 3).

As noted with both species of parasites, the resulting number of progeny decreased with older host ages. This is attributed to dorsal closure being complete in the host embryo, which prevented complete development of such eggs as observed by Wishart and Van Steenburgh (1934) in their studies of *Chelonus annulipes* parasitizing *Ostrinia nubilalis.*

Effect of Food, Water on Adult Parasite Fecundity

This study showed that for both species a carbohydrate source and free water are not prerequisites for progeny production.

Chelonus kellieae. Females subjected to starvation produced a mean total of 58.0 progeny after 3 days, as on the fourth day mortality occurred. Females subjected to honey and free water produced a mean total of 64.8 progeny after 3 days.

Chelonus phthorimaeae. Although only eight females were subjected to starvation, they produced a mean total of 71.1 progeny after 3 days, and, as in the previous study, mortality occurred on the fourth day. Females given access to honey and free water produced a mean total of 65.0 progeny after 3 days.

Number of progeny resulting from mated, unmated adult parasites

Daily progeny production from mated and virgin females of *C. kellieae* and *C. phthorimaeae* and their survivorship are shown in figures 6 and 7, respectively. This study also showed that virgin females of both species produced only male progeny; therefore both species are arrhenotokous.

Chelonus kellieae. Mean total number of progeny produced from virgin females was 304.2, consisting entirely of males; that from mated females was 315.6, consisting of males and females. Mean longevity of both virgin and mated females was 42.2 days (range, 33-55) and 36.8 days (range, 10-53), respectively. The reproductive period, expressed as the percentage of the number of days ovipositing of the longevity, was 48.0 percent and 67.6 percent for virgin and mated females, respectively.

Virgin females produced more progeny per day than mated females during the first few days after adult emergence (fig. 6).

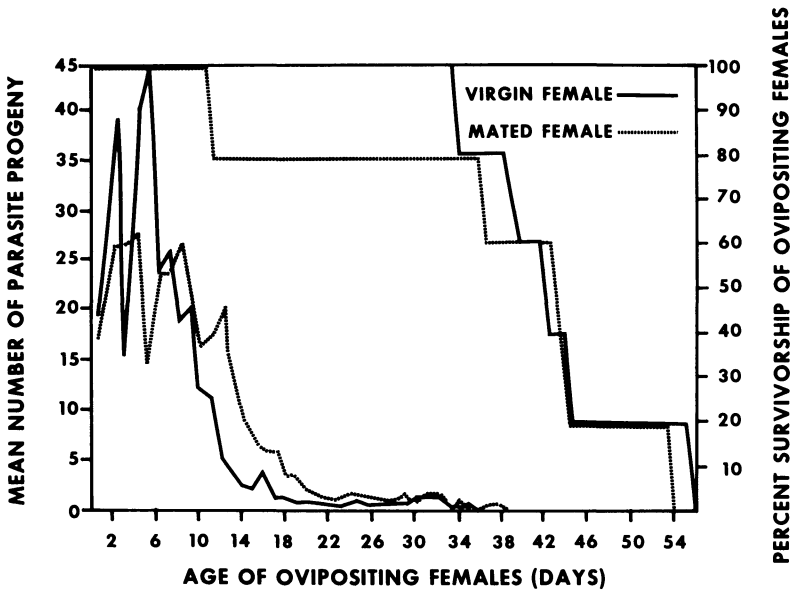

Fig. 6. Mean daily progeny production and survivorship of virgin and mated females of *Chelonus kellieae.*

Chelonus phthorimaeae. Mean total number of progeny resulting from virgin females was 448.7, consisting entirely of males while progeny resulting from mated females was 568.3, consisting of males and females. Mean longevity of both virgin and mated females was 21.7 days (range, 8-33) and 16.5 days (range, 8-27), respectively. The reproductive period was 86.8 percent and 90.5 percent for virgin and mated females, respectively.

During the first few days of adult life, mated females produced more progeny per day than virgin females (fig. 7).

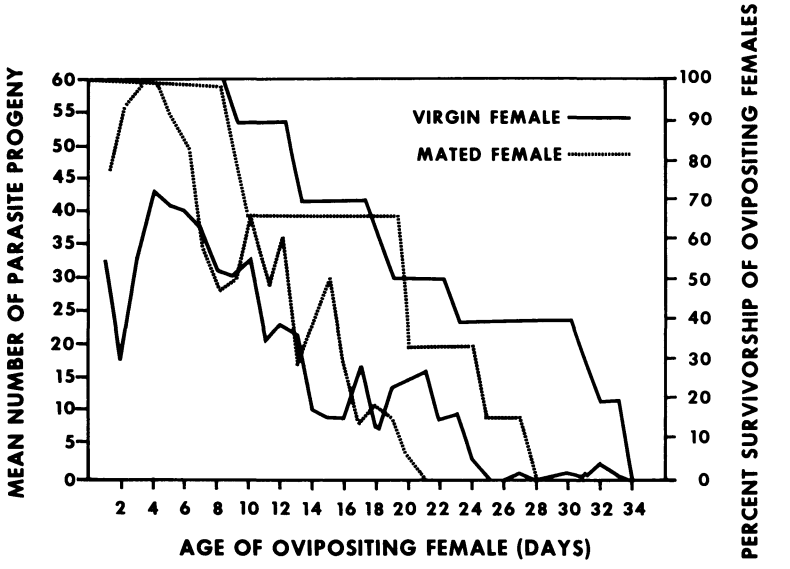

Fig. 7. Mean daily progeny production and survivorship of virgin and mated females of *Chelonus phthorimaeae.*

Preoviposition Period

Chelonus kellieae. Mated females first produced male progeny 1-2 hours postemergence and then continuously through 6-7 hours and 9-12 hours postemergence. Female progeny were first produced 4-5 hours postemergence and continuously through 6-7 and 9-12 hours postemergence. Virgin females first produced male progeny 1-2 hours postemergence and then continuously through 6-7 hours. At 7-8 and 8-9 hours postemergence, no progeny were produced from either mated or virgin females.

Chelonus phthorimaeae. Mated females first produced male progeny 0-1 hours postemergence. However, no progeny were produced at 1-2 hours. From 2-3 hours through 11-12 hours postemergence, progeny were again produced. Female progeny were first produced 2-3 hours postemergence and continuously through 10-11 hours postemergence. During the last hour (11-12 hours postemergence), no progeny were produced. Virgin females first produced male progeny 0-1 hours postemergence and continuously until termination of the study.

These results show that there is essentially no preoviposition period for mated females of both parasite species to produce male progeny. Female progeny are not produced until a few hours postemergence. Virgin females also exhibited essentially no preoviposition period for production of male progeny. Vance (1932), Malek (1947), and Broodryk (1969) also found that other species of *Chelonus* do not have a preoviposition period.

Comparison of Parasite Biologies

Chelonus phthorimaeae is native to North America, *C. kellieae* to Central America. Despite their geographical isolation, both are similar in biology, morphology of immature stages, and behavior. Both species are primary, solitary, egg-larval endoparasites of *P. operculella;* both have three larval instars. The early first instar is mandibulate-caudate, later becoming mandibulate-vesiculate. Second and third instars are mandibulate. The third instar completes its development by feeding externally on the remains of the host larva.

Both species of females had a maximum longevity (*C. kellieae,* 37.2 days; *C. phthorimaeae,* 39.6 days) when given access to honey and free water.

Females of *C. phthorimaeae* produced the greatest mean number of progeny (42.2) when exposed to 150 host eggs, 0-24 hours old; *C. kellieae* females produced a maximum of (29.0) when exposed to 50 host eggs, 0-24 hours old.

Females of both species are arrhenotokous and neither host feeds. Neither species requires honey and free water for progeny production. Both species produced approximately equal numbers of progeny, whether given access to honey and free water or starved, *C. kellieae* producing 64.8 and 58.0 progeny, respectively, and *C. phthorimaeae* producing 65.0 and 71.1 progeny.

Virgin and mated *C. phthorimaeae* produced a mean total of 448.7 and 568.3 progeny, respectively, while *C. kellieae* produced 304.2 and 315.6 progeny. Virgin females of *C. kellieae* produced more progeny during the first few days of adult life than mated females, while mated females of *C. phthorimaeae* produced more progeny than virgin females during a similar period.

Both species exhibited a preovipositional period, being 1-2 hours and 0-1 hour prior to production of male progeny for *C. kellieae* and *C. phthorimaeae,* respectively. Female

progeny were produced 2-3 hours and 4-5 hours postemergence for *C. phthorimaeae* and *C. kellieae,* respectively.

Effects of temperature on development and life table studies

Chelonus kellieae. Mean developmental time in days from egg to adult female emergence at 21.1±1, 23.9±1, 26.7±1, 29.4±1, and 32.2±1°C is shown in table 4. Data show that mean developmental time decreased as the temperature increased, the greatest change in percent development per day occurring between 23.9±1°C and 26.7±1°C.

Survivorship of ovipositing females subjected to these various temperatures is shown in figures 8, 9, and 10. Female survivorship was longest at 21.1±1°C, decreasing at 26.7±1°C. However, survivorship at 23.9±1°C was less than that at 32.2±1°C. These survivorship curves (l_x) suggest mortality of the population occurs when limits of physiological longevity are reached, at which time the entire population dies quickly. This type of survivorship curve (Type I) was discussed by Pearl (1928).

In construction of the life tables at each of the various temperatures, immature survivorship, based on 50 known parasitized host eggs at 21.1±1, 23.9±1, 26.7±1, 29.4±1, and 32.2±1°C, was 17.1, 45.0, 34.6, 42.0, and 27.5 percent, respectively. Due to internal development of the larvae and pupae stages, no assumptions could be made on separation of mortality associated with each stage.

Mean total progeny (males and females) produced throughout the females' lifespan was 148.2, 230.0, 255.0, 291.6, and 384.9, respectively, at 21.1±1, 23.9±1, 26.7±1, 29.4±1, and 32.2±1°C. Mean percentage of females of the total progeny was 31.6, 43.3, 37.6, and 35.3 percent, respectively, at 21.1±1, 23.9±1, 26.7±1, and 29.4±1°C. No female progeny were produced at 32.2±1°C.

Mean number of female progeny produced daily (m_x) (expressed as age specific fecundity) and survivorship (l_x) curve for ovipositing females at each of the respective temperatures are shown in figures 8, 9, and 10. At 21.1±1°C most female progeny were produced in the first 25 days. At 23.9±1°C, most female progeny were produced in the first 15 days with a distinct peak in production at 8 days. At 26.7±1°C, most female progeny were produced in the first 14 days, with a distinct peak in progeny at 8 days. At 29.4±1°C, all female progeny were produced in the first 25 days, with a distinct peak in progeny at 7 days. At all temperatures studied, female progeny were produced before 50 percent mortality of the ovipositing population had occurred. No female progeny were produced at 32.2±1°C.

TABLE 4. DEVELOPMENTAL TIME OF FEMALE *CHELONUS KELLIEAE* AT VARIOUS TEMPERATURES (±1°C). EXPERIMENTS CONDUCTED AT 50 PERCENT RH AND 12-HOUR PHOTOPERIOD

Temperature °C	Number reared	Developmental time (days)			Percent development per day
		Range	$\bar{X}$	±sd	
21.1	59	40 - 56	50.7	2.36	1.97
23.9	25	36 - 39	37.7	0.95	2.64
26.7	52	25 - 28	26.8	1.02	3.72
29.4	44	22 - 24	22.6	0.84	4.41
32.2	108	19 - 21	19.6	0.66	5.09

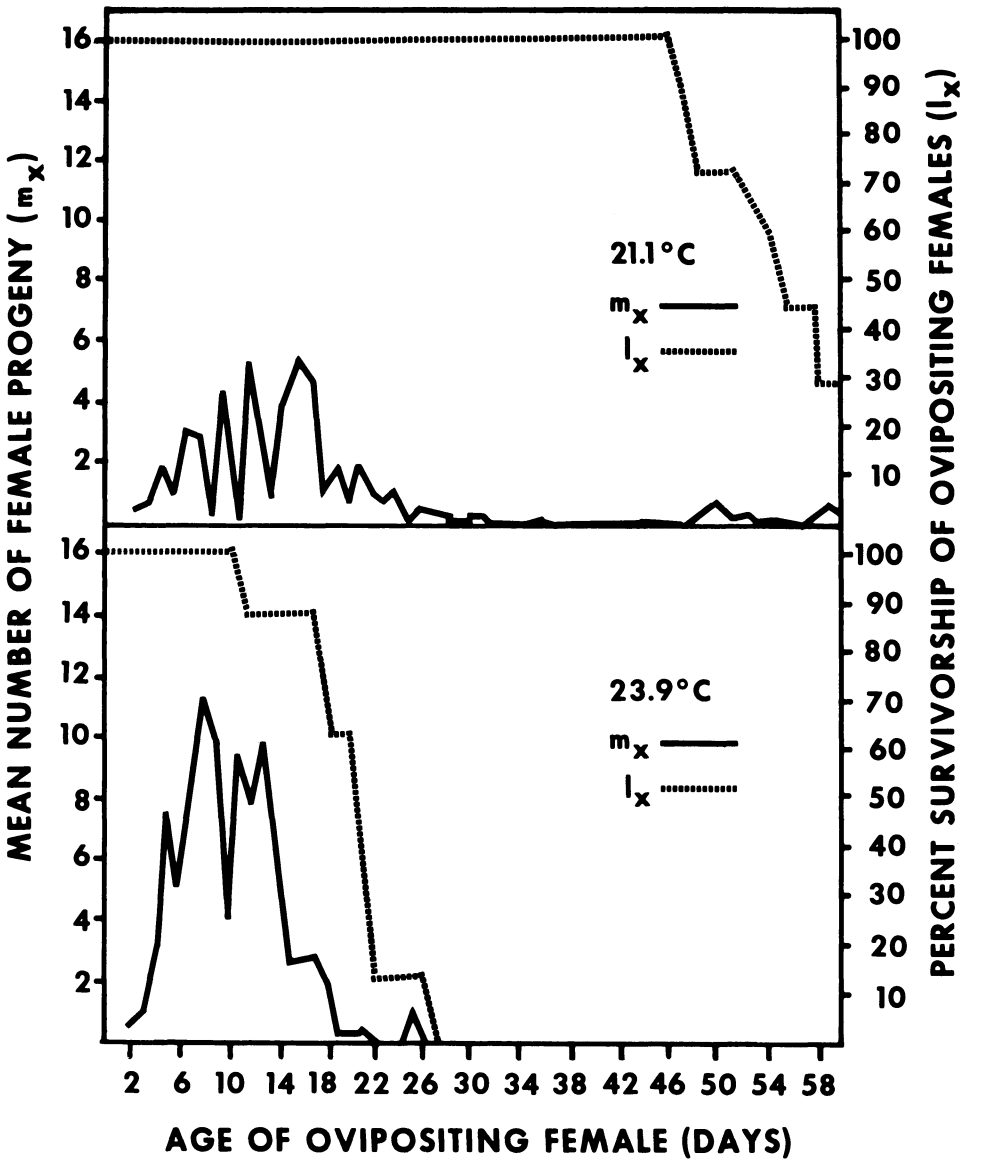

Fig. 8. Mean daily female progeny and survivorship curves for females of *Chelonus kellieae,* exposed daily to 50 host eggs (0-24 hours old) at 21.1 and 23.9 (±1°C), 50% RH and 12-hour photoperiod.

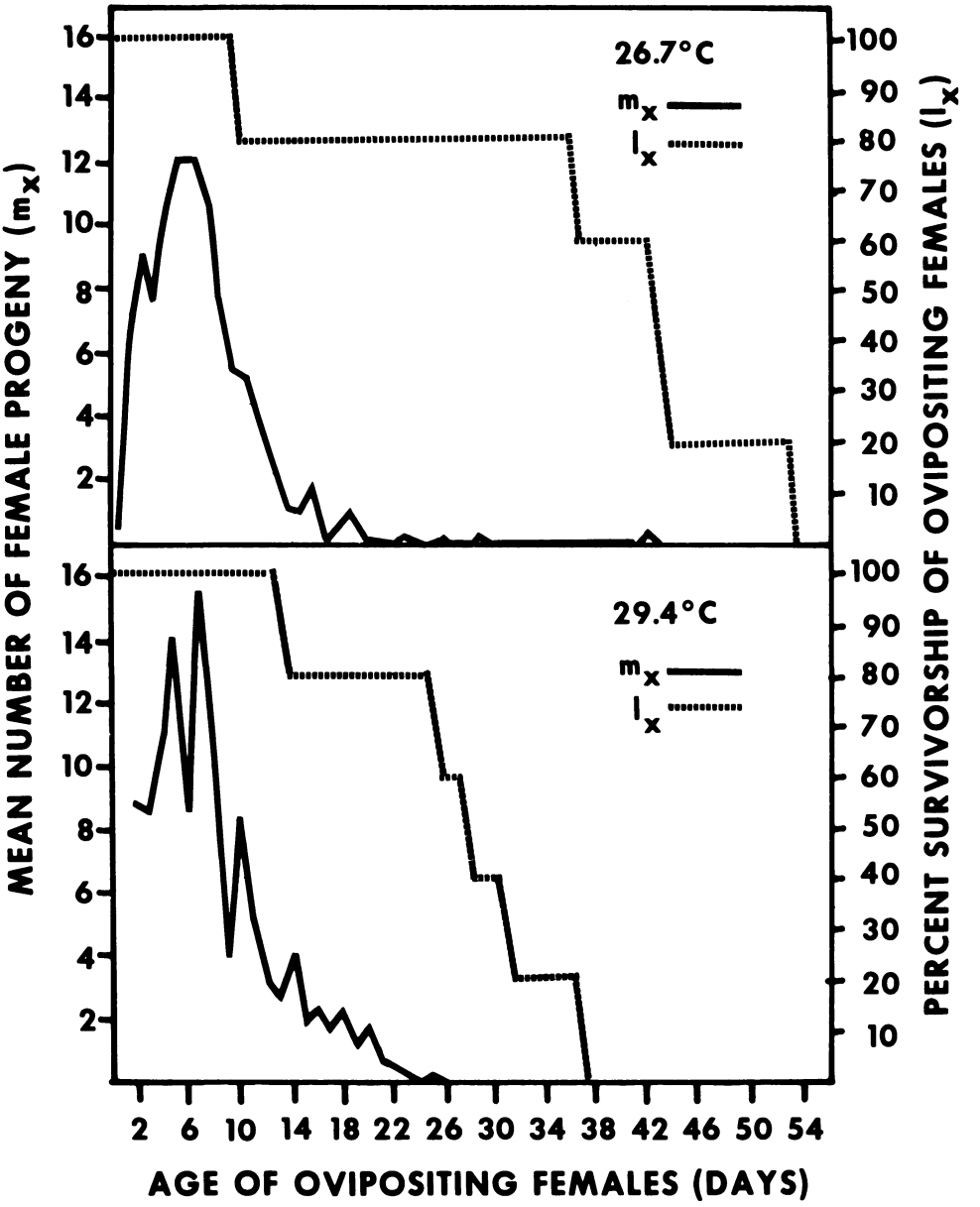

Fig. 9. Mean daily female progeny and survivorship curves for females of *Chelonus kellieae,* exposed daily to 50 host eggs (0-24 hours old) at 26.7 and 29.4 (±1°C), 50% RH and 12-hour photoperiod.

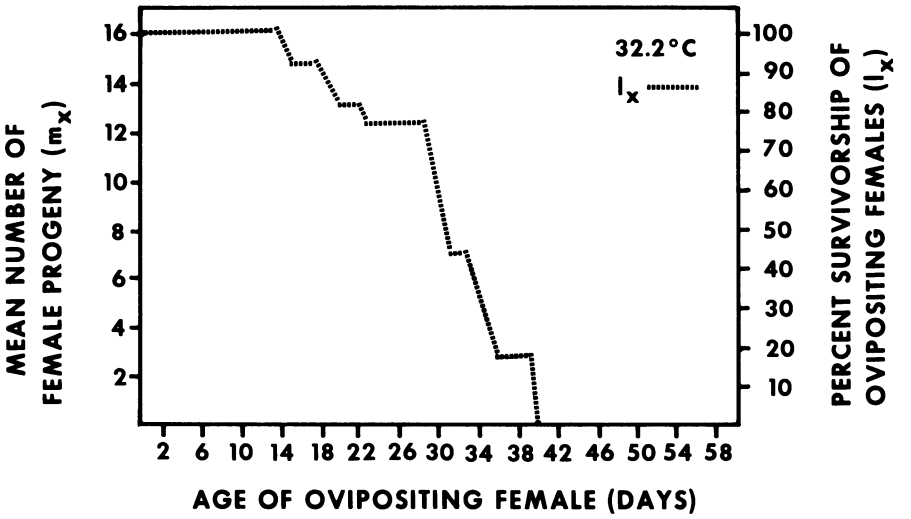

Fig. 10. Mean daily female progeny and survivorship curves for females of *Chelonus kellieae,* exposed daily to 50 host eggs (0-24 hours old) at 32.2°C (±1°C), 50% RH and 12-hour photoperiod. No female progeny produced at 32.2°C.

Age-specific survivorship was used to calculate other population growth statistics at the various temperatures; net reproductive rate (R_0), innate capacity for increase (r_m), gross reproductive rate (GRR), mean generation time (T), and finite rate of increase (λ) were calculated for each life table (table 5). Values of mean total progeny increased with increases in temperature. The R_0 and GRR values reached their maximum value at 29.4±1°C. However, R_0 value was lower at 26.7±1°C than that at 23.9±1°C. This may be due to the cohorts' fecundity and survival rate at this temperature compared with those at 23.9±1°C and 29.4±1°C. There also were differences between R_0 values and GRR values at each temperature except at 32.2±1°C. A maximum number of progeny was produced at 32.2±1°C; however, they were all male progeny.

TABLE 5. EFFECT OF VARIOUS TEMPERATURES (±1°C) ON SEVERAL POPULATION GROWTH STATISTICS OF *CHELONUS KELLIEAE.* EXPERIMENTS CONDUCTED AT 50 PERCENT RH AND 12-HOUR PHOTOPERIOD

Population growth statistic	Temperature (°C)				
	21.1	23.9	26.7	29.4	32.2
Mean total progeny/female	148.20	230.70	255.00	291.60	384.90
Gross reproductive rate (GRR)	52.32	95.60	101.80	116.80	0.00
Net reproductive rate (R_0)	8.58	40.37	35.39	47.66	0.00
Mean generation time (days) T	62.3	44.9	32.1	28.7	*
Innate capacity for increase r_m	0.035	0.083	0.113	0.140	negative
Finite rate of increase λ	1.04	1.09	1.12	1.15	0.00

*No female progeny produced at 32.2°C.

The r_m value (rate of increase of the population under constant environmental conditions in which food and space are nonlimiting and a stable age distribution has been obtained) was calculated. Because r_m is greater than zero in the range of 21.1±1°C to 29.4±1°C, this implies that *C. kellieae* can persist and increase as temperatures are increased within this range. The r_m value is near zero at 21.1±1°C, suggesting that this temperature is approaching the unfavorable lower limit, and lower temperatures could result in zero or negative r_m values. As *C. kellieae* did not produce female progeny at 32.2±1°C, a zero or negative value must occur somewhere between 29.4±1°C and 32.2±1°C. The maximum r_m value (0.140) at 29.4±1°C is due to the shorter developmental period (22.6 days) and, consequently, a shorter mean generation time (28.7 days) and a higher R_o value (47.66). At 21.1±1°C, the minimum r_m value (0.035) is due to the longer developmental period (50.7 days) and, consequently, a longer mean generation time (62.3 days) and a lower R_o value (8.58). Thus, r_m values are due to the effect of temperature on the developmental cycle. Since the natural log of λ equals r_m, it exhibits the same trends as r_m and indicates the number of times the population multiplies itself per unit of time, from a low λ value of 1.04 at 21.1±1°C to a peak λ value of 1.15 at 29.4±1°C.

This demonstrates that *C. kellieae* persists from generation to generation under given environmental conditions from at least 21.1±1°C to a temperature between 29.4±1°C to 32.2±1°C. Optimal temperature for population growth in this study was 29.4±1°C.

Chelonus phthorimaeae. Mean developmental time, as previously defined at the previously stated temperatures, is shown in table 6. Developmental time decreased as temperature increased, with the greatest change in percent development per day occurring between 23.9±1°C and 26.7±1°C.

TABLE 6. DEVELOPMENTAL TIME OF FEMALE *CHELONUS PHTHORIMAEAE* AT VARIOUS TEMPERATURES (±1°C). EXPERIMENTS CONDUCTED AT 50 PERCENT RH AND 12-HOUR PHOTOPERIOD

Temperature °C	Number reared	Developmental time (days)			Percent development per day
		Range	$\bar{X}$	±sd	
21.1	22	44 - 50	47.0	1.64	2.12
23.9	25	32 - 34	32.7	0.68	3.06
26.7	65	22 - 26	23.5	0.94	4.26
29.4	67	18 - 21	19.3	1.05	5.18
32.2	78	16 - 20	17.0	0.74	5.88

Survivorship of ovipositing females subjected to 21.1±1, 23.9±1, 26.7±1, 29.4±1, and 32.2±1°C is shown in figures 11, 12, and 13. Survivorship of ovipositing females shows a decrease from the longest survivorship at 21.1±1°C to the shortest survivorship at 32.2±1°C.

Immature survivorship was 31.8, 31.3, 44.6, 48.2, and 42.4 percent at 21.1, 23.9, 26.7, 29.4, and 32.2±1°C, respectively. As previously stated, separation of mortality at each stage could not be ascertained.

Mean total progeny (males and females) resulting from exposing ovipositing females to 21.1±1, 23.9±1, 26.7±1, 29.4±1, and 32.2±1°C was 246.9, 286.5, 549.7, 552.5, and 580.3, respectively. Mean percentage of females of the total progeny obtained at these temperatures was 50.3, 48.3, 32.1, 31.5, and 26.3 percent, respectively.

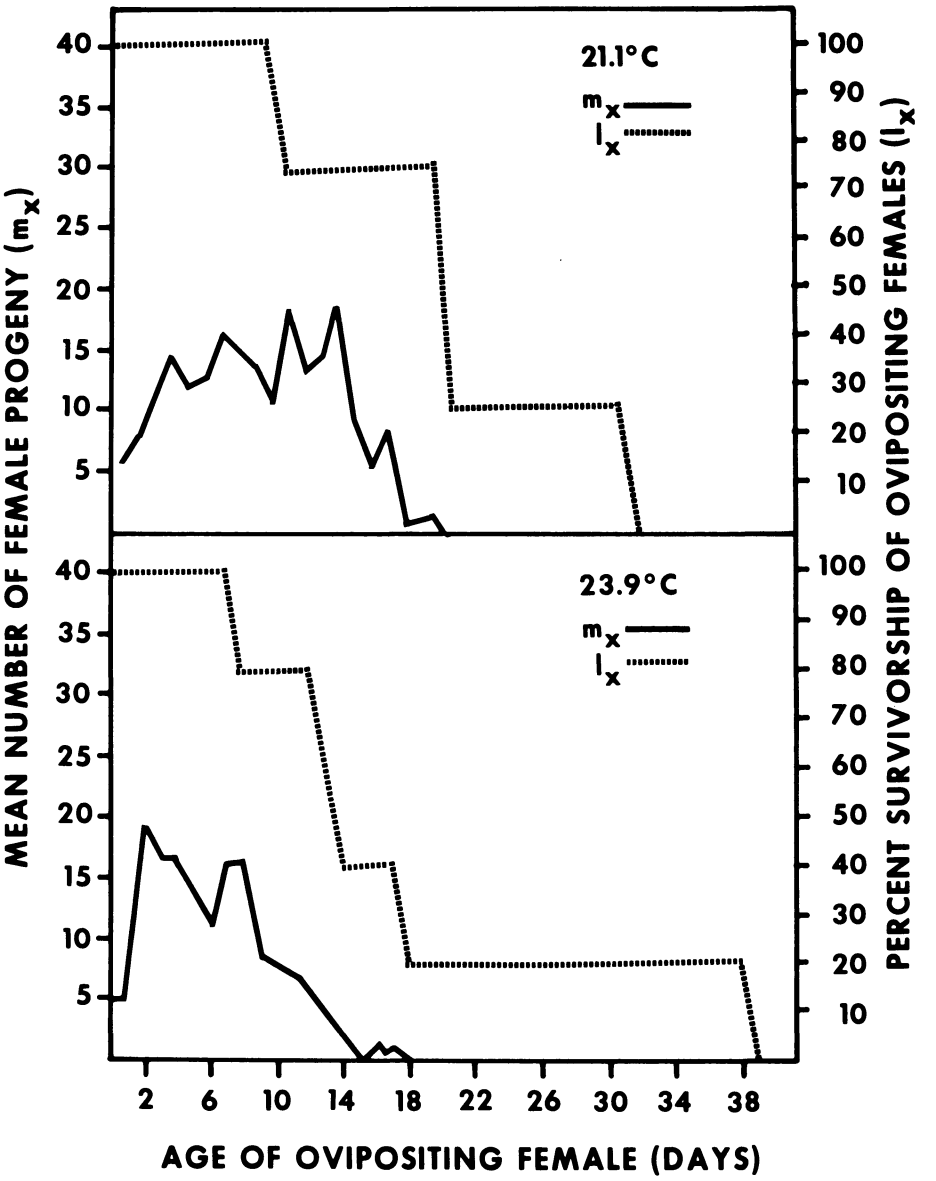

Fig. 11. Mean daily female progeny and survivorship curves for females of *Chelonus phthorimaeae,* exposed daily to 150 host eggs (0-24 hours old) at 21.1 and 23.9 (±1°C), 50% RH and 12-hour photoperiod.

Mean number of female progeny produced daily are shown in figures 11, 12, and 13. At 21.1±1°C, most female progeny were produced during the first 15 days. At 23.9±1°C, a peak in female progeny occurred the second day. At 26.7±1°C, the peak in female progeny occurred the third day, followed by two additional peaks in female progeny produc-

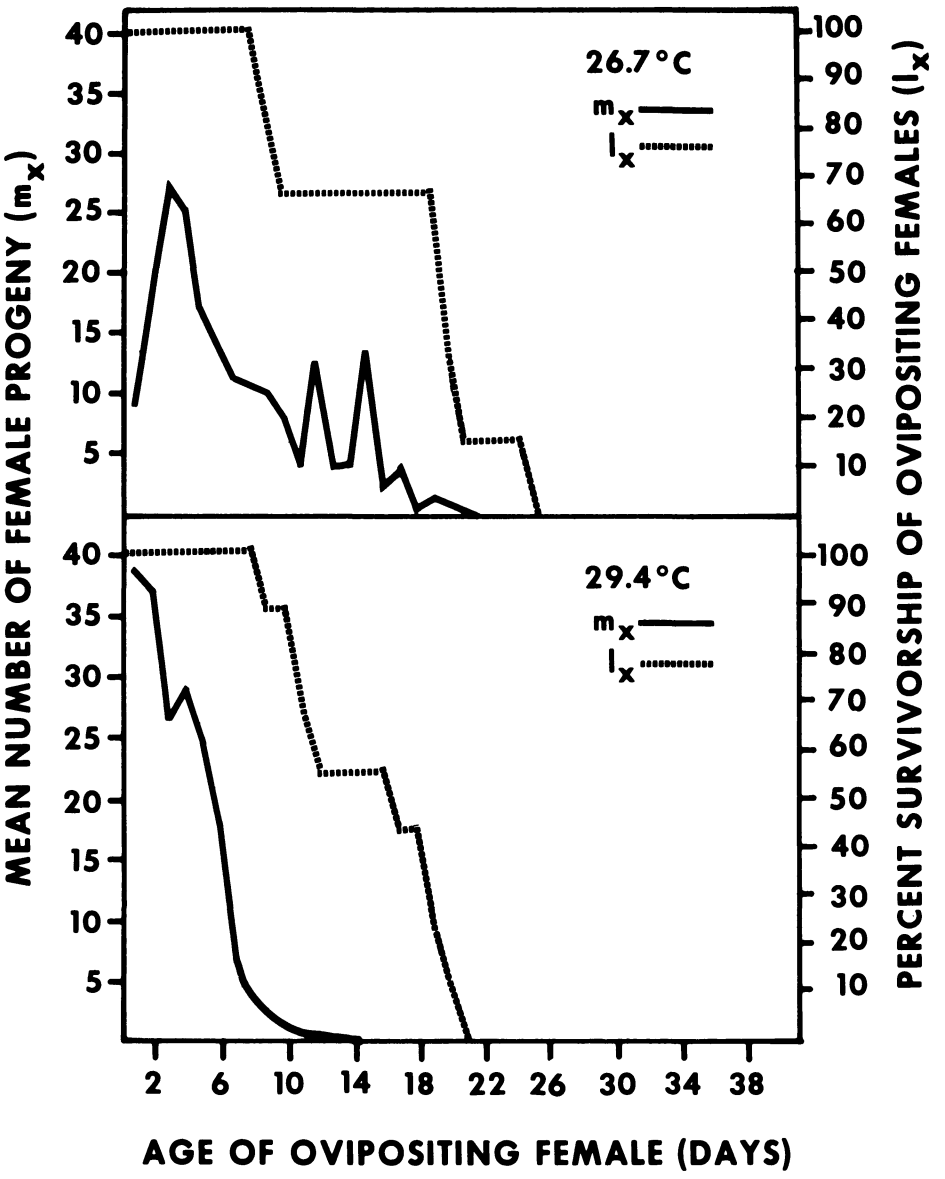

Fig. 12. Mean daily female progeny and survivorship curves for females of *Chelonus phthorimaeae,* exposed daily to 150 host eggs (0-24 hours old) at 26.7 and 29.4 (±1°C), 50% RH and 12-hour photoperiod.

tion at 12 and 15 days. At 29.4±1°C, the highest peak in female progeny production occurred the first day. At 32.2±1°C, the peak in female progeny production occurred the second day. In all cases, most of the progeny were produced before 50 percent mortality of the ovipositing female population had occurred.

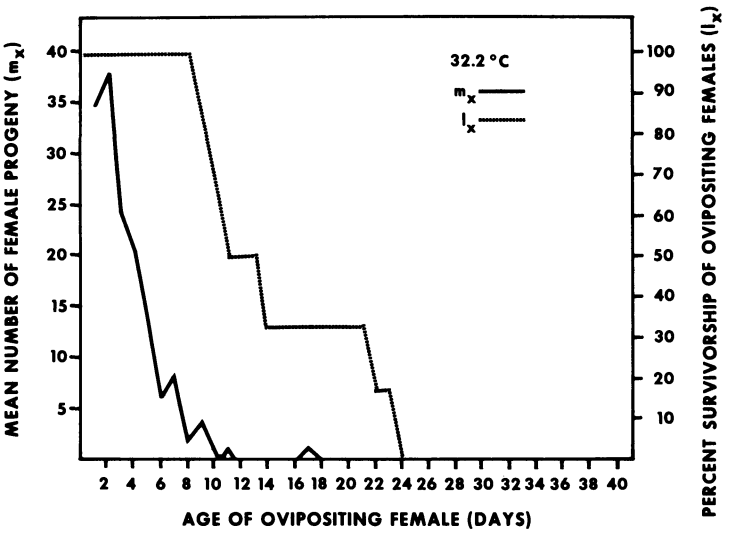

Fig. 13. Mean daily female progeny and survivorship curves for females of *Chelonus phthorimaeae,* exposed daily to 150 host eggs (0-24 hours old) at 32.2 (±1°C), 50% RH and 12-hour photoperiod.

Population growth statistics are presented in table 7. Mean total progeny increased with an increase in temperature.

TABLE 7. EFFECT OF VARIOUS TEMPERATURES (±1°C) ON SEVERAL POPULATION GROWTH STATISTICS OF *CHELONUS PHTHORIMAEAE.* EXPERIMENTS CONDUCTED AT 50 PERCENT RH AND 12-HOUR PHOTOPERIOD

Population growth statistic	Temperature (°C)				
	21.1	23.9	26.7	29.4	32.2
Mean total progeny/female	24.9	286.5	549.7	552.5	580.3
Gross reproductive rate (GRR)	210.55	154.10	199.40	189.60	152.98
Net reproductive rate (R_o)	59.75	44.17	79.58	90.93	64.33
Mean generation time (days) T	52.7	35.8	28.32	20.5	18.2
Innate capacity for increase r_m	0.079	0.107	0.161	0.225	0.234
Finite rate of increase λ	1.08	1.11	1.17	1.25	1.26

The maximum r_m value (0.234) at 32.2±1°C is due to the shorter developmental period (17.0 days) and a shorter mean generation time (18.2 days). At 21.1±1°C, the minimum r_m value (0.079) is due to the longer developmental period (47.0 days) and the longer mean generation time (52.7 days). This relationship was discussed by Birch (1948), Cole (1954), and Messenger (1964).

As with r_m, λ showed the same relationship of increasing values with increasing temperatures from a minimum λ value of 1.08 at 21.1±1°C to a maximum value of 1.26 at 32.2±1°C. This implies, therefore, that *C. phthorimaeae* can persist and reproduce at temperatures ranging from at least 21.1±1°C to 32.2±1°C, the latter temperature being optimal for population growth for this species within the range of temperatures studied.

Development and life tables of parasites and host compared

Cardona and Oatman (1975) studied temperature responses of *P. operculella* and constructed life tables for this species at 23.9±1, 26.7±1, 29.4±1, and 32.2±1°C. Data from their life tables and from those constructed at 21.1±1°C for *P. operculella* in the present study were used in comparison to those of *C. phthorimaeae* and *C. kellieae*.

Comparisons were made of mean developmental time (days), mean generation time (days), net reproductive rate (R_o), and innate capacity for increase (r_m). Comparisons of the mean developmental time (days) of *C. phthorimaeae, C. kellieae,* and their host, *P. operculella,* are shown in figure 14. The relationship of temperature and developmental time for both species is similar and indicates that *C. phthorimaeae* had a developmental time slightly less than that of *C. kellieae* at all temperatures except 23.9±1°C. Both parasites developed more slowly than did their host at 21.1±1°C and 23.9±1°C, resulting in their emergence a few days after their host; at 26.7±1, 29.4±1, and 32.2±1°C developmental time was similar for *C. phthorimaeae* and its host, while at these temperatures *C. kellieae* developed more slowly than its host.

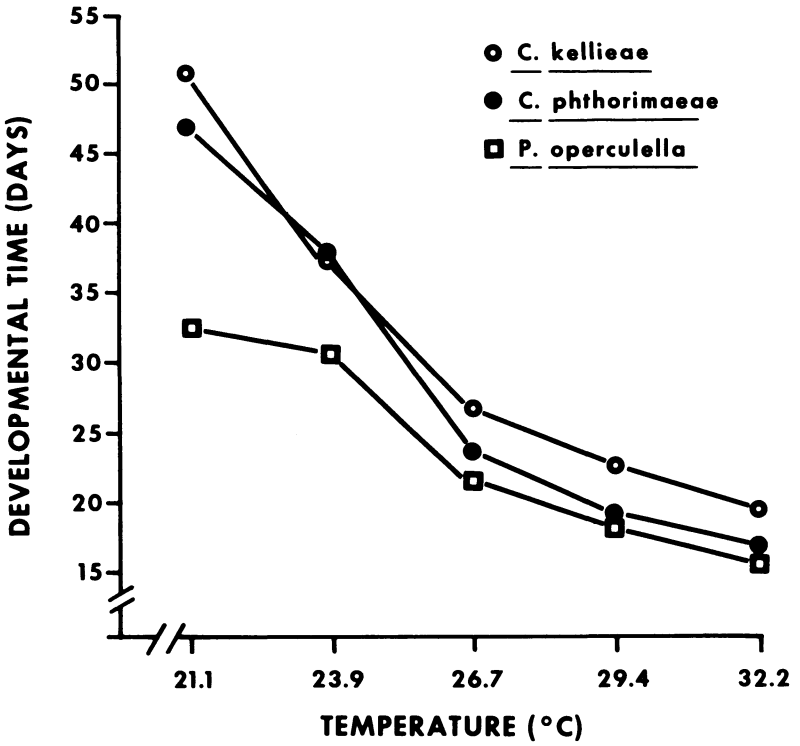

Fig. 14. Mean developmental times of *Chelonus kellieae, C. phthorimaeae,* and their host, *Phthorimaea operculella,* at various temperatures (±1°C), 50% RH and 12-hour photoperiod.

Mean generation times are compared in figure 15. *Chelonus phthorimaeae* had a shorter generation time than *C. kellieae* at all temperatures studied. Their host, *P. operculella,* had a shorter generation time than either parasite. There is no generation time value for *C. kellieae* at 32.2±1°C as female progeny were not produced at this temperature.

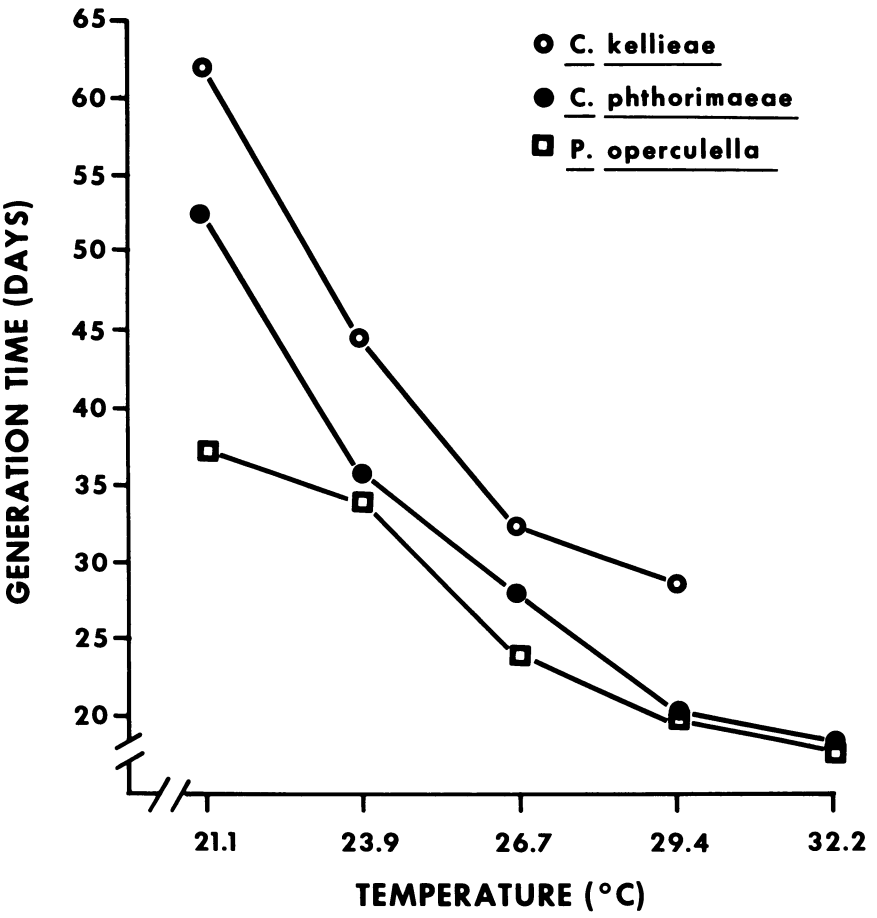

Fig. 15. Generation times of *Chelonus kellieae, C. phthorimaeae,* and their host, *Phthorimaea operculella,* at various temperatures (±1°C), 50% RH and 12-hour photoperiod.

Net reproductive rate (R_0) is shown in figure 16. This value included survivorship and progeny sex ratio and is a better estimate of the reproductive ability of an organism (Cole 1954). The R_0 value for both species of parasites was highest at 29.4±1°C. *Chelonus kellieae* produced no female progeny at 32.2±1°C, resulting in an R_0 value of 0. Although R_0 is a measure of the species' reproductive power, it cannot be used to compare two different populations under any given condition, except where generation times are equal.

The pattern of acquisition of r_m was analyzed by progressively summing the proportionate age specific contributions from the adult at age 0, thus finding the period in days required to reach 95 percent of the ultimate growth rate (King 1982). At 21.1±1°C, the period required to reach 95 percent of the ultimate growth rate of r_m is 15 days for *C. phthorimaeae* and 25 days for *C. kellieae.* At 23.9±1°C, 95 percent of the growth rate is reached in 9 days for *C. phthorimaeae* and in 14 days for *C. kellieae.* At 26.7±1°C, this 95 percent value is reached in 10 days for *C. phthorimaeae* and in 12 days for *C. kellieae.* At 29.4±1°C, it is reached in 7 days for *C. phthorimaeae* and in 11 days for *C. kellieae.* At 32.2±1°C,

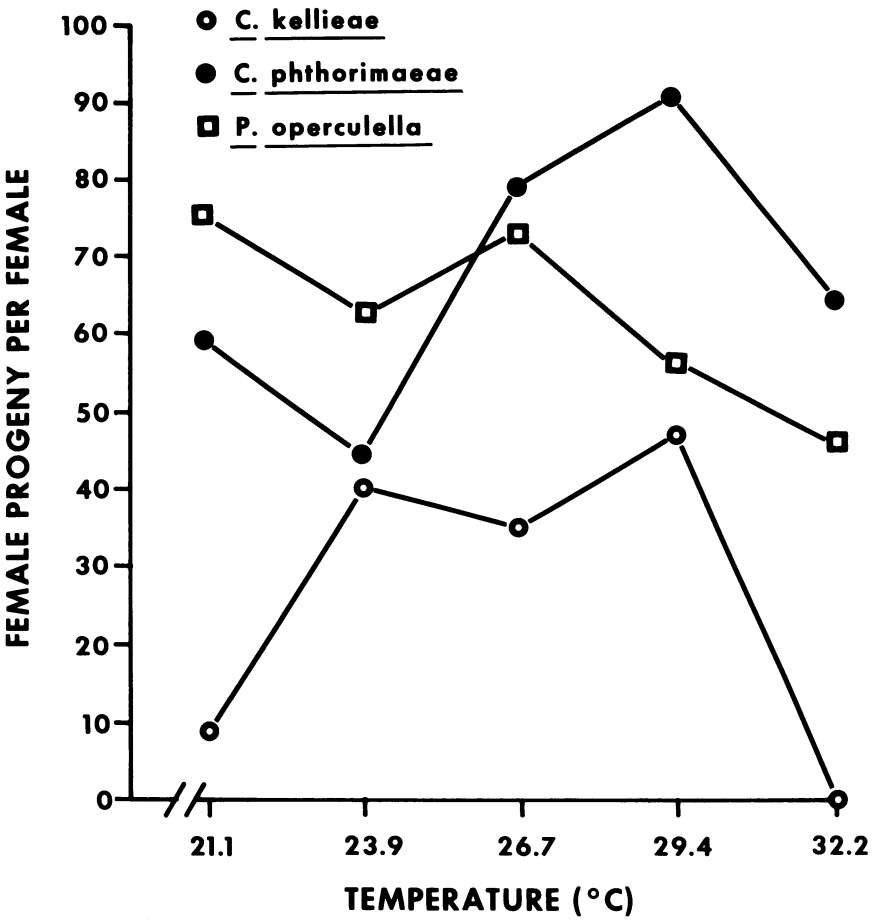

Fig. 16. Net reproductive rates (R_o) of *Chelonus kellieae, C. phthorimaeae,* and their host, *Phthorimaea operculella,* at various temperatures (±1°C), 50% RH and 12-hour photoperiod.

95 percent of the ultimate growth rate for *C. phthorimaeae* was reached in 6 days; there was no value for *C. kellieae* as it produced no female progeny at this temperature.

The innate capacity for increase (r_m) is used to compare responses of different populations under a given set of conditions. The r_m values in figure 17 show that the potential for population increase of the host, *P. operculella,* was far greater than that for *C. kellieae* and *C. phthorimaeae* at 21.1 ±1, 23.9±1, and 26.7±1°C. This is a result of the shorter mean developmental time of the host and, to a lesser extent, its higher net reproductive rate (R_o) values. At 29.4±1°C and 32.2±1°C, the host's potential for population increase was less than that of *C. phthorimaeae.* This may be attributed to the higher net reproductive rate (R_o) values of this parasite at these temperatures. At all temperatures studied, the potential for innate capacity of increase (r_m) of *C. phthorimaeae* and the host was greater than that for *C. kellieae.* This is reflected in the shorter mean time of the development and higher net reproductive rate compared to that of *C. kellieae.* These comparisons of the innate capacity for increase (r_m) show *C. phthorimaeae* having greater r_m values at temperatures of 29.4±1°C and 32.2±1°C than for *C. kellieae* or their host.

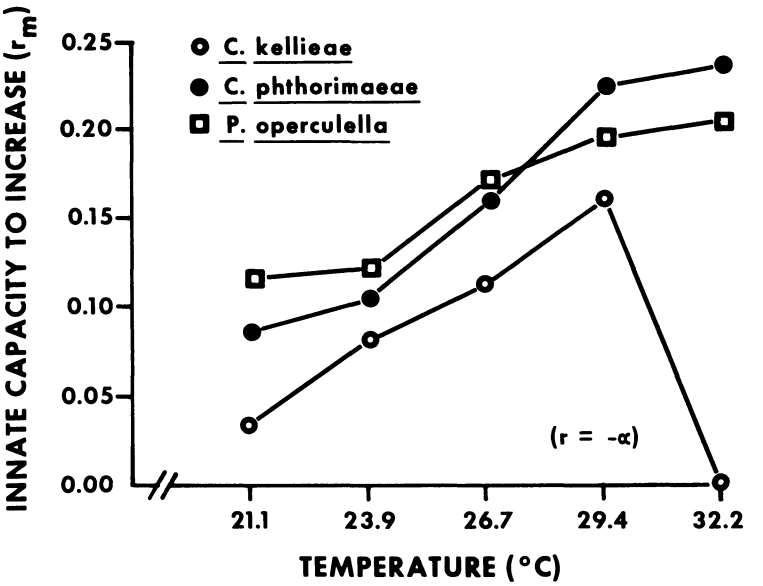

Fig. 17. Innate capacity for increase (r_m) for *Chelonus kellieae, C. phthorimaeae,* and their host, *Phthorimaea operculella,* at various temperatures (±1°C), 50% RH and 12-hour photoperiod.

These data suggest that within the range of temperatures studied, population growth potential, based on r_m values, is greater at higher temperatures for *C. phthorimaeae* compared with *C. kellieae,* indicating that *C. phthorimaeae* has a greater population growth potential than its ecological homologue at higher temperatures, which prevail in southern California.

Various researchers (Huffaker, Rabb, and Logan 1977) have discussed parasite fecundities or intrinsic rate of increase and believe such studies may not realistically assess the parasite's ability to regulate its host population. Although natural populations are much more complex, the importance of the intrinsic rate of increase or innate capacity for increase lies mostly in its use as a model for comparison. In the present study, such comparisons yielded information concerning the biologies and population growth potential at various temperatures, although such information may not be used to predict success or failure. Previous studies by Cardona and Oatman (1975), Odebiyi and Oatman (1977), and Flanders and Oatman (1982) on indigenous and introduced parasites of *P. operculella* in southern California analyzed the extent of parasite adaptability to various temperatures in reference to their biologies and population growth potential. Additional factors that can affect population growth were listed by Messenger (1964) and DeBach (1966); among these are searching capacity and initial host parasite ratio. Oatman and Platner (1974), Cardona and Oatman (1975), Odebiyi and Oatman (1977), and Flanders and Oatman (1982) discussed host range and competition with other parasites as being additional factors that can affect population growth.

Results of studying the indigenous parasite, *C. phthorimaeae,* and the introduced parasite, *C. kellieae,* show that they have similar biologies. However, their potentials for population increase differ. This difference may only indirectly affect their potential for establishment. The competitive interactions of these two parasite species and that of the parasite complex of *P. operculella* should be investigated further.

SUMMARY AND CONCLUSIONS

Comparative studies of the biologies and host relationships of the indigenous *C. phthorimaeae* and the introduced *C. kellieae* were studied at 26.7±1°C, 50% ± 5% RH and 12-hour photoperiod. Comparisons of the population growth potential of both species of parasites and their host, *P. operculella,* were made at five different temperatures.

Both species of parasites are primary, solitary, egg-larval endoparasties of the potato tuberworm. The egg of both species is hymenopteriform. There are three instars, the first being caudate-mandibulate finally becoming vesiculate-mandibulate; the second and third are mandibulate; the third instar possesses spines and setae. The pupa is exarate. Descriptions and measurements of immature stages are given. Superparasitism of the host egg occurred in experimental conditions, but only one parasite larva was found in a host larva. The parasite larva developed in the haemocoel of the still living host. The mature parasite larva emerged from the first instar host and continued feeding externally. It then formed a silver-white cocoon within that of its host.

Descriptions of both species of parasites are given by Marsh (1979) for *C. kellieae* and by Gahan (1917) for *C. phthorimaeae.*

Parasitization of the host by either species did not affect duration of development of *P. operculella* larvae. However, both parasites affected size of the fourth instar host as indicated by reduction in both the head capsule width and body length of the fourth instar.

During the light phase of the photoperiod, adult males of both species emerged from their cocoons 2 days before females. Courtship and mating behaviors of both species were described. Previously mated females did not permit the male to mount and copulate. Males were polygamous. The searching and ovipositional behaviors of both species were described. Once ovipositional activity started, it increased in intensity.

The female of both species of parasites exhibited maximum longevity when given access to carbohydrates and free water. Neither species was observed to host feed. Also, access to carbohydrates and free water was not a prerequisite for progeny production by either species.

One-hundred fifty host eggs, 0-24 hours old, were optimal for *C. phthorimaeae* progeny production (42.2); 50 host eggs, 0-24 hours old, were optimal for *C. kellieae* progeny production (29.0). *Chelonus phthorimaeae,* therefore, produced more progeny when exposed to a greater number of host eggs.

Mated females of *C. kellieae* produced 315.6 progeny compared with 304.2 for virgin females. Virgin females produced more progeny per day than mated females during the first few days after adult emergence. Mated females of *C. phthorimaeae* produced more progeny (568.3) than virgin females (448.7). During the first few days of adult life, mated females produced more progeny than did virgin females. Both species exhibited essentially no preoviposition period for mated females to produce male progeny. Female progeny were not produced until a few hours postemergence. Virgin females also exhibited essentially no preoviposition period.

Both species of parasites were arrhenotokous as virgin females produced only male progeny.

Studies of the population growth potentials for *C. phthorimaeae* and *C. kellieae* were conducted at 21.1±1, 23.9±1, 26.7±1, 29.4±1, and 32.2±1°C, 50% ± 5% RH and 12-hour photoperiod.

Phthorimaea operculella had the shortest developmental and generation time under the given set of environmental conditions. *Chelonus phthorimaeae* had a shorter developmental

time than did *C. kellieae* at all temperatures, except 23.9±1°C, and a shorter generation time than its ecological homologue at all temperatures.

Population growth statistics were calculated based on immature parasite mortality under each of the given temperature conditions for both parasite species. Net reproductive rate, innate capacity to increase, gross reproductive rate, mean generation time, and finite rate of increase were calculated to compare both parasite species to each other and to their host. Results indicate that under the given set of environmental conditions, *C. phthorimaeae* demonstrates a greater innate capacity to increase at 29.4±1°C and 32.2±1°C compared with that for its host and *C. kellieae,* especially so at 32.2±1°C in comparison with *C. kellieae.* At the lower temperatures (21.1±1, 23.9±1, and 26.7±1°C), the host, *P. operculella,* demonstrates the greatest innate capacity for increase compared with both parasites. The finite rate of increase for *C. phthorimaeae* demonstrates the greater growth potential at higher temperatures compared to that for *C. kellieae.*

Comparison of the biologies of both *C. phthorimaeae* and *C. kellieae* shows that the only significant difference is that the population growth potential of *C. phthorimaeae* is greater than that of *C. kellieae* at all temperatures studied, but less than that of its host at 21.1±1, 23.9±1, and 26.7±1°C. This demonstrates the adaptability of *C. phthorimaeae* at higher temperatures of 29.4±1°C and 32.2±1°C. *Chelonus kellieae* produced no female progeny at 32.2±1°C. These studies should not be used as the only indication of success or failure of these parasites to regulate their host. Because of their biological similarities, studies of their competitive interactions should be investigated.

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