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Biology and Physical Ecology of *Apanteles subandinus* Blanchard (Hymenoptera: Braconidae), with Notes on Temperature Responses of *Apanteles scutellaris* Muesebeck and its Host, the Potato Tuberworm

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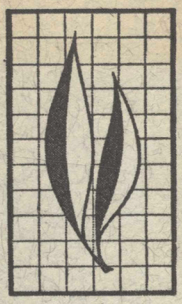

Laboratory investigations were conducted on the biology of *Apanteles subandinus* Blanchard and the effect of temperature and relative humidity on its bionomics. Temperature responses of this parasite were compared with those of *Apanteles scutellaris* Muesebeck and their common host, the potato tuberworm, *Phthorimaea operculella* (Zeller). Responses of the parasites and their host to physical factors were evaluated by using the intrinsic rate of natural increase (r) as a bioclimatic index. At 80°F and 50 per cent relative humidity (R.H.) the mean duration of the life cycle of *A. subandinus* from egg to adult was 15 days; egg, 1 day; first instar, 4.5 days; second instar, 2.5 days; third instar, 2 days; prepupa, 0.5 days; and pupa, 4.5 days. The parasite egg is deposited at random in the body cavity of the host larva where the parasite larva develops. There are three instars, the first being mandibulate-caudate and the other two hymenopteriform. The mature larva emerges from the host, killing it in the process, and spins a silver-white cocoon. There is essentially no preoviposition period in *A. subandinus* and the parasite is an arrhenotokous species, the virgin female producing only male progency. Between 60 and 90°F, speed of development was directly related to temperature. A constant temperature of 95°F prevented development of the parasite beyond the first instar. Longevity and reproductive periods were inversely related to temperature, longevity following the pattern of the curve of physiological longevity. Production of progeny was maximum at 80°F. As determined by calculations of the intrinsic rate of natural increase, *A. subandinus* persisted and increased in numbers between 60 and 90°F. Optimal temperature for the parasite was 85°F. Relative humidity did not affect development. At 80 and 85°F, maximum progeny production occurred at 50 per cent R.H.

(continued inside back cover)

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Biology and Physical Ecology of *Apanteles subandinus* Blanchard (Hymenoptera: Braconidae), with Notes on Temperature Responses of *Apanteles scutellaris* Muesebeck and its Host, the Potato Tuberworm[1]

INTRODUCTION

APANTELES SUBANDINUS Blanchard was first reared in the United States from larvae of the potato tuberworm, *Phthorimaea operculella* (Zeller), which were received in quarantine at the Division of Biological Control, Department of Entomology, University of California, Riverside, on March 16, 1964. The host material had been collected from potatoes in the locality of Ayacucho, Argentina. The parasite was released from quarantine on April 4, 1964, and a stock culture was initiated in the insectary. Shipments of *A. subandinus* were received from Peru in November, 1964, and additional shipments from Argentina in May and December, 1965. The species was first described by Blanchard (1947). Its only known host is the potato tuberworm.

Although high numbers of *A. subandinus* were released in the principal potato growing areas of southern California in 1964, 1965, and 1967, it apparently was not established. However, it was established in India, Cyprus, Australia, and other countries to which it had been shipped from California via India (Rao and Nagaraja, 1968). No biological or ecological studies have been published on this species.

Apanteles scutellaris was described by Muesebeck (1920). This parasite attacks the potato tuberworm and the tomato pinworm, *Keiferia lycopersicella* (Walsingham). It is generally regarded as being indigenous to southern California and is abundant on both hosts throughout the region (Graf, 1917; Elmore and Howland, 1943; and Oatman, 1970). *Apanteles scutellaris* has also been reported from Bulgaria (Stanev and Kaitazov, 1962), Hawaii (Pemberton, 1938), and India and Cyprus (Rao and Nagaraja, 1968). The Commonwealth Institute of Biological Control made shipments of this species to Australia and New Zealand for release against the potato tuberworm (Rao and Nagaraja, 1968). A detailed account of the biology and temperature responses of *A. scutellaris* as a parasite of the tomato pinworm was reported by Djamin (1970).

The potato tuberworm, *Phthorimaea operculella* (Zeller), is a serious pest of potatoes throughout the world. Numerous papers have been published on this pest. Detailed descriptions of its biology, economic importance, and natural enemies were provided by, among others, Picard (1913), Trouvelot

[1] Submitted for publication January 2, 1974.

(1924), Graf (1917), Hofmaster (1949), El Sherif (1961), and Stanev and Kaitazov (1962). However, a detailed account of its temperature relationships has not been published.

Many biological and ecological factors can prevent the establishment of imported parasites in a new agroecosystem. Among them, climate and interspecific competition are usually cited as two of the more important ones (DeBach, 1964). As *A. subandinus* was not established in southern California, whereas it was in other parts of the world, it is possible that climatic conditions or interspecific competition by the native *A. scutellaris* was responsible for the lack of success in California. A major portion of the present study was therefore concerned with basic and detailed laboratory investigations on the biology of *A. subandinus* and the effect of temperature and relative humidity on its bionomics.

Because *A. scutellaris* and the potato tuberworm host have been extensively studied, only the effect of a few selected temperatures on their biologies was studied to provide data for comparisons between the potential for population growth of the two parasite species under different environmental conditions, and between their potential and that of their common host. These comparisons are greatly simplified through the calculation of life tables. Messenger (1964) stated that life tables combined with fertility rates are the best index to rate the performance of organisms in each environment. In this type of study, data are accumulated on developmental rates, fecundity rates, survival and longevity, and from these the intrinsic rate or natural increase (r) is calculated. This particular statistic is the most conclusive bioclimatic index and is a precise measure of the response of a particular organism to different sets of environmental conditions.

A. subandinus and *A. scutellaris* are closely related species not only morphologically but also in their habits, biologies, and host relationships, thus suggesting that competition between them could be intense. Studies of these two species might therefore illustrate controversial but basic principles in biological control such as the competitive displacement principle. Hopefully, data presented herein can be used as the basis for such studies.

MATERIALS AND METHODS

General Insectary Procedures

Environmental conditions

Stock cultures of the host and parasites were maintained in an insectary room at 80 ± 1°F and 50 ± 2 per cent R.H. (relative humidity). Light was supplied by eight 40-watt, white-cool, fluorescent tubes and regulated by an automatic time switch set for alternating periods of 12 hours of light and darkness. A small electric fan was used to prevent stratification of air in the room, augmenting the air-conditioning system.

Mass culture of the host

The potato tuberworm was used as the host and was obtained from stock cultures maintained on White Rose variety potato tubers in the insectary, using techniques developed by Platner and Oatman (1968). From this culture, egg-sheets were obtained daily and kept in tight plastic containers until the eggs hatched. The resulting larvae were used for establishing sub-cultures of the parasites or for infesting potato tubers for specific experiments.

Parasite sub-cultures

A. subandinus and *A. scutellaris* were handled identically throughout these studies. A culture of *A. subandinus* has been kept in the insectary of the Division of Biological Control, University of California, Riverside, since April, 1964. The parasite is produced by using techniques described by Leong and Oatman (1968) and by Oatman *et al.* (1969). The initial stock of *A. scutellaris* was obtained from host material collected from potato plants in a pesticide-free experimental field on the University of California's Moreno Experiment Station near Riverside.

Sub-cultures of the parasites were maintained in wooden cages (16½″ × 16½″ × 14″) that had a glass top, lateral panels of muslin cloth for ventilation, and a detachable round section in each side to facilitate manipulation of material inside the cage without letting the insects escape. White sand was distributed evenly over the bottom of the cage to facilitate pupation of larvae. To initiate a parasite sub-culture, potato tubers infested with newly-emerged potato tuberworm larvae were placed in the cage for oviposition by the parasites. After 48 hours exposure, the tubers were removed and placed on an inverted tray made of ½″ galvanized wire mesh inside a cage similar to that described above. White sand was provided to facilitate pupation of the parasitized and non-parasitized larvae. These operations were repeated periodically, using two rearing units per each species. In this manner, parasite material was available in large numbers. When needed, virgin females of the parasites were obtained by isolating cocoons in gelatin capsules (size 000) until the parasites began to emerge.

General Experimental Procedures

Temperature cabinets

Most of the experiments were conducted in constant temperature cabinets made from modified apartment-size refrigerators (Platner, *et al.*, 1973). As no apparatus for controlling humidity existed in these cabinets, air humidity was regulated by means of sulfuric acid solutions which kept the relative humidity within 2 or 3 per cent of the desired level. At low temperatures (60 to 75° F), the solutions lasted for 3 or 4 weeks but, at high temperatures (85 to 95° F), they usually had to be changed on a weekly basis.

Experimental rearing units

To rear specific numbers of the host, medium size potato tubers of the White Rose variety were punctured with a tack-studded device (Finney, *et al.*, 1947) to insure even and adequate larval infestation. After puncturing, the tubers were impaled lengthwise on nails that had been driven through a sheet of ½″ plywood, leaving 2 inches protruding to provide support for each tuber during the study. The tubers were pressed down on the nails, leaving an adequate space between the tuber and the surface so that the female parasite had access to the entire tuber (fig. 1).

Before placing the potato tubers on the nails, the top of a plastic Petri dish, in which a hole had been centrally bored, was placed on a nail and pushed down until it rested on the plywood base to serve as a collection unit. The inside of the dish was then lined with paper and fine white sand was distributed evenly over it to facilitate pupation of the host larvae. The potato tuber was then inserted on the nail and infested with the number of host larvae required for a given experiment. The newly-emerged potato tuberworm larvae were

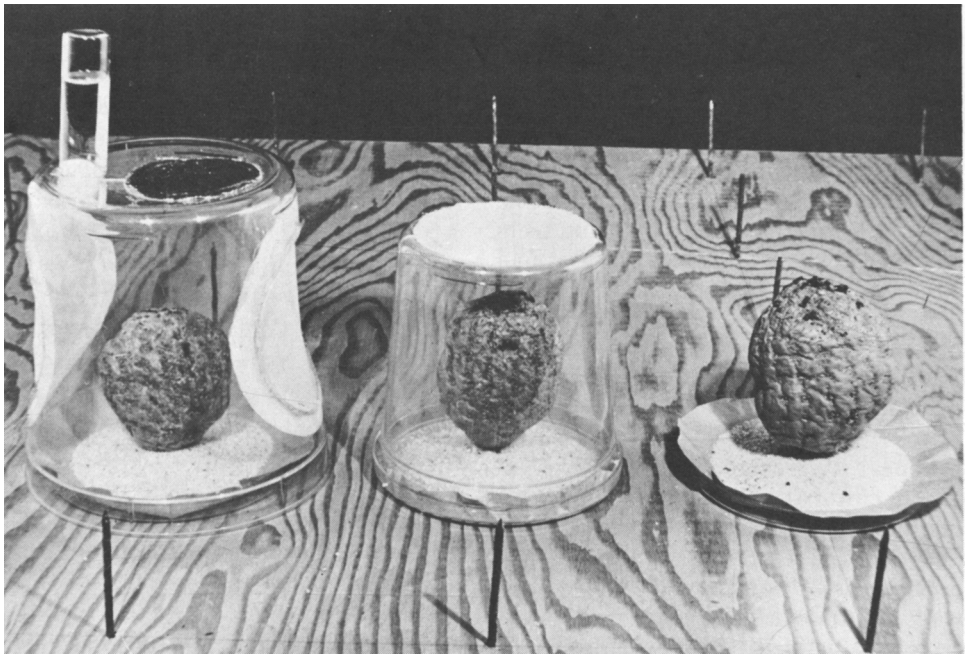

Fig. 1. Experimental setup utilized to rear specific numbers of the potato tuberworm host.

transferred from the emergence containers to the tubers with a camel's hair brush (size 0000).

The infested tubers were then covered with holding cages which consisted of clear, polystyrene, 1-pint containers. The bottom of the container had been cut off and vented by covering the opening with organdy. The containers measured 2¾″ in diameter at the bottom, 3½″ in diameter at the top and 3¾″ high. To prevent the mature, pupating host larvae from escaping, the holding cage was inverted and pressed down so that the rim of the unit fit tightly inside the rim of the paperlined Petri dish.

Parasite oviposition units

Clear, polystyrene, 1-quart containers were used as oviposition cages for the parasites. These units were vented on opposite sides by 2″ holes covered with organdy, and each unit had 1½″ openings cut in its bottom. These openings were covered with a 100-mesh brass screen through which pure honey was forced to serve as food for the parasites. Tap water was supplied in a cotton-stoppered 2-dram glass vial inserted upside down in a ½″ hole cut in the bottom of the container. When infested tubers were to be exposed to the parasite females, the holding cages (previously described) were removed and replaced by oviposition cages with their rim resting on the plywood sheet. The parasites were then introduced through the ½″ opening from gelatin capsules or with the aid of an aspirator. After oviposition, the oviposition units and the parasites were removed and the holding cages were again placed over the tubers. After pupation of healthy and/or parasitized host larvae occurred, the Petri dish top was removed and its hole covered with tape. The excess sand was then discarded and the pupae were enclosed with the bottom of the Petri dish. The emergence unit thus formed was stored until the host and parasite adults

had emerged and died. The adults were then removed, counted, and sexed.

The oviposition cages were also utilized for isolation of virgin individuals, for mating observations, and for studying the effect of food on longevity by closing the units with a polystyrene lid.

Parasite adults were never anesthesized and were always manipulated with the aid of a mouth aspirator.

The rearing and ovipositional experimental setup was modified for use in the temperature cabinets by utilizing smaller plywood sheets which fit on metal racks inside the cabinets.

Determination of optimal host age and density for exposure to parasites

The age and density of the host larvae apparently influence the oviposition rate of a parasite (Leong and Oatman, 1968; Oatman, *et al.*, 1969). To determine the most suitable age of the host to be exposed to the parasite, potato tubers, each infested with 50 potato tuberworm larvae of a known age, were exposed to a single mated parasite female for 24 hours. The numbers of resulting moths and parasites were recorded. The experiment was replicated 10 times for each host age group.

After learning the optimal host age, optimal host density was determined by infesting potato tubers with different host numbers. When the larvae reached the most suitable age, they were exposed to single mated parasite females for 24 hours. After development, the numbers of parasites and moths produced were recorded. The experiment was replicated 10 times for each host density. These two experiments were conducted in the insectary under the physical environmental conditions described previously.

Life Table Studies

Life tables were constructed for each species and combination of environmental conditions being studied. This required the daily observation of a cohort of individuals of the same species and the compilation of the following data: duration of development; daily survival; daily progeny production; longevity of the adult female; progeny sex ratio; and the effect of superparasitism (parasites only).

As the temperature and/or R.H. at which parasite females were reared might have a marked effect on their biology, especially progeny production, the females utilized to start temperature and humidity studies were themselves reared from egg to adult at the given environmental conditions.

Determining duration of development

To study the effect of physical factors on the developmental rates of *A. subandinus* and *A. scutellaris*, tubers were infested with the optimal host density and held in the insectary until host larvae reached the optimal age for exposure to the parasite. They were then transferred to the respective temperature cabinet and placed in a cage with a large adult parasite population. After 4 hours exposure, the parasites were removed. One tuber was then taken from the cabinet and the host larvae recovered by using the heat-extraction technique developed by Platner, *et al.* (1969). This procedure was repeated at 12, 18, and 24 hours and every 24 hours thereafter until development was completed. The host larvae, prepupae, and pupae thus obtained were placed directly in 75 per cent ethanol for preservation. Later, this material was dissected to follow the development of the parasite. In all cases, some tubers were left undisturbed in the cabinets until complete development of the parasites occurred and the

adults emerged. These adults were then utilized to initiate the parasite reproduction studies.

To measure the duration of development of the potato tuberworm, moths were collected from the stock culture cages and placed in the respective temperature cabinet in an oviposition unit (Platner and Oatman, 1968) for 12 hours. The resulting egg sheet was cut in small pieces, containing known numbers of eggs. Each piece was then placed on top of a freshly punctured potato tuber, covered with a holding cage of the type described previously, and immediately returned to the cabinet. On hatching, the larvae penetrated the tuber and started feeding. The duration of the egg stage was then recorded. After hatching, tubers were removed from the cabinet every 24 hours. Larvae were recovered from the tubers by heat extraction, killed in alcohol, and their head capsules measured with the aid of a calibrated eyepiece micrometer in a dissecting microscope. Dyar's law was applied to detect the occurrence and number of instars. When pupation began, the formation of prepupae and pupae was carefully noted. Some of the potato tubers were left undisturbed until the moths emerged. The rest were used for the collection of pupae for sexing. Separation of sexes in the adult stage is extremely difficult in the potato tuberworm but can be easily distinguished in the pupal stage with a microscope. After sexing, the pupae were separated in emergence units and returned to the temperature cabinets. The resulting moths were utilized to initiate reproduction studies.

Reproduction studies

Parasite adults from the development studies were placed in feeding and mating units and returned to their respective temperature cabinet. After 4 or 6 hours, cohorts of 15 males and 15 females were selected and one male and female per each pair (15 pairs per temperature) were placed in separate oviposition units and exposed to a potato tuber infested with the optimal host number of the optimal host age. Every 24 hours, each parasite pair was transferred to another oviposition unit, containing an identical number and kind of new hosts. This operation took from 5 to 10 minutes so that disturbance of the experimental system and the cabinets was minimal. The exposed tubers were held in the insectary until the emergence of progeny had occurred. The operation was repeated daily until all female parasites in the cohort died. This provided data on daily progeny production, sex ratios, longevity, and survival of adults.

Cohorts of 35 males and 35 females of the potato tuberworm which emerged from development studies were selected and one male and female per each pair (35 pairs per temperature) were placed in separate oviposition units. These units consisted of 45-dram plastic vials. Each vial was supplied with a cotton-stoppered 1-dram glass vial of water. Honey was streaked on the sides of the unit to serve as food. After introduction of a pair of moths, each vial was covered with a small sheet of unbleached muslin cloth stretched tightly over the top and secured with a ruber band. The females were induced to oviposit on the underside of the cloth by rubbing potato juice on the top of the cloth. Every 24 hours the oviposition units were removed from the cabinets, the moths lightly anesthesized with CO_2, and the egg-sheets changed. Anesthetization apparently has no deleterious effect on adults of the potato tuberworm (Platner, unpublished data). The resulting eggs were counted and a portion of the sample was reared in the insectary until the insects reached the pupal stage. The pupae were then separated from the sand with sodium hypochloride and their numbers and sexes recorded. As with the parasites, these procedures were continued until the last female in the cohort died.

Construction of Life Tables

The methods of Birch (1948) were used in constructing life tables and in calculating intrinsic rates of natural increase. In the life tables, the basic data on development, survival, and fertility were used as follows:

x = the age of the individuals in days (age interval column)

1_x = the proportion of individuals still alive at age x

m_x = the number of female offspring produced per female in the age interval x.

The calculation of immature survival for the pre-reproductive period in the 1_x column posed a special problem in the case of the potato tuberworm and its parasites. The host completes its larval development inside the tuber, and parasites develop internally in the host throughout their immature stages. Thus, it was impossible to know exactly the initial number of parasites and, hence, to calculate the immature mortality. This value had to be estimated, using results from previous experiments which had indicated that a newly-emerged female produced an average of 37 to 40 progeny in a period of 8 hours at 80° F and 50 per cent R.H. This value was taken as 100 per cent survival and entered in the life tables as $1_x = 1.00$. To obtain the 1_x values for the immature stages at a given temperature, a series of 20 tubers was infested and exposed to the parasites at 80° F and 50 per cent R.H. for 8 hours. The potato tubers were then immediately placed in the respective temperature cabinet and left undisturbed until development was completed and adult parasites had emerged. The number of parasites obtained was recorded and compared with the 80° index already mentioned. When emergence was substantially lower than the number that theoretically should have been obtained, egg and larval mortality was assumed to have occurred and was introduced into the 1_x column of the life tables.

As the m_x value of life tables might be greatly influenced by superparasitism, its incidence was measured in detail by dissection of large samples of parasitized hosts.

Barlow (1962) and Messenger (1964) stated that sex ratios are important in the calculation of life tables as they affect the values in the m_x column. Therefore progeny sex ratios were carefully recorded. Daily sex-ratio correction factors (percentage of females in the mean total daily progeny) were then calculated. The mean total daily progeny multiplied by the corresponding sex-ratio correction factor thus gave the corrected m_x value of the life table.

The following statistics were computed from each life table:

a) the Gross Reproductive Rate (GRR) which is the sum of the m_x column and represents the total number of female eggs produced by the average female without taking survival values into account.

b) the Net Reproductive Rate (R_o) which is the sum of the $1_x m_x$ column. This value represents the number of female decendants that an average female leaves in one generation. It has also been called the Replacement Rate.

c) the intrinsic rate of natural increase (r). This has been defined by Andrewartha and Birch (1954) as the actual rate of increase of a population under specified constant environmental conditions in which space and food are unlimited. This statistic is computed from the data of the life table according to the formula:

$$\sum e^{-rx} 1_x m_x = 1$$

Since this formula involves a series of trial and error computations, Birch's

(1948) method of calculation was used, but as modified by Watson (1964). The values of r obtained for the different environmental conditions were used to estimate the responses of the organisms to the particular set of conditions. The highest value of r was then used as a climatic index based on the fact that the organism reaches its maximum value of r when placed in an optimal environment (Macfadyen, 1963).

d) Generation time (T) which is the mean length of a generation (birth to weighted mean reproductive age in the adult) was calculated from the formula:

$$T = \frac{\log_e R_o}{r}$$

Immature Stages of *A. subandinus*

To follow the development of the parasite, dissections were made every 12 hours. Host material, containing different immature stages of *A. subandinus,* was dissected in a 0.9 per cent saline solution. Parasite eggs and larvae were removed from the host and measured with a calibrated eye piece micrometer in a compound microscope. Larval stages were mounted in Hoyer's solution on microscopic slides and their morphology studied.

The larvae were cleared by boiling them for 10 to 15 seconds in a 10 per cent KOH solution. After washing in distilled water, they were mounted on microscope slides. The head capsules and mandibles were measured with a calibrated eyepiece micrometer in a compound microscope. First and second instar larvae were stained with acetocarmine.

The head structures of the last instar larva were studied by excising the heads and immersing them in a lactophenol solution for 8 to 24 hours. They were then washed with distilled water and mounted in a drop of Hoyer's solution in the cavity of a monoconcave microscope slide.

To study the prepupae and pupae, cocoons were opened longitudinally by the use of microdissecting scissors. The prepupae and pupae thus obtained were measured and observed.

All drawings were made with the aid of a drawing tube attachment on a Wild compound microscope.

RESULTS AND DISCUSSION

Apanteles subandinus Blanchard

I. Biology and Morphology

Life cycle and host parasite relationship

The basic biology and the morphology of immature stages of *A. subandinus* were studied at 80° F, 50 per cent R.H., and 12 hours photoperiod. Under these conditions, the mean duration of the life cycle from egg to adult emergence was 15 days. The shortest period from egg to adult was 14 days and the longest, 16 days. Emergence of males usually preceded the females by one day. The mean duration of the developmental stages was as follows: egg, 20 to 24 hours; first instar, 4½ days; second instar, 2½ days; third or last instar, 2 days; prepupa, ½ day; and pupa, 4½ days.

The egg was always found floating free in the body cavity of the host. Usually only one egg was deposited per host, but occasionally 2 or 3 eggs were found, indicating that superparasitism may occur. As several first instars of the same size could be found in a single host, hatching of eggs apparently was not

prevented by superparasitism. However, intraspecific competition in the form of destruction of supernumerary larvae occurred because their remains were found, and because no more than 1 late first instar larva was ever found in a host; also, no more than one parasite ever emerged from a single cocoon. Females did not oviposit in host eggs or pupae.

The larvae of *A. subandinus* were found floating free in the body cavity of the host larvae, but mature individuals were located primarily in the posterior half of their host. The parasite apparently does not feed on vital organs of the host until ready to emerge for pupation. Mature parasitized host larvae did not differ noticeably in behavior from healthy individuals. The parasite larvae probably do feed on secondary tissue (fat) because parasitized host larvae were almost always smaller than healthy ones. However, when the host was ready to pupate and started to spin its cocoon, the parasite fed on vital organs and finally killed the host by cutting its way out along the lateral line of the host. The remains of the host, consisting of the integument and the head capsule, were usually found attached to the parasite cocoon.

These observations indicate that *A. subandinus* is a primary, solitary, larval endoparasite of the potato tuberworm.

Development of the parasite was well synchronized with that of the host at all temperatures tested. Almost invariably, emergence of the parasite occurred 1 day prior to that of the potato tuberworm.

Morphology of Immature Stages

Egg

Both the ovarian and the newly-deposited egg are elongated and translucid. The cephalic or anterior end is somewhat rounded but the posterior end presents an elongated, translucid stalk or pedicel. The chorion is smooth, thin, and transparent. The ovarian egg is somewhat smaller than the newly-deposited egg. The mean length of 22 eggs, 0- to 4-hours old, was 0.322 mm (range: 0.260 to 0.380 mm) and the mean width at the widest point was 0.065 mm (range: 0.059 to 0.083 mm).

The contents of recently-deposited eggs are homogeneous, but as development proceeds a deep zone differentiates in the central part. As the embryo develops, the egg increases in size. Thus, at 20 hours after oviposition, the mean length of 39 eggs was 0.345 mm (range: 0.261 to 0.404 mm); mean width, 0.092 mm (range: 0.059 to 0.119 mm). Mean length of 14 mature, 24-hour-old eggs was 0.346 mm (range: 0.285 to 0.428 mm); mean width, 0.108 mm (range: 0.095 to 0.143).

Hatching of most eggs apparently took place between 20 and 24 hours after oviposition because almost all individuals found during this time were either early first instar or mature eggs in which the first instar could be seen through the membrane.

First instar larva

The early first instar corresponds with Clausen's (1940) definition of the mandibulate type. However, as it also possesses a caudal horn in its early stages, it could also be classified as being mandibulate-caudate. It has a translucent body that tapers gradually toward the caudal horn. The body (fig. 2) consists of a broad quadrate head, 3 thoracic and 7 abdominal segments, and a caudal horn. The last abdominal segment is about twice as long as the others and appears to be composed of two subsegments faintly divided. As growth proceeded, this segment clearly divided into two

distinct segments. A prominent caudal horn projects from the first abdominal segment. No tracheal system is apparent.

The head is a strong, quadrate structure (fig. 2) bearing a pair of anterolateral labral processes. Labium and labrum are present and there are two anteroventral, sharp-pointed, sickle-shaped mandibles with broad bases (fig. 2). The tips of these mandibles are more sclerotized than their bases. Their bases are supported by rod-like structures and their tips are directed inwardly.

Early first instars changed little in size or appearance until they were 1.5 days old. Newly emerged first instars had a mean length of 0.307 mm and a mean width of 0.144 mm (table 1). These dimensions gradually increased as growth proceeded. The mean length of late first instars was 1.335 mm and their width, 0.276 mm. The entire body became more opaque, the head narrower than the rest of the body and less prominent. The segmentation became more marked and eleven segments could now be counted (fig. 2). As development continued, the caudal horn gradually decreased in size and evolved into a large, conspicuous, bladder-like vesicle (fig. 2). According to Narayanan, *et al.* (1956) this vesicle, a caudal projection of the proctodaeum, seems to have a respiratory function in some parasite Hymenoptera.

Measurements of the head capsules and the right mandibles of 30 early, 25 intermediate, and 39 late first instars showed that no molt occurred during this period. Despite considerable changes in body size and appearance, the width of the head capsule did not change significantly from early to late first instar. The size and configuration of the mandibles also did not change. The mean width of the head capsule of 94 individuals was 0.151 mm (range: 0.144 to 0.153 mm). The mean length of their mandibles was 0.065 mm (range 0.063 to 0.067 mm) and their mean width, 0.020 mm (range: 0.019 to 0.023 mm).

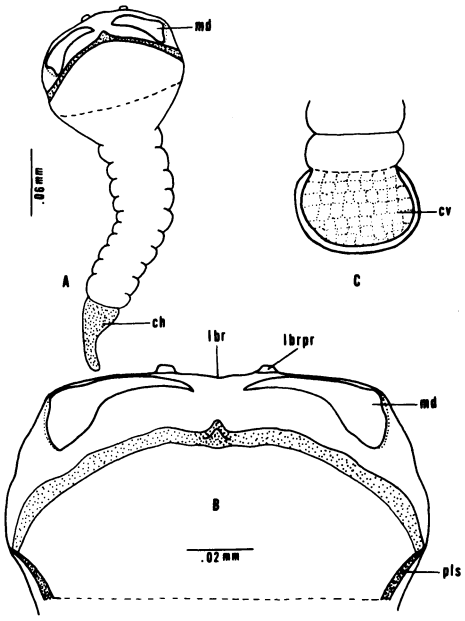

Fig. 2. First instar larva of *A. subandinus*. A, early first instar; B, detail of head of early first instar; C, posterior of late first instar. (ch, caudal horn; cv, caudal vesicle; lbr, labrum; lbrpr, labral process; md, mandible; pls, pleurostoma).

Second instar larva

The general appearance of the second instar resembles that of Clausen's (1940) hymenopteriform type. The body of the larva is creamy-white and consists of a head as wide as the rest of the body, 13 well-defined segments, and a prominent anal vesicle. The head capsule and mouthparts are very weakly scelerotized. For this reason, a long process of clearing with lactophenol was required to detect and observe the mandibles which are sickle shaped and anteroventral in position.

The second instar first appeared 5.5 days after oviposition and lasted 2.5 days. The mean length of early second instar was 1.865 mm and the mean width at the widest point, 0.337. The

TABLE 1

BODY MEASUREMENTS OF LARVAE OF *A. SUBANDINUS*

Age (days)	Number measured	Length (mm)			Width (mm)		
		Range	$\bar{x}$	SD	Range	$\bar{x}$	SD
			first instar				
Just emerged	30	0.261—0.357	0.307	0.027	0.119—0.166	0.144	0.011
0.5	14	0.261—0.357	0.307	0.030	0.119—0.190	0.148	0.019
1	22	0.285—0.476	0.325	0.040	0.119—0.166	0.147	0.015
1.5	25	0.380—0.423	0.361	0.045	0.142—0.166	0.148	0.008
2	10	0.471—0.595	0.511	0.037	0.142—0.166	0.149	0.005
2.5	25	0.476—0.595	0.547	0.062	0.142—0.166	0.177	0.018
3	10	0.619—0.823	0.707	0.086	0.142—0.190	0.177	0.015
3.5	9	0.714—1.040	0.820	0.131	0.142—0.238	0.186	0.025
4	11	1.166—1.385	1.335	0.229	0.283—0.404	0.276	0.045
			second instar				
Early	45	1.714—2.071	1.865	0.257	0.261—0.523	0.337	0.085
Mature	37	2.142—2.690	2.278	0.306	0.357—0.595	0.457	0.075
			third instar				
Mature	119	2.666—4.465	3.241	0.580	0.733—1.333	0.906	0.105

mature second instar reached a mean length of 2.278 mm and a mean width of 0.457 mm (table 1). The general configuration of early and mature second instars was similar except for size. The mean width of the head capsule of 31 individuals was 0.231 mm (range: 0.208 to 0.237 mm) and did not change from early to mature stages of the instar. The mean length of their right mandibles was 0.094 mm (range: 0.092 to 0.095 mm); mean width, 0.057 mm (range: 0.053 to 0.060 mm).

The main internal structures are the mid-intestine which occupies the central portion, a pair of salivary glands, and the tracheal system. The paired salivary glands surround the mid-intestine and form a series of loops that fill the major portion of the body cavity. The extensive tracheal system forms a network and consists of two main lateral-longitudinal trunks and a number of midlateral trunks which later subdivide. This system does not extend into the anal vesicle. No spiracles were seen. The body lacks spines or setae.

Third instar larva

The third instar is hymenopteriform (fig. 3). Early stages of the instar have an anal vesicle but this is absent in mature specimens. The body of the last instar is strong, stout, and tapering towards both ends. It is creamy-white and consists of the head, 13 well-defined segments and, in early stages, an anal vesicle. The head, which seems to be telescopic, is small compared to the rest of the body and not as prominent as in the first instar. It presents a well sclerotized tentorium and mouthparts which are well developed and sclerotized. The mandibles are bifid at the tips and bear a row of saw-like teeth on the dorsal edge of the blade. The average length of the last instar was 3.241 mm and the mean width, 0.906 mm (table 1). The right mandibles of 18 individuals averaged 0.127 mm (range: 0.103 to 0.139 mm) in length and 0.062 mm (range: 0.053 to 0.068 mm) in width. The mean width of the head capsules of 10 individuals was 0.442 mm (range: 0.395 to 0.492 mm).

The first thoracic segment is the longest one of the body. Except for the last abdominal segment, all body segments bear a row of minute setae which are more prominent on the dorsum.

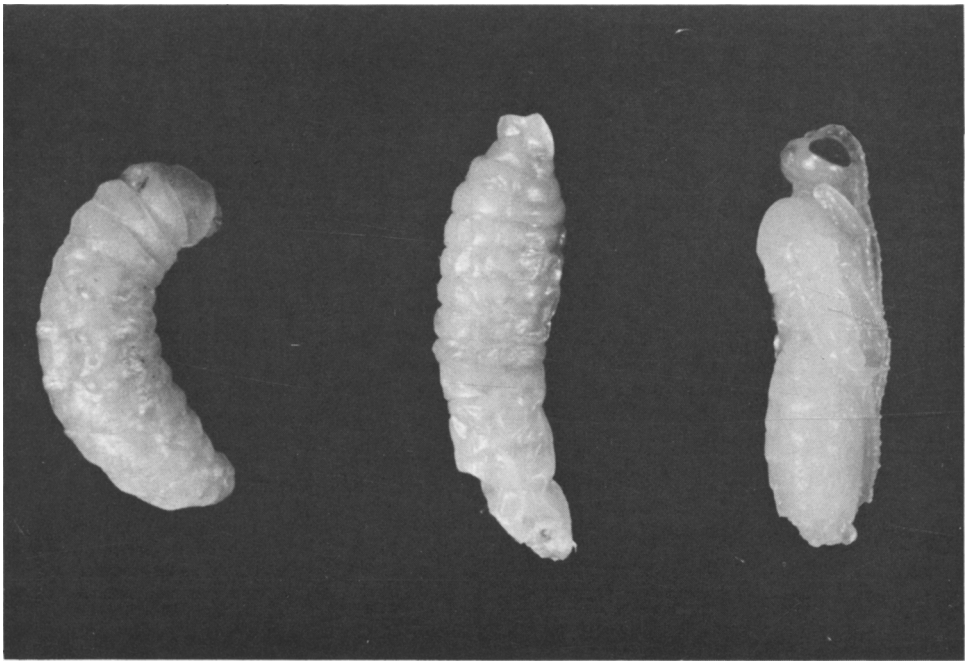

Fig. 3. Third or last instar (left), prepupa (center), and pupa (right) of *A. subandinus*.

The digestive system consists of the mouth, a slender esophagous, a prominent mid-intestine, and the anus. A pair of coiled, tubular silk glands occupies a large portion of the body cavity. These glands extend from the eighth abdominal segment, uniting approximately at the level of the second abdominal segment. The united silk glands then form a common salivary duct which extends to the pharynx and reach the mouth. The tracheal system, although similar to that of the second instar, is open in the third. Eight pairs of spiracles are present; one in the second thoracic segment and one in each of the first seven abdominal segments.

The third and last larval instar appeared on the 8th day after oviposition and lasted 2 days.

Head structures of the last instar larva

The terminology of Short (1952, 1953) is used to describe the head structures of the last instar larva (fig. 4). The mandibles are well sclerotized, bifid, and bear a series of strong teeth. The pleurostoma, with which the mandibles articulate, show a marked differentiation between anterior and posterior processes. The hypostoma, which is long, extends laterally, curves upwards, and forms a semicircle partially surrounding the stipital sclerites. The sclerotic spur of the hypostoma is an extension of the hypostoma toward the stipital sclerite. The labial sclerite is U-shaped and occupies the central portion of the structure; from it the paired stipital sclerites project laterally toward the hypostoma. The labial sclerite encloses the region of the prelabium, the paired papilose labial palpi, and the well-developed silk press. A pair of smaller papilose maxillary palpi are located close to the dorsal end of the labial sclerite. Antennae are absent.

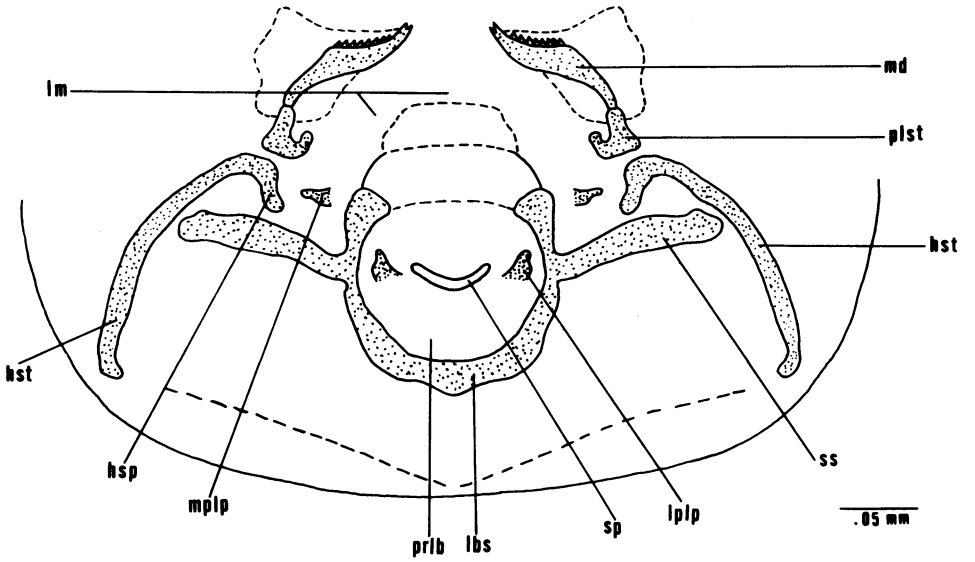

Fig. 4. Schematic representation of last instar larva head structures of *A. subandinus* (hsp = sclerotic spur of hypostoma; hst = hypostoma; lbs = labial sclerite; lm = labrum; lplp = labial palp; md = mandible; mplp = maxillary palp; plst = pleurostoma; prlb = prelabium; sp = silk press; ss = stipital sclerite). Terminology according to Short (1952, 1953).

Cocoon

The cocoon is spun by the mature last instar larva inside that of the host, soon after it emerges from the host. The cocoon is rounded at both ends, cylindrical, silver-white, dense, and strong. The mean length of 59 cocoons was 4.412 mm and the mean width, 1.74 mm. The meconium of the larva was found at one extreme end of the cocoon.

Prepupa

The prepupal stage appeared on the 10th day after oviposition and lasted for about 12 hours. It appears soon after discharge of the meconium by the last instar larva. Soon thereafter the prepupa differentiates from the last instar by the appearance of a constriction in the middle portion of the larval body, and by the appearance of spots corresponding to the future location of the pupal eyes (fig. 3). The average length of 15 prepupae was 3.800 mm and the average width, 1.168 mm.

Pupa

The pupa of *A. subandinus* is of the exarate or "free" type. Although creamy-white at first, it gradually darkens as development proceeds. The mean length of 84 pupae was 3.600 mm and the mean width 1.727 mm. It appeared for the first time 10.5 days after oviposition and lasted from 4 to 6 days. Male pupae developed faster than did females, and emergence of males usually preceded females by one day. They are easily distinguished by sexual characters.

The morphology of the immature stages of *A. subandinus* is generally quite similar to that of *A. dignus* (Cardona and Oatman, 1971) and to that of *A. scutellaris* (Djamin, 1970). The main differences are in the egg stage and in the characteristics of the head structures. The larval stages, especially the first instar of *A. subandinus* and *A. scutellaris,* could not be distinguished.

Characteristics of adults

A. subandinus males and females were described in detail by Blanchard (1947). Both are black with palps and tibiae less dark. Females (fig. 5) measure approximately 3.864 mm from the tip of the head to the tip of the abdomen. The average length of the ovipositor is 0.635 mm. The male (fig. 5) is somewhat smaller with an average length of 3.635 mm. Both are similar to males and females of *A. scutellaris*. A detailed account of the morphological differences between these two closely related species was given by Rao and Nagaraja (1968).

General behavior of adults

Emergence of adults of *A. subandinus* was stimulated by light. Soon after emergence the adults cleaned their bodies and fed if food was available. However, mating sometimes preceded both activities, especially if fully-fed males were exposed to emerging females. This commonly occurred, as males usually emerged 1 day before the females. The presence of virgin females excited males highly. Prior to mating, the male fanned his wings and walked in this manner towards the female. If the female was receptive, the male mounted her, bent his abdomen towards the female's genital area, and copulated with her. Copulation usually lasted 50 to 60 seconds. Males were observed to mate with several females in a single day or with several females on different days. However, mated females were reluctant to copulate.

Determination of preoviposition period

To ascertain if there is a preoviposition period in *A. subandinus,* the following experiment was conducted: cocoons of the parasite were isolated in gelatin capsules and left until the adults emerged. Immediately after emergence,

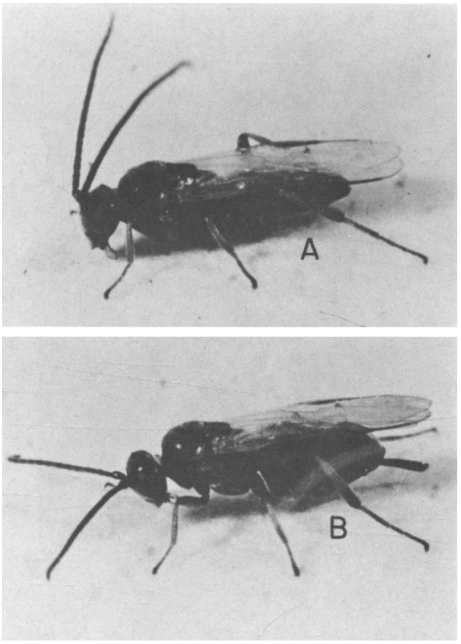

Fig. 5. Adults of *A. subandinus*. A, male; B, female.

10 females were each isolated with a fully fed male for 20 minutes in the presence of honey to assure mating.

A series of units, containing potato tubers each infested with fifty 2- to 3-day-old host larvae was prepared. Each newly-emerged but already fed and mated female was then confined in the first unit for 1 hour. Afterwards, she was transferred to a new unit. The host larvae were exposed in this manner when the parasite females were 0 to 1, 1 to 2, 3 to 4, and 7 to 8 hours old. After pupation of the host larvae occurred and the parasite had emerged, the numbers of parasites and hosts were recorded. The same procedure was followed with virgin parasite females.

Both virgin and mated parasite females produced viable progeny within 80 minutes after emergence (table 2). All the mated and virgin females laid eggs with oviposition being uniform throughout this period. The data thus indicate that there is essentially no pre-

TABLE 2

DETERMINATION OF PREOVIPOSITION PERIOD AND NUMBER OF PROGENY PRODUCED BY MATED AND VIRGIN FEMALES OF *A. SUBANDINUS* DURING FIRST 8 HOURS OF LIFE

Age of female (hours)*	Average number of progeny produced per unit†			
	Mated females		Virgin females	
	Males	Females	Males	Females
0—1	4.6	4.2	8.3	0
1—2	4.2	5.0	9.6	0
3—4	3.8	4.8	8.3	0
7—8	4.8	5.6	9.0	0

* Ten mated and 10 virgin females were each allowed 20 minutes for feeding and/or mating before exposure to host.

† Each unit contained 1 potato tuber infested with 50, 2- to 3-day-old potato tuberworm larvae.

oviposition period in this species. The data also show that the progeny of virgin females consisted entirely of males. Thus, *A. subandinus* is an arrhenotokous species.

Ovipositional behavior of the adult female

When exposed to potato tubers containing potato tuberworm larvae, females of *A. subandinus* actively walked about tapping the surface of the tuber with her antennae and ovipositor. The frass produced by the tunneling host apparently attracts the female. Upon contacting a pile of frass, the female stopped and examined it carefully. Usually, she then probed with her ovipositor. If a host was contacted, she inserted her ovipositor and quickly deposited an egg. Probing was repeated if a host was not contacted. These activities were repeated until most of the surface of the tubers was contacted.

Effect of food on longevity

Tests on the effect of food on longevity were conducted by placing 10 newly-emerged males and 10 females in each of a series of clear polystyrene units. The parasite adults were then supplied with either water or honey, or a combination of both. The effect of complete starvation was also recorded. Initially, 30 males and 30 females were to be tested in each treatment but, as a high variability was noted, the experiment was conducted with as many individuals as were available. The mortality of each sex was recorded every 24 hours.

None of the treatments had a differential effect on longevity of the sexes (table 3). Water alone did not significantly increase longevity over that recorded for starved individuals. Individuals lived approximately 3 days longer on honey than those provided only water. Their life span was prolonged considerably when given both honey and water, increasing from a mean longevity of about 5 days with honey to a mean of about 17 days. Therefore, honey and water were provided for the adults of *A. subandinus* in all subsequent experiments.

TABLE 3

EFFECT OF FOOD ON LONGEVITY OF *A. SUBANDINUS*

Type of food	Males			Females		
	Number studied	Longevity (days)		Number studied	Longevity (days)	
		Range	Mean		Range	Mean
None	53	1—3	1.80	66	1—3	1.85
Water	48	1—3	2.16	44	1—3	2.16
Honey	54	4—8	4.96	42	4—7	4.99
Water and honey	116	4—35	17.38	123	4—27	16.97

TABLE 4
EFFECT OF AGE OF POTATO TUBERWORM LARVAE ON PARASITIZATION BY *A. SUBANDINUS*

Age of host larvae at exposure (days)	Mean number of individuals emerged per replicate*		Per cent of host larvae parasitized†	Per cent of total individuals emerging‡
	Moths	Parasites		
0—1	13.1	22.3	62.9	70.8
1—2	14.4	25.8	64.1	80.4
2—3	13.5	26.6	66.3	80.2
3—4	15.3	25.4	62.4	81.4
4—5	24.0	17.7	42.4	83.4
5—6	35.0	4.7	11.8	79.4
6—7	38.4	3.6	8.6	84.0
7—8	40.0	0.7	1.7	81.4
8—9	42.7	0.0	0.0	85.4
Control	39.5	0.0	0.0	79.0

* Mean of 10 replicates. Each replicate consisted of 50 potato tuberworm larvae of a given age exposed to a female parasite for 24 hours.
† Calculated on the basis of the total number of individuals emerged (significant differences discussed in text).
‡ Mean per replicate.

Determination of optimal host age for parasitization

Potato tubers, each infested with 50 potato tuberworm larvae of a known age, ranging from less than 1 day to 8- to 9-days old, were exposed to a single mated parasite female for 24 hours. After development, the numbers of moths and parasites were recorded. The experiment was replicated 10 times, including also a control (non-exposed).

The results are summarized in table 4. Although significant differences were obvious, an analysis of variance was conducted on the mean per cent of parasitization to compare the means. The F test was highly significant. Duncan's (1955) multiple range test indicated that the means for age groups from 0 to 1 up to 3 to 4 days were not significantly different at the 1 per cent level from all other means. The test also revealed that the age group 4- to 5-days old was significantly different from all other groups. The data thus show that parasite effectiveness was not significantly affected by host age until the host reached 3 to 4 days of age. The data also show that 4 to 5 days was a critical host age since progeny production beyond this point decreased rapidly. This suggests that larvae 5- to 6 days-old and older have penetrated the tuber to depths beyond the reach of the parasite's ovipositor. For convenience in handling, and because the highest percentage of parasitization and the highest number of parasites were obtained with larvae 2- to 3-days-old, this age was chosen as the most suitable age for exposure to the parasite. On this basis, 2- to 3-day-old larvae were used in all other studies with *A. subandinus*. Later experiments showed that potato tuberworm larvae, 2- to 3-days-old, were late first instars.

Determination of optimal host density for parasitization

To determine the optimal number of potato tuberworm larvae to be exposed to a single parasite female to obtain the maximum parasite progeny, potato tubers were infested with 50, 100, 150, or 200 potato tuberworm larvae. When the larvae were 2- to 3-days-old (most suitable age), they were exposed to a newly emerged pair of *A. subandinus* for 24 hours. The experiment was replicated 10 times. Control series for each host density were also replicated 10 times.

TABLE 5
EFFECT OF HOST DENSITY ON PARASITIZATION BY A SINGLE MATED FEMALE OF *A. SUBANDINUS*

Test group*	Number of tubers per replicate	Host density per tuber†	Total host density exposed	Per cent emergence of moths and parasites	Mean number of individuals per replicate	
					Moths	Parasites‡
A	1	50	50	75.0	12.8	24.7 a
B	1	75	75	78.0	26.3	32.2 b
C	2	50	100	81.0	38.4	42.6 b
D	1	100	100	79.5	33.4	46.1 b
E	1	150	150	86.6	88.9	41.0 b
F	1	200	200	78.2	120.0	36.4 b
Control A	1	50	—	79.2	39.6	—
Control B	1	75	—	82.0	61.5	—
Control C	2	50	—	73.2	73.2	—
Control D	1	100	—	79.4	79.4	—
Control E	1	150	—	74.8	112.2	—
Control F	1	200	—	73.0	146.0	—

* Each test group replicated 10 times.
† Two- to 3-day-old host larvae exposed to parasite for 24 hours. Control groups non-exposed.
‡ Means followed by the same letter in a vertical line are not significantly different at the 5 per cent level.

An analysis of variance was conducted on the mean number of parasite progeny produced (table 5). The F test was significant only at the 5 per cent level. The Duncan's multiple range test revealed that only a host density of 50 larvae was significantly different (5 per cent level). However, oviposition by *A. subandinus* increased with the increase in the number of hosts available until a host density of 150 was exposed (table 5). A decrease in progeny production occurred when 150 or more larvae were offered. The mean progeny produced was highest (46.1) when one tuber infested with 100 larvae was exposed. This value was higher than that obtained when two tubers infested with 50 larvae each were used (42.6). Therefore, division of the number of hosts available into separate tubers did not essentially affect parasite progeny production.

Consequently (and for convenience in handling) a host density of 100 larvae per tuber was selected as the optimal density to be exposed to the parasite. This density was then used in all other studies involving this species.

Parthenogenicity

Preoviposition studies with virgin females had shown that *A. subandinus* is an arrhenotokous species, the virgin female producing only male progeny. The fecundity, longevity, and reproductive period of six virgin parasite fe-

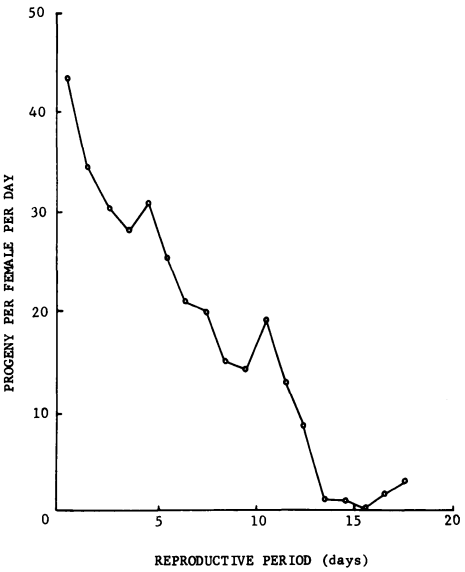

Fig. 6. Mean daily production of progeny by virgin females of *A. subandinus*.

males was studied at 80° F and 50 per cent R.H. as follows: potato tubers were each infested with 100 potato tuberworm larvae (optimal density). When the larvae were 2- to 3-days-old (most suitable age), they were exposed to a single virgin female for 24 hours. Afterwards, the parasite was transferred to a new oviposition unit containing new, identically infested material. This procedure was repeated daily until the last female died. The exposed material was held in rearing units in the insectary until pupation and emergence of adults occurred and their numbers were then recorded.

The mean total progeny of six females, consisting entirely of males, was 295.3 individuals. Longevity of the females ranged from 10 to 19 days (mean: 14.0). The reproductive period was essentially the same as the longevity period, with most females laying eggs until 1 day prior to their death. The mean reproductive period was 12.6 days (range: 9–18). The maximum mean daily progeny (43.6) occurred during the first day of life (fig. 6). This value then decreased as the female aged. The ovipositional behavior of virgin females was identical to that of mated females.

A. subandinus

II. Temperature Studies

All temperature studies were conducted in constant temperature cabinets at a constant relative humidity of 50 per cent and 12 hours photoperiod.

Effect of temperature on development

The developmental periods of each stage of *A. subandinus* were measured at 60, 70, 75, 80, 85, 90, and 95° F. The effect of temperature on the length of development of each stage is graphically represented in figure 7. In general, as temperature increased the speed of development increased. However, in the prepupal and pupal stages the developmental velocity changed little above 75° F. At 85 and 90° F, the duration of the prepupal and pupal stages was practically the same, indicating that unfavorable temperatures were being approached.

Newly-emerged larvae of the parasite were eventually killed when exposed to 95° F. The egg stage survived this temperature and some individuals developed quickly during the first 12 hours. However, growth of the parasite larvae soon became disorganized, most of them died, and only a few reached the late first instar larval stage. None of the larvae molted to the second instar. Consequently, adult parasites were not obtained at this temperature and a life table could not be calculated. Host larvae did complete their life cycle at 95° F and adults were obtained. Apparently, only unparasitized hosts were able to develop.

The duration of the total life cycle is a better estimate of the effect of temperature on development. In table 6, the mean developmental time in days from egg to adult female emergence is expressed in terms of velocity of development or per cent development per day. The data indicate that the percentage of development per day increased progressively as the temperature increased, rising by a factor of about 1.2 per each 5° F increase in temperature. The rate of development was reduced at higher temperatures. The mean developmental time ranged from a mean of 11.9 days at 90° F to 55 days at 60° F.

When the velocity of development was plotted against temperature and

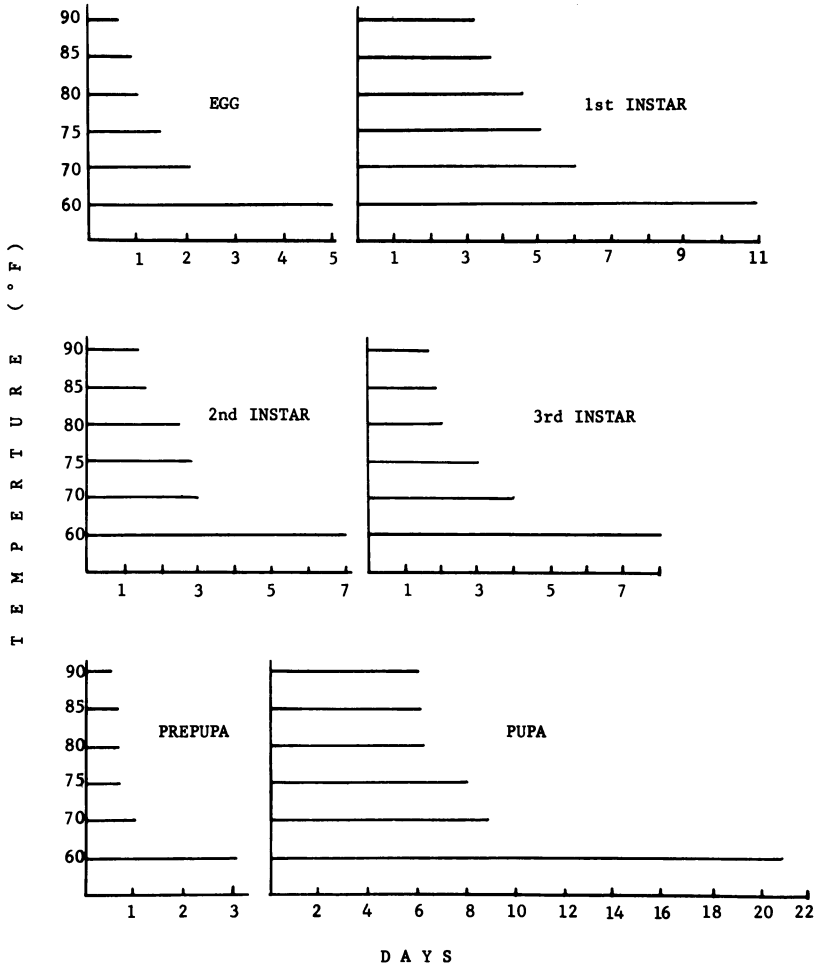

Fig. 7. Duration of development of immature stages of *A. subandinus* at different constant temperatures.

TABLE 6

DEVELOPMENTAL TIMES OF *A. SUBANDINUS* FEMALES AT SEVERAL CONSTANT TEMPERATURES, 50 PER CENT R.H. AND 12-HOUR PHOTOPERIOD

Temp. (°F)	Number reared	Developmental time (days)		Per cent development per day
		Range	Mean ± S.D.	
60	83	54—57	55.0 ± 0.58	1.81
70	93	23—26	24.8 ± 0.44	4.03
75	68	20—22	21.2 ± 0.50	4.71
80	150	14—16	15.1 ± 0.50	6.62
85	81	12—15	13.3 ± 0.85	7.51
90	80	10—13	11.9 ± 0.83	8.48

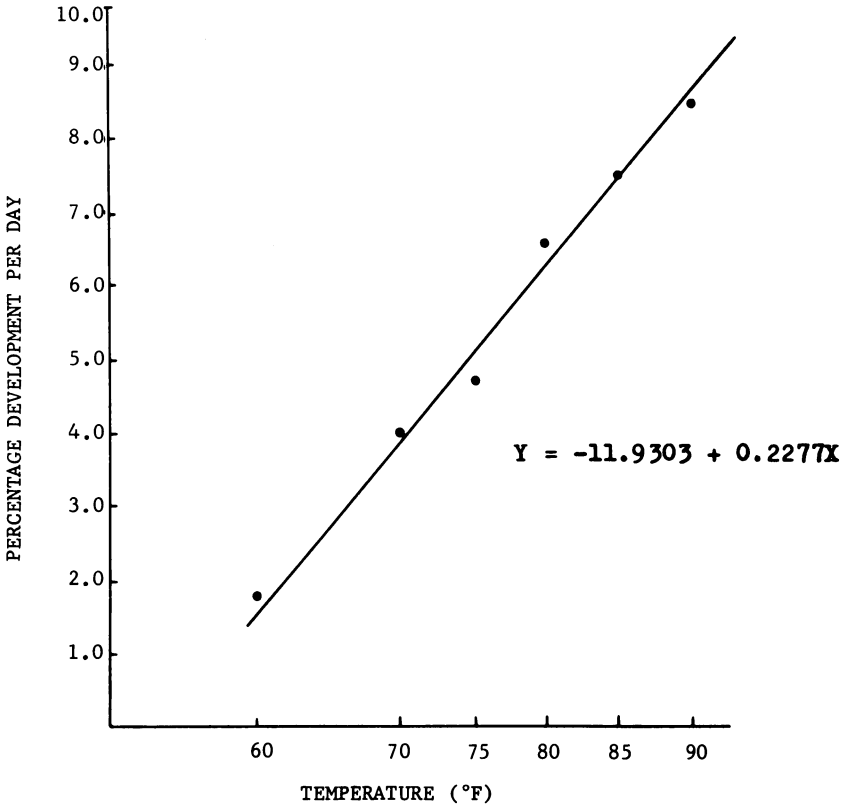

Fig. 8. Relationship between temperature and the velocity of development of *A. subandinus* from egg to adult emergence (relative humidity: 50 per cent).

a regression analysis of percentage development per day was made for each temperature, a linear relationship was found (fig. 8). The best-fitting line was given by the equation $Y = -11.9303 + 0.2277\ X$. The regression was highly significant (0.1 per cent level) ($t = 19.33$; 4 *d.f.*). The data thus show a direct relationship between temperature and speed of development.

Though the upper and lower thermal limits for development of *A. subandinus* were not established, the upper thermal limit is between 90 and 95° F as development was normal at 90° F but failed at 95° F. The lower thermal limit was estimated by solving the regression equation for $Y = O$. This operation gave a value of 52.3° F as the lower thermal limit. As this value is an approximation, all the hazards of extrapolation (Snedecor and Cochran, 1967) must be considered in its interpretation.

None of the parasites entered into diapause at any of the temperatures tested. From these developmental studies, the mean weighted developmental times of female parasites (table 6) were obtained and used in the construction of life tables. Males usually emerged 1 day earlier, indicating that they developed at a slightly faster rate than the females.

Mortality of the immature stages was also calculated by comparing the percentages of emergence at each temperature with those obtained at 80° F and which were taken as $1_x = 1.00$. The values thus obtained were utilized in the calculation of the 1_x column of the life

TABLE 7

EFFECT OF EXPOSURE OF IMMATURE STAGES OF *A. SUBANDINUS* TO A CONSTANT TEMPERATURE OF 95°F, 50 PER CENT R.H., AND 12-HOUR PHOTOPERIOD

Time of exposure to 95°F (days)	Mean number of individuals emerged per replicate*		Per cent total mortality
	Moths	Parasites	
1	43	46	11.0
2	46	28	26.0
3	50	22	28.0
4	56	6	38.0
5	55	0	45.0
6	54	0	46.0
7	48	0	52.0
8	46	0	54.0

* Emerged at 80°F; each replicate consisted of a potato tuber infested with 100, 2- to 3-day-old potato tuberworm larvae exposed to parasite females for 4 to 5 hours.

tables. According to these calculations no mortality occurred at 75, 80, and 85° F. It reached 32.5 per cent at 60° F, 4.4 per cent at 70° F, and 34 per cent at 90° F. As noted previously, it was 100 per cent at 95° F.

To study in more detail the lethal effect of 95° F on the development of *A. subandinus,* two experiments were conducted. The first one was to determine the maximum time of exposure to this temperature that parasite immatures could survive. For this purpose, a series of potato tubers were each infested with 100 host larvae and placed in a constant temperature cabinet at 95°F. When the host larvae were 2- to 3-days old, they were exposed to a large parasite population. After 4 to 5 hours exposure, the parasites were discarded. One tuber was then removed every 24 hours so as to give different times of exposure, ranging from 1 day to 9 days. The removed tubers were placed at 80° F until development and emergence occurred. The experiment was replicated three times.

There was little deleterious effect when time of exposure was 1 day (table 7). With succeeding days exposure, the number of parasites which emerged decreased gradually so that only six individuals were obtained from tubers exposed for four days. No parasites emerged from material exposed for five days and more. The mean number of hosts obtained, however, remained fairly constant and hosts were produced throughout the range of exposure (Table 7). The fact that host emergence remained more or less uniform suggests that mortality of healthy individuals remained approximately the same. This in turn suggests that parasitized larvae were the ones which failed to complete development. These results thus support previous observations on the development of this parasite at 95° F.

A second experiment involved the determination of the stage or stages of the parasite which were more susceptible to exposure to 95° F. For this test, potato tubers were each infested with 50 larvae and held at 80° F. When the larvae were 2- to 3-days old they were exposed to a large parasite population. After exposure, one of the tubers was placed at 95° F. This operation was repeated every 24 hours. In this manner, as the life cycle at 80° F was well-known, each of the immature stages from egg to late pupa was exposed to 95° F. This experiment was replicated four times.

Only the prepupal and pupal stages survived this temperature. No parasites emerged from material containing ear-

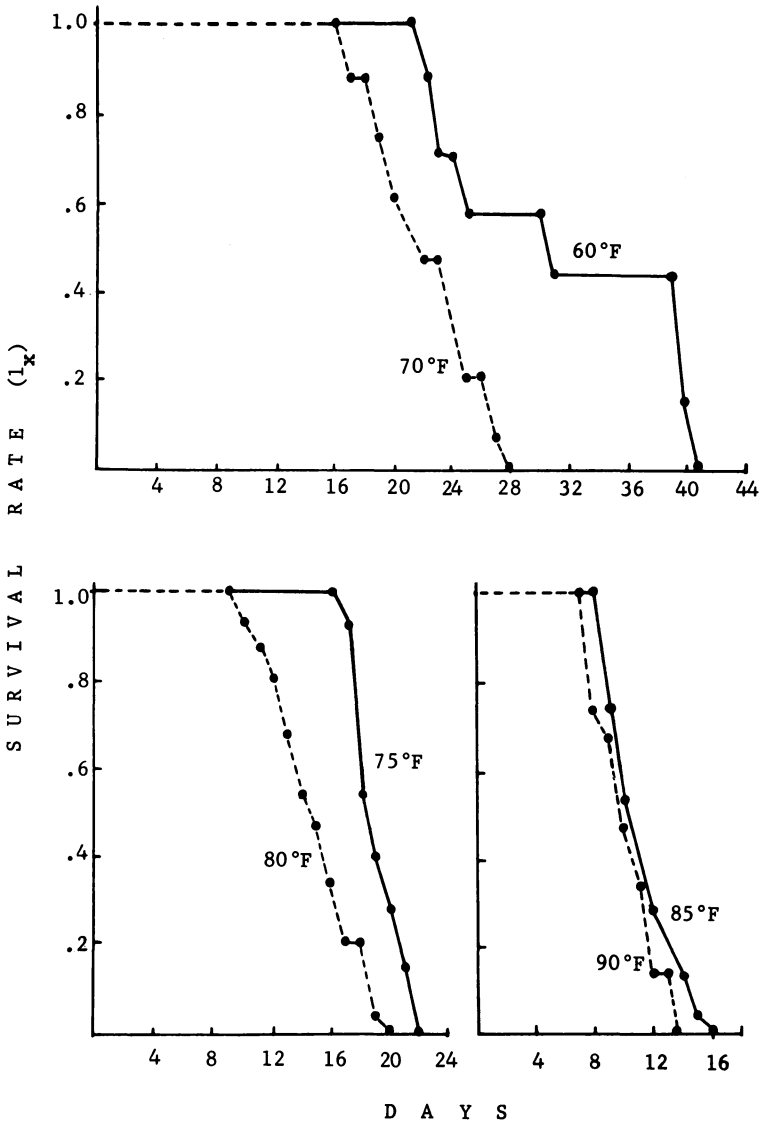

Fig. 9. Survivorship curves for adult females of *A. subandinus* at different constant temperatures and 50 per cent R.H. (based on cohorts of 15 individuals).

lier stages. There were also differences in survival between the prepupal and pupal stage, and within the pupal stage. Only four parasites emerged from material exposed in the prepupal stage. This value increased to a mean of 11.2 when early pupae were used and to 40.8 when late pupae were utilized. Failure to acclimate (Bursell, 1964) is the most likely physiological explanation for these results.

These and previous results demonstrate that a constant temperature of 95° F prevents development of *A. subandinus* beyond the late first instar larval stage; that 4 days is the maximum time that parasite immatures can survive exposure to this temperature;

TABLE 8

EFFECT OF DIFFERENT CONSTANT TEMPERATURES ON LONGEVITY OF OVIPOSITING FEMALES OF *A. SUBANDINUS*

Temperature (°F)	Female longevity (days)		Time required for 50 per cent mortality (days)
	Range	Mean*	
60	22—42	32.0 a	31.0
70	16—28	21.3 b	22.0
75	16—21	18.2 b	18.0
80	9—20	14.1 c	14.0
85	8—15	10.3 c	10.0
90	7—12	9.3 c	9.8

* Based on a cohort of 15 individuals; means followed by the same letter on a vertical line are not significantly different at the 1 per cent level.

and that only the prepupal and pupal stages survived when transferred from 80 to 95 ° F.

Effect of temperature on longevity

Survivorship curves for adult females of *A. subandinus* are shown in figure 9. These curves represent the longevities recorded for the females utilized in the studies of the effect of temperature upon reproduction and in the construction of life tables.

There was an inverse relation between temperature and longevity. Mean longevities ranged from 9.3 days at 90° F to 32.0 days at 60° F (table 8). An analysis of variance on the mean longevities gave a significant F value. An application of Duncan's multiple range test indicated that the mean longevity at 60° F was significantly different at the 1 per cent level from all other means. No significant difference was found between 70 and 75° F but these two temperatures were different at the same level from all others. It is important to note that there were no significant differences for the mean longevities obtained in the range of temperatures between 80 and 90° F. The difference was even less evident at the highest temperatures. The mean longevity of females at 85° F (10.3 days) was close to that recorded at 90° F (9.3 days).

Thus, statistically speaking, differences in longevity were not as marked as a visual analysis might indicate. Nevertheless, table 8 does show the inverse relationship between temperature and longevity. This type of relationship has been discussed by Bodenheimer (1938) and Clark and Rockstein (1964). Longevity is generally inversely proportional to the intensity of life or metabolic rate of an insect. For example, the curve for adults at 90° F (fig. 9) shows that at this high temperature activity and metabolism apparently occur at such a high rate that senescence is reached within a short period of time by the entire population.

Observations of the populations indicated in fact that individuals placed at 90° F exhibited a high degree of activity, whereas those placed at 60° F remained motionless for long periods of time.

A comparison of survivorship curves in figure 9 indicates that all of them conform well with the so-called curve of physiological longevity discussed by Deevey (1947), Clark and Rockstein (1964), and other authors. In this type of curve, the mortality of the population is nil until limits of physiological longevity are reached. Beyond this point the entire population soon dies, thus producing a convex, rectangular, survivorship curve. This situation occurred at all temperatures tested, especially at 85 and 90° F. The curve at 60°

TABLE 9
INFLUENCE OF SEVERAL CONSTANT TEMPERATURES ON REPRODUCTION OF *A. SUBANDINUS*

Temperature (°F)	Mean total progeny*	Mean per cent of females in total progeny*	Mean reproductive period*
60	64.85 a	11.29 a	15.3 a
70	181.33 b	32.77 b	18.5 a
75	257.46 b	37.94 b	16.4 a
80	345.53 c	41.56 b	14.4 a
85	237.20 b	44.86 b	9.4 b
90	203.86 b	14.92 a	7.7 b

* Means followed by the same letter on a verical line are not significantly different at the 1 per cent level.

F, though of the same type as the others, departs from the general configuration because the intervals between deaths of individuals were longer. This was probably due to the very low level of activity observed at this temperature.

The effect of temperature on longevity is also expressed by estimating from the survivorship curves (fig. 9) the time necessary for the population to reach 50 per cent mortality. These values (table 8) are similar to the mean longevity values. Again, there was no major difference between 85 and 90° F. However, in the range of temperatures between 70 and 85° F, longevity decreased 4 days as the temperature rose 5°F.

Effect of temperature on reproduction

Table 9 summarizes the influence of temperature on several phases of the reproductive ability of *A. subandinus*. Analysis of variance was conducted on the mean total progeny, the mean percentage of females in the total progeny, and the mean reproductive period. Significant values of F were obtained in all cases. Consequently, Duncan's multiple range test was conducted to compare the means. Significant differences at the 1 per cent level of confidence are shown in the same table.

Total progeny production

The mean total progeny per female followed a pattern in which an optimum temperature was found at which progeny production was maximum (table 9). Progeny production declined at lower or higher temperatures. Thus, the mean total progeny increased gradually from a value of 64.85 individuals per female at 60° F to a peak of 345.53 individuals per female at 80° F and then decreased to 203.86 individuals per female at 90° F.

Within each temperature tested, variability was not very high. The coefficients of variation ranged from 16 per cent at 80° F to 28 per cent at 60° F. Statistical analysis (table 9) indicated that 60° F greatly affected the reproductive capacity of *A. subandinus*. The mean total progeny at this temperature was significantly different at the 1 per cent level from all other means. The intermediate temperature of 80° F favored progeny production by this parasite. The mean total progeny produced at 80° F was significantly different from all other means. No other significant differences were found.

On a daily basis, the mean total progeny per female per day reached its highest value in the first day of life of the parent female at all temperatures tested. The maximum progeny per female per day was 42.2 at 80° F and the minimum was 8.9 at 60° F. After the first day, daily production of progeny decreased gradually. Reproduction usually continued until 2 days before the

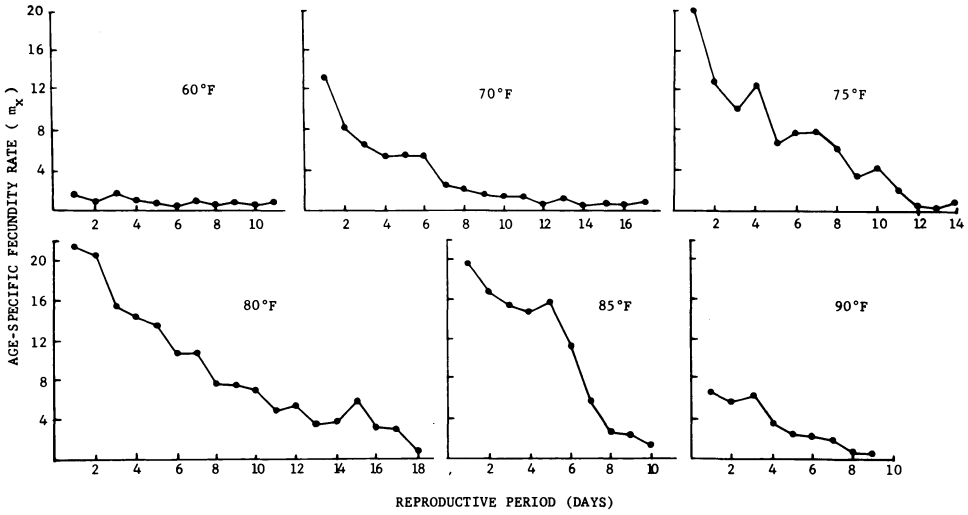

Fig. 10. Influence of temperature on age-specific fecundity rate of *A. subandinus*.

death of the female, but in some cases females oviposited until the day they died. At 60° F a remarkable difference between longevity and reproductive period occurred: females lived an average of 32 days but oviposited only during the first 15 days.

Female progeny and progeny sex ratios

In respect to population growth, total progeny is not the best indicator of the organism's capacity to increase in numbers. The ability of the female to produce a large number of female descendants is considerably more important. Thus, the intrinsic rate of natural increase (r) and other population growth statistics are calculated on the basis of female progeny. Males are assumed to always be available. For these reasons, the determination of sex ratios and sex-ratio correction factors is extremely important.

The age-specific fecundity rate or the number of female descendants produced per female per day (m_x column of a life table) is shown in figure 10. At all temperatures tested, the peak of female progeny production occurred on the first day of life. Production of female progeny was very low at 60° F. It was never higher than 1.8 individuals per female per day, and the curve did not follow the same general pattern of other temperatures. Oviposition remained very low throughout the reproductive period. The sex ratio at this temperature was very poor with only 11.29 per cent of the individuals, being females (table 9). This indicates that the reproductive capacity of *A. subandinus* is very low at 60° F.

Production of female progeny at the other temperatures tested followed the same general pattern as that of total progeny (males + females). Total female progeny increased gradually from 70 to 75° F, reached a peak at 80° F, decreased slightly at 85° F, and then fell abruptly at 90° F.

During the first 6 days of reproduction, the total female progeny was higher at 85° F than the total female progeny during the same period at 80° F (fig. 10). This is very important because, as noted by Birch (1948), Andrewartha and Birch (1954), Barlow (1962) and other authors, the value of the intrinsic rate of natural increase (r)

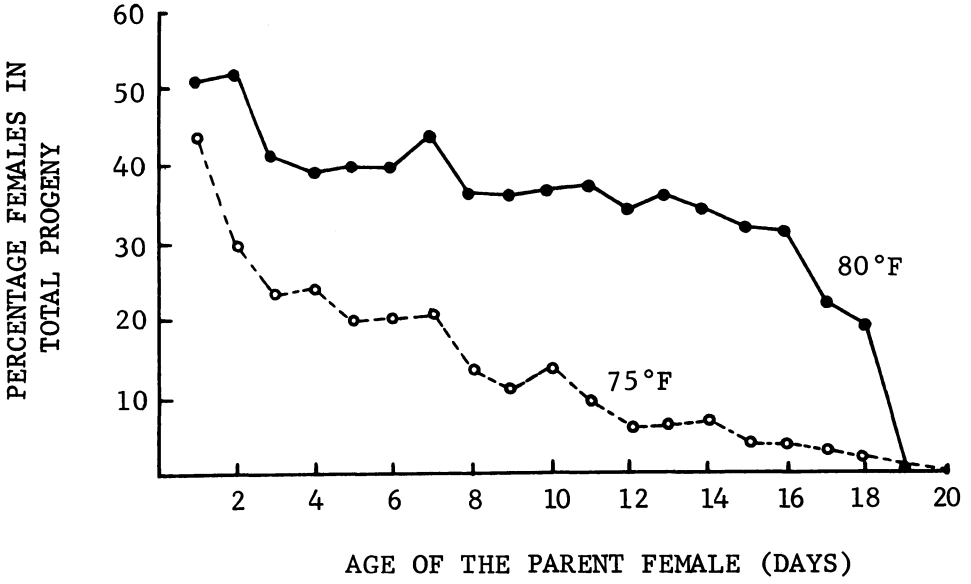

Fig 11. Effect of temperature and age of the parent female on progeny sex ratio of *A. subandinus.*

is largely determined in the first days of adult life. The more the female progeny produced during this period, the higher the value of *r*. The contribution of later age groups is less important. The difference between 80 and 85° F in relation to total female progeny produced during the first 6 days of life will be reflected in their respective calculations of *r*.

The statistical analysis on over-all sex ratios, expressed as percentage females in total progeny, showed no significant differences among the temperatures between 70 and 85° F (table 9). It did shown that the extreme temperatures of 60 and 90° F were unfavorable for the production of female progeny. The percentages of females in the total progeny at 60 and 90° F were 11.29 and 14.92 per cent, respectively. The case at 90° F demonstrates why total progeny production can be a misleading statistic. If total progeny alone were used to evaluate the influence of environmental conditions on the reproductive capacity of *A. subandinus,* it could be concluded that the parasite performed similarly at 70, 75, 85, and 90° F (table 9). The sex ratio clearly indicates that this was not true.

The progeny sex ratios varied from day to day at all temperatures. There was a marked tendency for older parent females to produce an excess of male progeny (fig. 11). For simplicity, the effect of parent age on the percentage of females in total progeny is shown for only two temperatures (75 and 80° F). During the last 2 or 3 days of their life most females produced only male progeny, probably because of depletion of sperm in the spermatheca. The effect was less obvious at 80° F.

Effect of temperature on population growth

The effect of temperature on separate phases of the biology of *A. subandinus* revealed that development was linearly related to temperature in the range between 60 and 90° F (table 6). It was also shown that a constant temperature of 95° F was lethal and prevented de-

velopment of the parasite from egg to adult emergence (table 7). It was found that longevity generally decreased four days as the temperature rose 5° F (table 8). The production of total progeny and female progeny was maximum at 80° F and decreased at higher and lower temperatures (table 9, fig. 10). The highest percentage of females in the total progeny was obtained at 85° F.

However, as discussed by Messenger (1964), bioclimatic evaluation of the influence of physical factors on the biology of an insect, "... based upon differential rates of development, reproduction or survival, each considered separately, is inconclusive." This evaluation can be more simply and accurately accomplished by construction of life tables and subsequent calculation of the intrinsic rate of natural increase. This statistic combines all previous data and can then be used as a precise bioclimatic index (Bursell, 1964; Messenger, 1964).

Life tables for each environmental condition were calculated on these bases. Each table included developmental time, immature survival, longevity, and fecundity rate in terms of female progeny. Superparasitism was not considered in their calculation, as the percentage of superparasitism was negligible at the host density utilized throughout the studies. When it did occur, it was never higher than 1 or 2 per cent. The values of the intrinsic rate of natural increase (r) and generation time (T) were included in each of the life tables. These data were not analyzed statistically because statistical analyses have not been devised for them.

Table 10 summarizes data from the life tables. The effect of temperatures on the mean total progeny, the Gross Reproductive Rate (female progeny per female), and the Net Reproductive Rate (Gross Reproductive Rate corrected for survivorship) are shown in figure 12. The data show that all these measurements of the reproductive power of *A. subandinus* reached a peak at 80° F. As discussed earlier, there was a large difference between the mean total progeny and the Net Reproductive Rate. This difference was larger at 60 and 90° F and became less pronounced from 70 to 85° F.

The curves for Gross Reproductive Rate and Net Reproductive Rate were almost identical throughout the range of temperatures tested. This is due to the fact that survivorship values for the parent females remained the same throughout most of the reproductive period. This was especially true at 75° F. At this temperature, the values for GRR and R_o are the same because the 1_x value was 1.00 until the last day of production of female progeny.

The generation time (T) followed the same type of inverse relationship with temperature as did the developmental time, decreasing as temperature increased (table 10).

As stated before, all responses of the organism to a particular set of environmental conditions are summarized in the intrinsic rate of natural increase (r). The influence of temperature on this statistic is shown in table 10 and graphically illustrated in figure 13.

The effect of temperature on population growth is obvious. The value of r increased gradually from a low of 0.026 at 60° F to a high of 0.290 at 85° F. It then declined to 0.197 at 90° F. The fact that r was greater than zero in the range between 60 and 90° F indicates that *A. subandinus* can persist and increase in numbers in this range. However, it must be noted that the value of r at 60° F is close to zero. This suggests that this temperature is not only unfavorable to the parasite but also that a temperature slightly lower than 60° F would probably be the one where r would be zero or negative. When r is zero the population will not increase in numbers, and when r is negative it will rapidly decline to extinction. These aspects have

TABLE 10
EFFECT OF CONSTANT TEMPERATURES, 50 PER CENT R.H., AND 12-HOUR PHOTOPERIOD ON SEVERAL POPULATION GROWTH STATISTICS OF *A. SUBANDINUS**

Temperature (°F)	Mean total progeny (progeny per female)	Gross reproductive rate (GRR) (female progeny per female)	Net reproductive rate (R_o) (female progeny per female)	Mean generation time (T) (days)	Intrinsic rate of natural increase (r)
60	64.85	7.60	5.06	66.2	0.026
70	181.33	57.70	55.04	28.8	0.139
75	257.46	95.10	95.10	24.7	0.184
80	345.53	157.90	145.00	18.8	0.264
85	237.20	106.50	105.31	16.0	0.290
90	203.86	28.40	18.59	14.8	0.197

* Based on cohorts of 15 individuals.

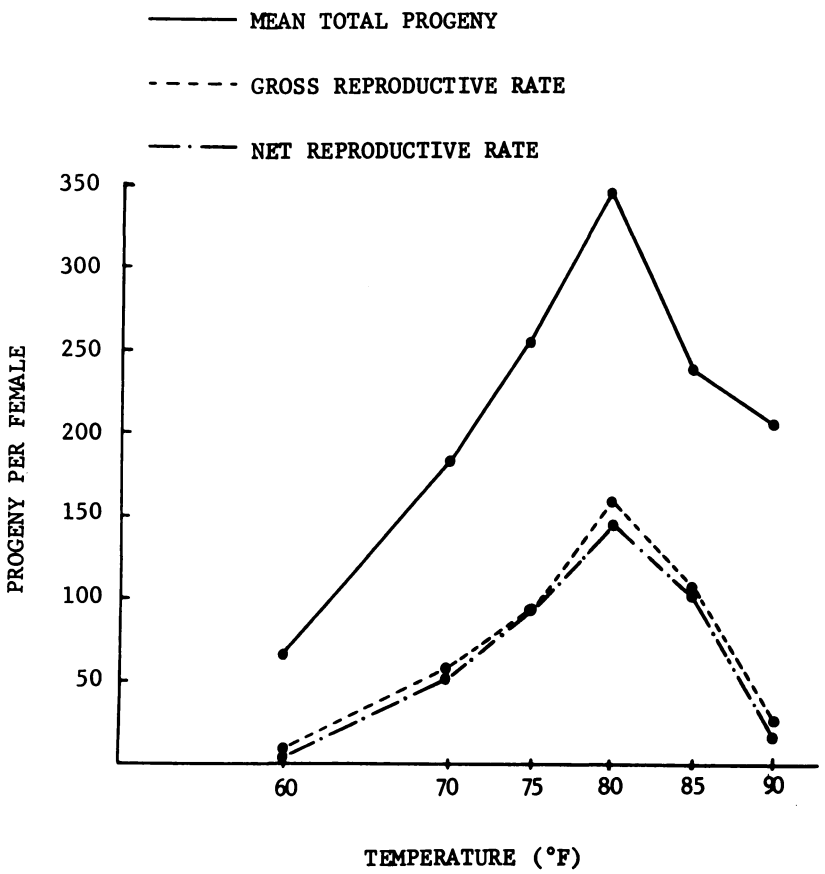

Fig. 12. Mean total progeny, Gross Reproductive Rate and Net Reproductive Rate of *A. subandinus* at several constant temperatures, 50 per cent R.H., and 12-hour photoperiod.

been extensively discussed by Birch (1948) and Cole (1954). The very low value of r at 60° F was due to the long developmental period (55 days) and the low value of the Net Reproductive Rate (5.06) which were recorded at this temperature.

A curve of the second degree poly-

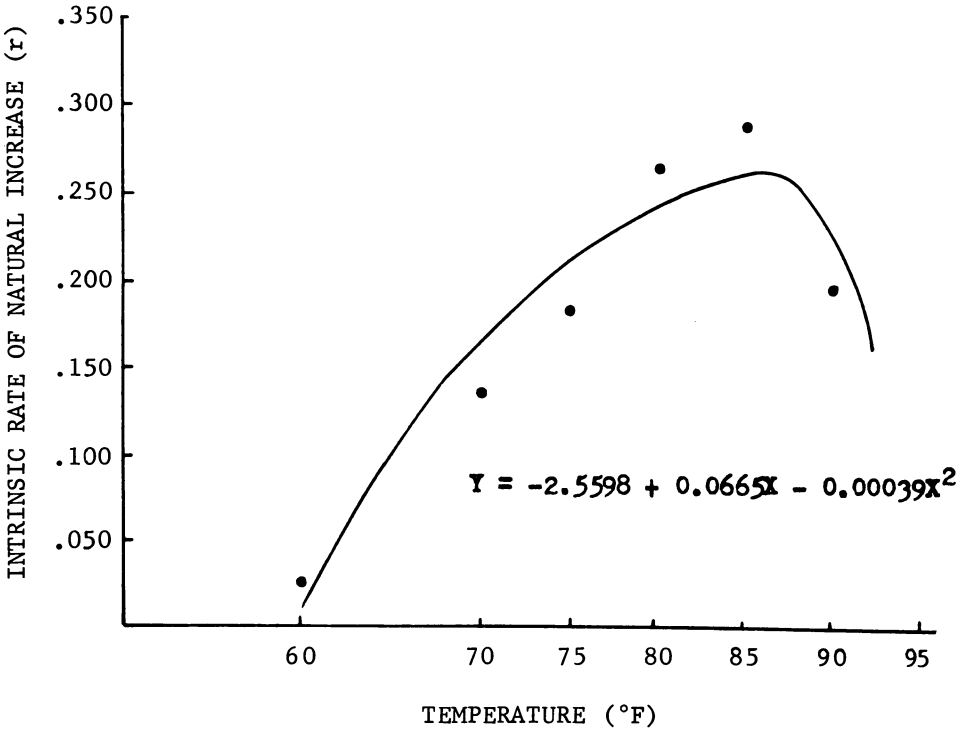

Fig. 13. Effect of constant temperatures on the intrinsic rate of natural increase of *A. subandinus*.

nominal ($Y = a + bX + cX^2$) was fitted to the data on figure 13. Possibly, a third degree polynomial would have given a better fit, but it was not calculated. No analysis of variance and test of significance were conducted on the regression equation. Consequently, its predictive value is limited. Nevertheless, there is a well-marked trend for the curve to bend at 85° F and drop abruptly between 85 and 90° F. The rapid fall in the curve agrees with previous results. Since *A. subandinus* does not develop at 95° F, there must be a temperature between 90 and 95° F at which r is zero or negative.

The maximum value of r (0.290) was obtained at 85° F, a temperature at which total progeny production, GRR and Net Reproductive Rate were not at a maximum (table 10). Thus, the intrinsic rate of natural increase was higher at 85° F than at 80° F though the reproductive power was highest at 80° F. This was due to the shorter developmental period (13 days) recorded at 85° F as compared to 15 days obtained at 80° F. Cole (1954) discussed this situation at length. Basically, it is explained from the nature of the calculation of r by the formula $r = \sum e^{-rx} 1_x m_x$. Other things being equal, the shorter the developmental period, the higher the value of r. Furthermore, r varies in linear inverse relation to generation time, which in turn is strongly affected by developmental time.

For the same reasons, r was higher at 90° F than at 75° F, though the reproductive power at 90° F was less than at 75° F (table 10).

From previous results, and using the intrinsic rate of natural increase (r) as a bioclimatic index, it can be concluded that *A. subandinus* can persist and reproduce at temperatures, ranging

from at least 60° F to a point between 90 and 95° F, and that 85° F was the optimal temperature for this species.

It is difficult to relate the results of the present study with natural situations. Many factors have to be considered. The intrinsic rate of natural increase, though a reliable bioclimatic index, has some serious limitations. It is based on assumption of unlimited food and space and a stable age distribution. These conditions depart from natural situations. Furthermore, the value of r is affected by many other factors besides temperature. Messenger (1964) lists 15 other factors of variable importance that can affect the growth of a population. Nevertheless, temperature is accepted as the most important factor affecting the distribution and, sometimes, the abundance of organisms (Bursell, 1964).

Despite its limitations, the intrinsic rate of natural increase calculated for laboratory conditions has sometimes proved to have a realistic value. This is illustrated by the works of Lamb (1961), Watson (1964), and Force and Messenger (1968). These authors found a close relationship between their laboratory studies and natural observations on distribution and real population growth rates.

As *A. subandinus* has not been established in southern Cailfornia, its performance in the laboratory is the only available information. Given the relatively mild climatic conditions of the inland valleys and coastal areas of southern California, the results of this study suggest that temperature is not a major reason for the failure of establishing this parasite in the potato-growing areas of this region.

Progeny production at 95° F

As *A. subandinus* could not develop at a constant temperature of 95° F, a life table at this temperature could not be calculated. However, it was important to study the reproductive capacity of the parasite at this high temperature. Females and males reared at 80° F were used in the study. Immediately after emergence, 10 females were placed at 95° F in the presence of males for mating and oviposition. The daily progeny production of each of the females was then recorded until the last female died.

The results indicated that *A. subandinus* females reared at 80° F. mated and produced progeny in a normal manner at 95° F. The mean total progeny per female was 145.6 (range: 100 to 204). The percentage of females in the total progeny was 37.5 per cent. All females had their peak of reproduction during the first day of life. The daily progeny production then decreased gradually to zero. The mean longevity was 7.3 days and the mean reproductive period 6.5 days. Most female progeny was produced during the first 4 days of life of the parent female.

A. subandinus
III. Humidity Studies

The effect of relative humidity on the basic biology of *A. subandinus* was studied at 80 and 85° F which were found to be the two most favorable temperatures for this species. A 12-hour photoperiod was maintained. The parasite was reared under conditions of relatively high humidity (70 per cent) and relatively low humidity (30 per cent). Results were then compared with data previously obtained at the level of 50 per cent R.H. The methods were exactly as those utilized in the temperature studies. Unfortunately, a constant relative humidity of 90 per cent could not be obtained in the temperature cabinets available for these studies.

TABLE 11
EFFECT OF RELATIVE HUMIDITY UPON DURATION OF DEVELOPMENT OF *A. SUBANDINUS*

Relative humidity	Number reared	Developmental time (days)		Per cent development per day
		Range	Mean ± S.D.	
		temperature 80°F		
30%	136	13—16	15.1 ± 0.64	6.63
50%	150	14—16	15.1 ± 0.50	6.62
70%	86	14—16	14.9 ± 0.66	6.68
		temperature 85°F		
30%	124	13—14	13.4 ± 0.47	7.46
50%	81	12—15	13.3 ± 0.85	7.51
70%	84	12—14	12.9 ± 0.73	7.81

Effect of humidity on development

Table 11 shows the influence of three different levels of humidity (at two temperatures) upon development of *A. subandinus*. The data show that relative humidity had little if any effect on development. The mean developmental period was about 15 days at 80° F and about 13 days at 85° F and the percentage development per day was about 6.6 and 7.5 per cent respectively.

The effect of relative humidity on the speed of development has been studied for many species of insects. Andrewartha and Birch (1954) and Bursell (1964) discussed in detail the types of responses of insects to relative humidity. The results summarized in table 11 suggest that *A. subandinus* belongs to that group of insects in which developmental rates are apparently unaffected by relative humidity.

Immature mortalities at the different relative humidities were estimated by a comparison of the emergence of adults with those obtained at 80° F and 50 per cent R.H. There was no appreciable difference. Consequently, a survival value of $1_x = 1.00$ for immatures was utilized in the construction of life tables.

Effect of humidity on longevity

There was an inverse relationship between relative humidity and longevity at 80° F. Thus, females of *A. subandinus* lived an average of only 8.8 days at 70 per cent R.H. (table 12). The mean longevity increased to 14.1 days at

TABLE 12
EFFECT OF RELATIVE HUMIDITY ON LONGEVITY OF OVIPOSITING FEMALES OF *A. SUBANDINUS*

Relative humidity	Female longevity (days)		Time to 50 per cent mortality (days)
	Range	Mean*	
	temperature 80°F		
30%	12—20	15.8	17.0
50%	12—18	14.1	14.7
70%	7—11	8.8	9.0
	temperature 85°F		
30%	10—15	12.3	13.0
50%	8—15	10.2	10.3
70%	5—8	6.6	6.9

* Based on a cohort of 15 individuals; statistical differences explained in text.

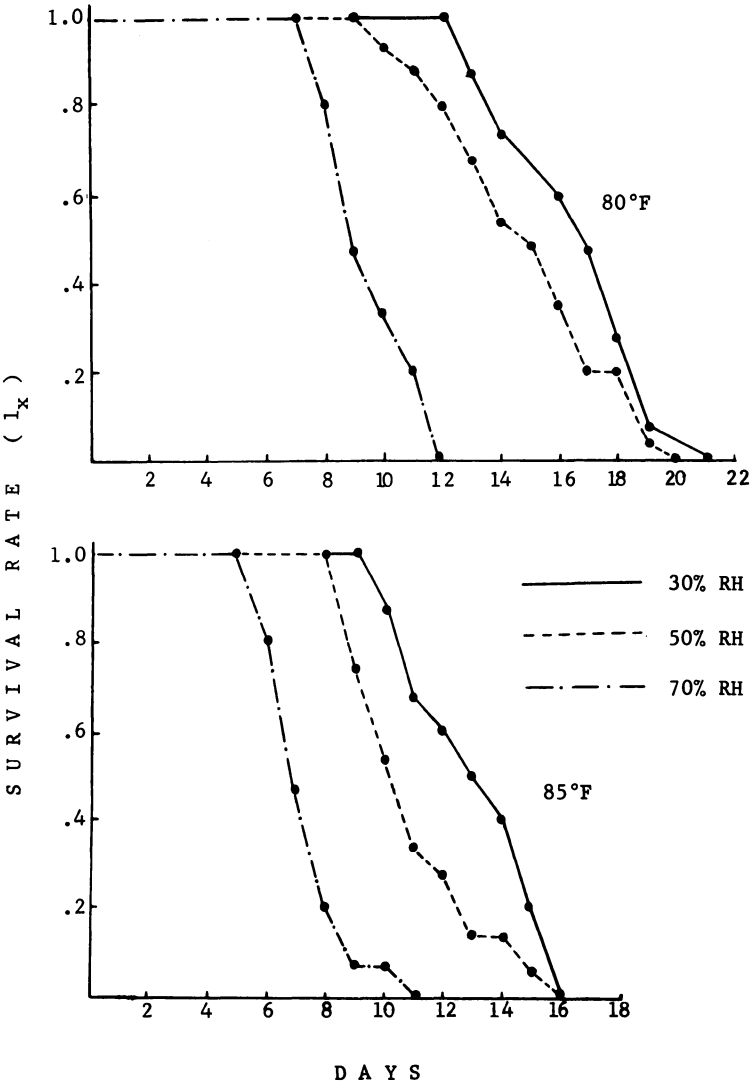

Fig. 14. Effect of relative humidity on longevity of adult females of *A. subandinus* at a constant temperature of 80° F (above) and 85° F (below).

50 per cent R.H. and 15.8 days at 30 per cent R.H. Statistically (multiple range test), mean longevities at 30 and 50 per cent R.H. were the same but both were significantly different at the 1 per cent level from the mean longevity recorded at 70 per cent R.H. (Table 12).

The inverse relationship between relative humidity and longevity or survival are also shown in figure 14 from which values to 50 per cent mortality (table 12) were estimated. The three curves follow the pattern of the curve of physiological longevity already discussed. The data show that senescence was reached faster as humidity increased, and that a relative humidity of 70 per cent does not favor longevity of ovipositing females of *A. subandinus*.

A similar response to humidity was

TABLE 13
EFFECT OF RELATIVE HUMIDITY ON REPRODUCTION OF *A. SUBANDINUS*

Relative humidity	Mean total progeny*	Mean per cent of females in total progeny*	Mean reproductive period*
	temperature 80°F		
30%	270.53	35.36	13.8
50%	345.53	41.56	13.4
70%	174.00	37.87	7.9
	temperature 85°F		
30%	232.46	34.35	11.4
50%	237.20	44.86	9.4
70%	158.60	43.83	6.1

* Statistical differences explained in text.

obtained at 85° F (table 12). The mean longevity of females at 30 per cent R.H. was 12.2 days, but decreased to 10.2 days at 50 per cent and to 6.6 days at 70 per cent R.H. There was no significant difference between longevities at 30 and 50 per cent R.H., but both were significantly different at the 1 per cent level from longevity recorded at 70 per cent R.H.

Figure 14 illustrates the unfavorable effect of high humidity at 85° F on longevity. Again, senescence was reached at an earlier age when females were exposed to 70° R.H. This is also reflected in the estimates for the times required to reach 50 per cent mortality (table 12). Differences in female longevity were really due to the effect of humidity. When the combined analysis was conducted, the interaction temperature-relative humidity failed to show significant differences.

The adverse effect of high humidity on the survival of adult females of *A. subandinus* is somewhat difficult to explain. The relationship between relative humidity and the biology of insects is generally less well understood than those of temperature. As discussed by Bursell (1964), the problem becomes one of balance between gains and losses of water, which is difficult to measure and was not attempted in this study. Nevertheless, the results agree with general observations and with some previous research. Thus, for example, Graham (1959) concluded that high humidities, as compared to low humidities, had a definite adverse effect upon survival of *Therioaphis maculata* (Buckton).

Effect of humidity on reproduction

Table 13 summarizes the influence of relative humidity on several aspects of the reproductive potential of *A. subandinus*. At 80° F, relative humidity had an appreciable effect on production of total progeny. Thus, the multiple range test indicated that there were significant differences at the 1 per cent level among all means. The data show that a high humidity of 70 per cent R.H. did not favor the production of progeny by *A. subandinus* and that the intermediate level of humidity (50 per cent) was optimal at this temperature.

The effect was not as obvious at 85° F as it was at 80° F. Again, maximum progeny production occurred at 50 per cent R.H. but the mean total progeny at this humidity was not significantly different from that recorded at 30 per cent R.H. (table 13). Both means were significantly different from the mean total progeny at 70 per cent R.H., but only at the 5 per cent level.

From these results, it was concluded that high humidity has an adverse effect

upon the reproductive capacity of *A. subandinus*, and that the parasite prefers intermediate levels of humidity.

The over-all sex ratios expressed in terms of percentage of females in total progeny are also summarized in table 13. Relative humidity did not have a major influence on sex ratios. No significant differences were found among the means at 80° or 85° F.

The effect of humidity on the reproductive period followed the same pattern as that on the longevity of adults (table 12). Thus, at both 80 and 85° F high humidity (70 per cent) caused a reduction in the reproductive period. There were no significant differences between the mean reproductive periods at 30 and 50 per cent R.H.

Female progeny production

Figure 15 shows the effect of relative humidity on the age-specific fecundity rate (female progeny per female) at 80 and 85° F. In all cases, production of female progeny reached a peak during the first day of life of the parent female and was followed by a gradual decrease. The curves at 80° F show that the maximum production of female progeny occurred at 50 per cent R.H. and the minimum at 70 per cent R.H. At 70 per cent R.H., the production of female progeny declined rapidly from the first day of oviposition.

The influence of humidity upon the production of total progeny (males + females) at 85° F was not as evident as that at 80° F, and this was also true in relation to female progeny production (fig. 15). As at 80° F, the highest number of female progeny was produced at 50 per cent R.H., but the curves at 30 and 70 per cent R.H. were similar.

Effect of humidity on population growth

Life tables were calculated for *A. subandinus* at each R.H. tested. The data from these tables, including the values

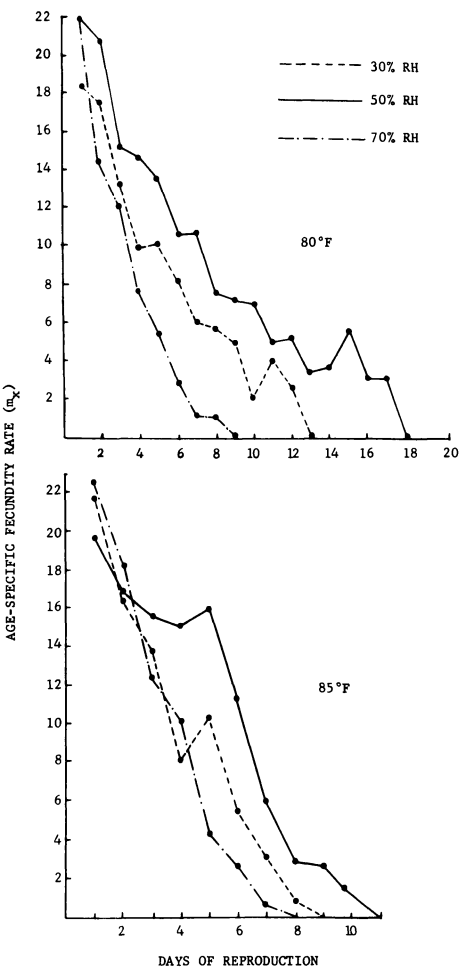

Fig. 15. Effect of relative humidity on age-specific fecundity rate of *A. subandinus* at a constant temperature of 80° F (above) and 85° F (below).

for the intrinsic rate of natural increase (r) and generation time (T), are summarized in table 14.

The Gross Reproductive Rate and the Net Reproductive Rate followed the same general pattern of the mean total progeny (table 14). High humidity (70 per cent) adversely affected the reproductive ability of females of *A. subandinus*. At both 80 and 85° F, reproductive rates were maximum at 50 per cent R.H.

TABLE 14

EFFECT OF RELATIVE HUMIDITY ON SEVERAL POPULATION GROWTH STATISTICS OF *A. SUBANDINUS*

Relative humidity	Mean total progeny (progeny per female)	Gross Reproductive Rate (GRR) (female progeny per female)	Net Reproductive Rate (R_o) (female progeny per female)	Mean generation time (T) (days)	Intrinsic rate of natural increase (r)
		temperature 80°F			
30%	270.53	99.60	99.60	18.5	0.249
50%	345.53	157.90	145.00	18.8	0.264
70%	174.00	66.30	66.08	17.3	0.242
		temperature 85°F			
30%	232.46	80.20	80.20	15.5	0.282
50%	237.20	106.50	105.31	16.0	0.290
70%	158.60	70.50	69.68	15.2	0.279

* Based on cohorts of 15 individuals.

The differential effect of humidity on the intrinsic rate of natural increase was less evident than the one on reproductive capacity. Thus, at 80° F the values of r at 30 and 70 per cent R.H. were similar (0.249 and 0.242, respectively), and neither differed much from that obtained at 50 per cent R.H. (0.264) (table 14). Differences at 85° F were even smaller, the values of r at 30 per cent R.H. (0.282) and 70 per cent R.H. (0.279) being almost identical to the one at 50 per cent R.H. (0.290).

This situation illustrates an important principle in population growth. Since developmental times were unaffected by relative humidity, it would be expected that declines in fecundity (table 14) would be reflected proportionately in the magnitudes of the intrinsic rate of natural increase. However, variations in fecundity do not exert similar proportional changes in r. This is because r varies only as the natural logarithm of changes in fecundity. Thus, for example, Messenger (1964), working with a hypothetical sex ratio 1:1, proved that a 50 per cent decline in fecundity rate resulted in only a 13.5 per cent decline in r.

Apanteles scutellaris Muesebeck

I. General Biology

The life history, morphology of immature stages, and temperature responses of *A. scutellaris* were studied in detail by Djamin (1970). His research on the parasite as a primary parasite of the tomato pinworm was conducted at different environmental conditions, using different experimental techniques than those utilized in the present study.

One of the main purposes of the present study was to investigate comparisons between *A. subandinus* and *A. scutellaris*. Therefore, it was necessary to conduct studies on the basic biology and temperature responses of *A. scutellaris* as a parasite of their common host, the potato tuberworm. The same experimental methods already described for *A. subandinus* were used. Results reported by Djamin (1970) were carefully noted so as to avoid unnecessary repetitions.

From observations accumulated during this study and from Djamin's (1970) research, the general biology of *A. scutellaris* is briefly summarized.

TABLE 15
EFFECT OF AGE OF POTATO TUBERWORM LARVAE ON PARASITIZATION BY *A. SCUTELLARIS*

Age of host larvae at exposure (days)	Mean number of individuals emerged per replicate*		Per cent of host larvae parasitized†	Per cent of total individuals emerging‡
	Moths	Parasites		
0—1	24.8	17.2	40.9 a	84.0
1—2	12.7	28.5	69.1 b	82.4
2—3	13.3	28.8	68.4 b	84.2
3—4	21.5	21.1	49.3 a	85.2
4—5	21.6	19.4	47.3 a	82.0
5—6	25.8	12.6	32.8 c	76.8
Control	40.2	0.0	0.0	80.4

* Mean of 10 replicates, each replicate consisting of 50 potato tuberworm larvae of a given age exposed to a female parasite for 24 hours.
† Calculated on the basis of total number of individuals emerged. Means followed by the same letter on a vertical line are not significantly different at the 1 per cent level.
‡ Mean per replicate.

The species is a primary, solitary, larvel endoparasite of the potato tuberworm and tomato pinworm. The egg is deposited at random in the body cavity of the host where the larva develops to maturity. When mature, the larva emerges by cutting its way out along the lateral line, thus killing the host.

A. scutellaris undergoes three larval instars in both hosts. The first instar is of the mandibulate-caudate type. The second and third instars are hymenopteriform. The three instars were described by Djamin (1970). The immature stages of *A. scutellaris* are very similar to those of *A. subandinus.*

After emergence from the host larva, the mature parasite larva spins a silver-white cocoon in which it pupates. The pupa is of the exarate type. Adult emergence from the cocoon is stimulated by light. The feeding, mating, and ovipositional behaviors of female *A. scutellaris* were virtually the same as those of *A. subandinus. A. scutellaris* is also an arrhenotokous species, the virgin female producing only male progeny. There is essentially no preoviposition period in this species.

At 80° F, 50 per cent R.H., and 12 hours photoperiod, the average duration of the life cycle of *A. scutellaris* was about 14 days. The length of the developmental stages was as follows: egg, 1 day; first instar, 4 days; second instar, 3 days; third instar, 1.5 days; prepupa, 0.5 days; and pupa, 4 days.

Before initiating the study of temperature responses of *A. scutellaris,* it was first necessary to determine optimal host age and optimal host density to be exposed to the parasite.

To determine the most suitable age of the host for parasitization, the following experiment was conducted at 80° F and 50 per cent R.H. Potato tubers, each infested with 50 larvae of a known age (ranging from 0–1 day to 5–6 days), were exposed to single mated parasite females for 24 hours. After development, the numbers of parasites and moths obtained were recorded. The experiment was replicated 10 times, including also a control (non-exposed).

Table 15 summarizes the results. The analysis of variance and Duncan's multiple range test indicated that host larvae 1- to 2-days and 2- to 3-days-old were the most suitable for exposure to the parasite. The mean percentages of larvae parasitized at these two ages were significantly different at the 1 per cent from all other means. There was no significant difference between them, suggesting that either one could be utilized as the most suitable age. Previous

TABLE 16
EFFECT OF HOST DENSITY ON PARASITIZATION BY A SINGLE MATED FEMALE OF *A. SCUTELLARIS*

Host density*	Per cent emergence of moths and parasites	Mean number of individuals per replicate	
		Moths	Parasites†
	Exposed‡		
50	76.0	16.2	21.8 a
75	79.6	27.4	29.3 b
100	81.2	47.9	33.3 b
150	79.3	88.8	30.2 b
	Non-exposed (control)§		
50	81.4	40.6	—
75	77.6	58.2	—
100	74.0	74.0	—
150	72.2	108.3	—

* Each host density replicated 10 times.
† Means followed by the same letter on a vertical line are not significantly different at the 5 per cent level.
‡ Host larvae exposed to a single parasite female for 24 hours.
§ Host larvae not exposed to parasite.

results with *A. subandinus* had shown that larvae 2- to 3-days-old were the most suitable for exposure to that parasite. Therefore, to facilitate comparisons and have uniform methods, this host age was utilized in subsequent experiments concerning *A. scutellaris*.

The optimal host density to be exposed to the parasite was determined by infesting potato tubers with 50, 75, 100, or 150 potato tuberworm larvae. When the host larvae were 2- to 3-days-old (most suitable age) they were exposed to single mated parasite females for 24 hours. The experiment was replicated 10 times. Control series (non-exposed) for each host density were also replicated 10 times.

Table 16 summarizes the results. Only a host density of 50 larvae was significantly different (5 per cent level). Thus, statistically, any of the other host densities could be utilized to obtain maximum parasitization. However, a host density of 100 larvae was selected because it produced the highest absolute number of parasites and because this density had been utilized in studies concerning *A. subandinus*.

A. scutellaris
II. Temperature Studies

The response of *A. scutellaris* to temperature was studied at 75, 80, 85, 90 and 95° F. A constant relative humidity of 50 per cent was utilized. This humidity had been previously found as optimal for *A. subandinus*.

Table 17 shows the relationship between temperature and velocity of development in *A. scutellaris*. The velocity of development, expressed as percentage development per day, increased in a direct manner with temperature. There was a reduction in the speed of development with increasing temperatures towards the upper range of temperature (90 and 95° F). This is usually interpreted as an indication that the upper threshold for development is being approached (Clark and Rockstein, 1964).

The data show that *A. scutellaris* developed at a constant temperature of 95° F (table 17). This is probably the most important difference between *A. scutellaris* and *A. subandinus*, as the

TABLE 17

DEVELOPMENTAL TIMES OF *A. SCUTELLARIS* FEMALES AT SEVERAL CONSTANT TEMPERATURES, 50 PER CENT R.H., AND 12-HOUR PHOTOPERIOD

Temperature (°F)	Number reared	Developmental time (days)*		Per cent development per day
		Range	Mean ± S.D.	
75	91	18—21	19.2 ± 0.67	5.20
80	114	13—16	14.0 ± 0.60	7.14
85	84	11—13	12.1 ± 0.70	8.26
90	110	9—12	10.5 ± 0.88	9.43
95	111	9—11	10.1 ± 0.52	9.82

* From egg to adult emergence.

latter species was incapable of developing at this high temperature.

The mean developmental times obtained (table 17) were later utilized in the preparation of life tables for *A. scutellaris*.

Immature mortality was calculated by a comparison of emergence of progeny with that obtained at 80° F which was considered as being 100 per cent survival. These estimates indicated that immature mortality was negligible at 75, 80, and 85° F, and that it was 7 per cent at 90° F and 23.9 per cent at 95° F.

The influence of constant temperatures upon the reproductive ability, sex ratio, longevity, and the reproductive period of *A. scutellaris* is summarized in table 18. Significant differences at the 1 per cent level are shown in the same table. The mean total progeny increased from 156.06 individuals at 75° F to a high of 194.53 individuals at 80° F, decreasing at the higher temperatures. The parasite produced the maximum number of progeny at 80° F with the mean total being significantly different from all other means. The only significant effect of temperature on sex ratios (expressed as percentage females in total progeny) was obtained at 95° F. The longevity of females was similar to their reproductive period. Both longevity and reproductive period followed an inverse relationship with temperature.

Effect of temperature on population growth

Life tables were calculated for *A. scutellaris* at each temperature tested. The data from these tables, including the values of generation time (T) and intrinsic rate of natural increase (r), are summarized in table 19. An analysis of the data indicates that the Gross Reproductive Rate (female progeny per female) and the Net Reproductive Rate (Gross Reproductive Rate corrected for

TABLE 18

INFLUENCE OF CONSTANT TEMPERATURES UPON SEVERAL PHASES OF THE BIOLOGY OF *A. SCUTELLARIS**

Temperature (°F)	Mean total progeny†	Mean per cent of females in total progeny†	Mean longevity of adults (days)†	Mean reproductive period (days)†
75	156.06 a	48.68 a	11.0 a	10.0 a
80	194.53 b	51.30 a	9.8 a	9.7 a
85	150.66 a	44.06 a	7.4 b	7.2 b
90	116.26 c	41.55 a	6.2 b	5.7 c
95	107.00 c	32.39 b	4.8 c	4.7 c

* Based on cohorts of 15 individuals.
† Means followed by the same letter on a vertical line are not significantly different at the 1 per cent level.

TABLE 19

EFFECT OF CONSTANT TEMPERATURES, 50 PER CENT R.H., AND 12-HOUR PHOTOPERIOD ON SEVERAL POPULATION GROWTH STATISTICS OF *A. SCUTELLARIS**

Temperature (°F)	Mean total progeny (progeny per female)	Gross Reproductive Rate (GRR) (female progeny per female)	Net Reproductive Rate (R_o) (female progeny per female)	Mean generation time (T) (days)	Intrinsic rate of natural increase (r)
75	156.06	77.70	76.34	22.1	0.196
80	194.80	105.80	99.62	16.9	0.271
85	150.66	73.30	67.62	14.7	0.287
90	116.26	49.80	45.86	13.0	0.294
95	107.00	35.10	26.26	11.9	0.273

* Based on cohorts of 15 individuals.

survivorship) were similar in all cases. Favorable survivorship of the parent females was probably responsible for this situation as nearly all the females were alive when the last day of female progeny production occurred.

Production of female progeny showed the same trend as that of production of total progeny (males + females). The Net Reproductive Rate increased with temperature from 75° F, reached a peak of 99.62 offspring at 80° F, and then declined with higher temperatures. Unfavorable sex ratios at 95° F are reflected in the large difference between the mean total progeny and the Net Reproductive Rate (table 19). The overall response of *A. scutellaris* to temperature is summarized in the different values of the intrinsic rate of natural increase. Figure 16 illustrates the effect of temperature on this statistic. It increased from a low of 0.196 at 75° F to a high of 0.294 at 90° F; then decreased to 0.273 at 95° F. The fact that the value of r remained high from 80 to 95° F indicates a good adaptability of this parasite to high temperatures.

The data in table 19 illustrate a principle of population growth that was previously discussed in relation to *A. subandinus*. Higher reproductive capacities do not necessarily translate into higher potentials for increase. Thus, the value of r reached a peak at 90° F, a temperature at which production of total progeny and of female progeny was lower than at 75, 80, and 85° F. This was due to lower developmental times at 90° F which more than offset the effect of reduced reproduction. For the same reasons, the intrinsic rate of natural increase at 95° F was higher than at 75 and 80° F.

The intrinsic rate of natural increase (r) is regarded as the most reliable index for rating the performance of organisms under different environmental conditions (Birch, 1948; Macfadyen,

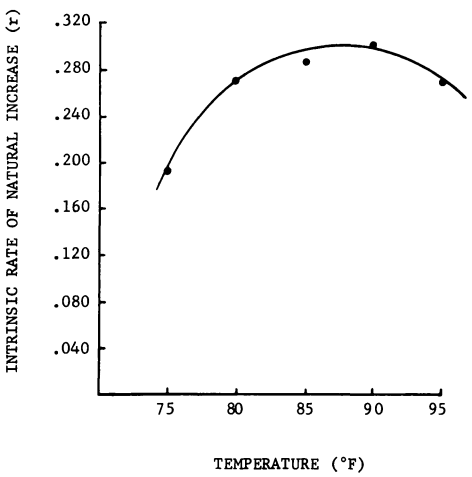

Fig. 16. Effect of constant temperatures on intrinsic rate of natural increase of *A. scutellaris* (50 per cent R.H. and 12-hour photoperiod).

1963). The optimal environment is one at which r reaches its highest value. Consequently, it is concluded that at a relative humidity of 50 per cent, the optimal temperature for *A. scutellaris* is 90° F.

Phthorimaea operculella (Zeller)

I. General Biology

The biology of the potato tuberworm has been extensively studied by a number of authors. Probably the most comprehensive study was done by Graf (1917). More recent works were published by Hofmaster (1949), El Sherif (1961) and Stanev and Kaitazov (1962). In the present study, the biology and the temperature responses of this species were studied in the laboratory to conduct comparisons with those of two of its parasites.

In the laboratory, larvae of the potato tuberworm completed their development in potato tubers. The mature larvae emerged from the tuber and pupated in sand that was provided to facilitate pupation. Development of males apparently occurred at a faster rate than that of females because males usually emerged 1 or 2 days earlier. Mating occurred soon after emergence and lasted for extended periods of time. Observations at different temperatures indicated that adult females mated more than once, usually two or three times during their life spans.

A pre-reproductive period apparently does not occur although, at high temperatures (85 and 90° F), most females laid eggs 1 day after emergence. Picard (1913) reported the occurrence of parthenogenesis in this species. However, in the present study the results of isolation tests indicated that none of the eggs laid by 35 virgin females hatched. This confirms the results obtained by Graf (1917).

To detect the occurrence of larval instars, the width of the head capsule of each of 50 larvae was measured every 24 hours with the aid of a calibrated eyepiece micrometer in a dissecting microscope. The process was repeated until pupation occurred. Application of Dyar's law to the head capsule measurements showed the occurrence of four instars at all temperatures tested. The average growth ratio for the species was 1.54.

The mean duration of developmental stages at 80° F and 50 per cent R.H. was as follows: egg, 4 days; first instar, 3 days; second instar, 2 days; third instar, 2 days; fourth instar, 3 days; prepupa, 0.5 days; and pupa, 7.5 days.

P. operculella

II. Temperature Studies

All temperature studies with *P. operculella* were conducted at 50 per cent R.H. and 12 hours photoperiod.

Table 20 shows the effect of temperature on development from egg to adult emergence and on immature mortality. There was a strong direct relationship between temperature and the velocity of development expressed as percentage per day. This velocity of development decreased somewhat at the upper thermal levels (90 and 95° F). Mean developmental times ranged from 30.8 days at 75° to 14.0 days at 95° F.

Percentages of immature mortality were calculated for each temperature by determining the difference between the number of initial eggs utilized and the number of moths obtained. Thus, these percentages reflect egg, larval,

TABLE 20

DEVELOPMENTAL TIMES FROM EGG TO ADULT EMERGENCE AND IMMATURE MORTALITY OF *P. OPERCULELLA* AT SEVERAL CONSTANT TEMPERATURES, 50 PER CENT R.H., AND 12-HOUR PHOTOPERIOD

Temperature (°F)	Number reared	Developmental time (days)		Per cent development per day	Per cent of immature mortality
		Range	Mean ± S.D.		
75	100	29—32	30.8 ± 0.93	3.26	24.5
80	65	21—23	21.9 ± 0.58	4.58	17.6
85	92	17—19	18.1 ± 0.70	5.50	20.4
90	77	14—17	15.9 ±0.56	6.28	27.8
95	60	13—15	14.0 ± 0.44	7.14	41.8

and pupal mortality. Most mortality apparently occurred in the larval and pupal stages because previous results indicated that only 3 to 4 per cent mortality occurred in the egg stage. The lowest percentage of immature mortality was recorded at 80° F (17.6 per cent) and the highest at 95° F (41.8 per cent) (table 20).

The mean developmental times and the immature mortalities thus estimated were later utilized in the calculation of life tables.

Table 21 summarizes the influence of temperature upon total progeny production, sex ratios, longevity, and reproductive period. Duncan's multiple range test was conducted on the mean total progeny and the mean percentage of females in total progeny. No significant differences were detected at the 5 per cent level. The data on longevity and on reproductive period did not quite follow the normal distribution. Consequently, the rank sum test illustrated by Snedecor and Cochran (1967) was utilized. No significant differences were found at the 5 per cent level.

The data thus show that temperatures between 75 and 90° F did not have a significant effect on reproductive capacity, sex ratios, and survival of the potato tuberworm. This is unusual, as temperature has had a marked influence on most insects studied (Bursell, 1964). The data also show that the potato tuberworm did not reproduce at 95° F. Moths reared from eggs at this temperature produced an average of 15 eggs per female, none of which hatched. These eggs were laid during the first 5 days of life of the females. Some of them appeared normal at deposition, but soon all the eggs shriveled and died. There-

TABLE 21

EFFECT OF CONSTANT TEMPERATURES ON TOTAL PROGENY PRODUCTION, PROGENY SEX RATIOS, LONGEVITY, AND REPRODUCTIVE PERIOD OF *P. OPERCULELLA* (50 PER CENT R.H., AND 12-HOUR PHOTOPERIOD)*

Temperature (°F)	Mean total progeny†	Mean per cent of females in total progeny†	Mean longevity of adults (days)†	Mean reproductive period (days)†
75	168.85 a	48.1 a	9.1 a	7.5 a
80	177.65 a	50.6 a	8.2 a	5.7 a
85	141.57 a	49.1 a	7.4 a	5.4 a
90	128.71 a	49.2 a	7.2 a	5.4 a
95	0.00	—	7.0 a	—

* Based on cohorts of 35 individuals.
† Means followed by the same letter on a vertical line are not significantly different at the 5 per cent level.

TABLE 22

EFFECT OF TEMPERATURE OF REARING ON VIABILITY OF THE PROGENY OF THE POTATO TUBERWORM

Cross*	Temperature at which mating and oviposition occurred (°F)	Mean number of eggs per female†	Per cent of eggs hatching
M80 × F80	80	173.0	96.8
M80 × F80	95	144.7	93.5
M80 × F95	80	78.4	94.6
M80 × F95	95	63.2	92.2
M95 × F80	80	18.0	0.0
M95 × F80	95	26.6	0.0
M95 × F95	80	24.1	0.0
M95 × F95	95	15.0	0.0

* Indicates sex of individuals and temperature at which they were reared from birth. For example, M80 indicates males reared at 80°F; F95 indicates females reared at 95°F.
† Means of 30 replicates.

fore, a life table at 95° F could not be calculated.

An experiment was conducted to study in more detail the adverse effect of high temperature (95° F) on the reproductive capacity of the potato tuberworm. Potato tubers were infested with a number of newly-hatched larvae which were reared at 80° F and the infested tubers were then immediately placed in a temperature cabinet at 95° F. At pupation, the pupae were sexed and separated to insure a supply of virgin females. The same methods were used to obtain pupal material reared at 80° F.

Immediately after emergence, all possible crosses were conducted (table 22). Each cross was replicated 30 times and was made at both 80 and 95° F to determine the effect of temperature on mating and oviposition. Data were gathered daily and only from oviposition units in which mating had been ascertained. The resulting eggs were kept in tight containers at 80° F and observed daily to measure percentages of hatching. The results indicate that the temperature at which mating took place did not appreciably affect mating and fertilization. The percentages of hatching remained approximately the same for all crosses irrespective of the temperature at which mating took place. Males reared at 80° F fertilized females born and reared at 95° F, whereas males born and reared at 95°F did not fertilize females born and reared at 80° F. This indicates that a constant rearing temperature at 95° F caused male sterility.

TABLE 23

EFFECT OF CONSTANT TEMPERATURES ON SEVERAL POPULATION GROWTH STATISTICS OF *P. OPERCULELLA**

Temperature (°F)	Mean total progeny (progeny per female)	Gross Reproductive Rate (GRR) (female progeny per female)	Net Reproductive Rate (R_o) (female progeny per female)	Mean generation time (T) (days)	Intrinsic rate of natural increase (r)
75	168.85	85.30	63.51	34.3	0.121
80	177.65	88.75	73.08	24.4	0.176
85	141.57	70.73	56.15	20.5	0.196
90	128.71	65.20	46.13	18.5	0.207
95	0.00	0.00	0.00	—	negative

* Based on cohorts of 35 individuals.

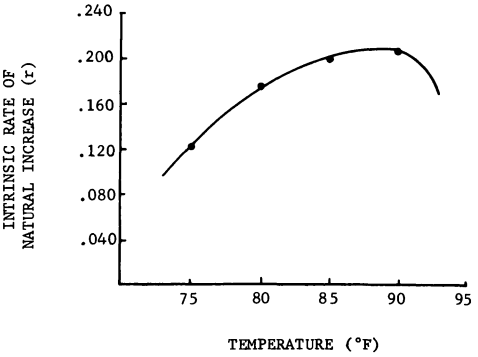

Fig. 17. Effect of constant temperatures on intrinsic rate of natural increase of *P. operculella* (50 per cent R.H. and 12-hour photoperiod).

Progeny production at temperatures between 75 and 90° F reached a peak during the second day of life of the parent females. The daily progeny sex ratios were not influenced by temperature and remained 1:1 throughout the reproductive period.

Effect of temperature on population growth

Life tables were calculated for the potato tuberworm at each temperature tested and data from these are summarized in table 23.

The non-significant effect of temperature on the reproductive capacity of the potato tuberworm was also reflected in the relatively small differences among the Net Reproductive Rates (table 23). Because the magnitude of the intrinsic rate of natural increase varies only as the logarithm of the Net Reproductive Rate, differences among values for r in table 23 are mainly due to differences among developmental times. Thus, the intrinsic rate of natural increase varied in direct proportion to temperature as did velocity of development. It increased from a low of 0.121 at 75° F to a high of 0.207 at 90° F; the optimal temperature. This is also illustrated in figure 17.

The intrinsic rate of natural increase at 95° F was negative because the potato tuberworm was unable to reproduce at this temperature. Thus, the population will decrease to extinction at this high temperature.

COMPARISON OF TEMPERATURE RESPONSES OF THE TWO PARASITES AND THEIR HOST

Developmental and generation times

Figure 18 illustrates the way in which developmental times of the three species varied with temperature. The curves are very similar in configuration, especially those of the two parasites between 75 and 90° F. *A. scutellaris* consistently developed at a faster rate than did *A. subandinus* and both parasites developed faster than did their host. As will be shown later, this had an important effect on their capacities for increase. The most important difference between *A. subandinus* and *A. scutellaris* was that the former could not develop at 95° F (fig. 18).

The same type of relationship was found for generation times mainly because the generation time is largely determined by the developmental time. There is no value for the potato tuberworm at 95° F in figure 18 because this species could not reproduce at this temperature.

Adult longevity

There were marked differences in regard to the effect of temperature on adult longevity (fig. 19). Ovipositing females of *A. subandinus* lived longer than did those of *A. scutellaris* and the potato tuberworm. However, high temperatures had more of an adverse effect

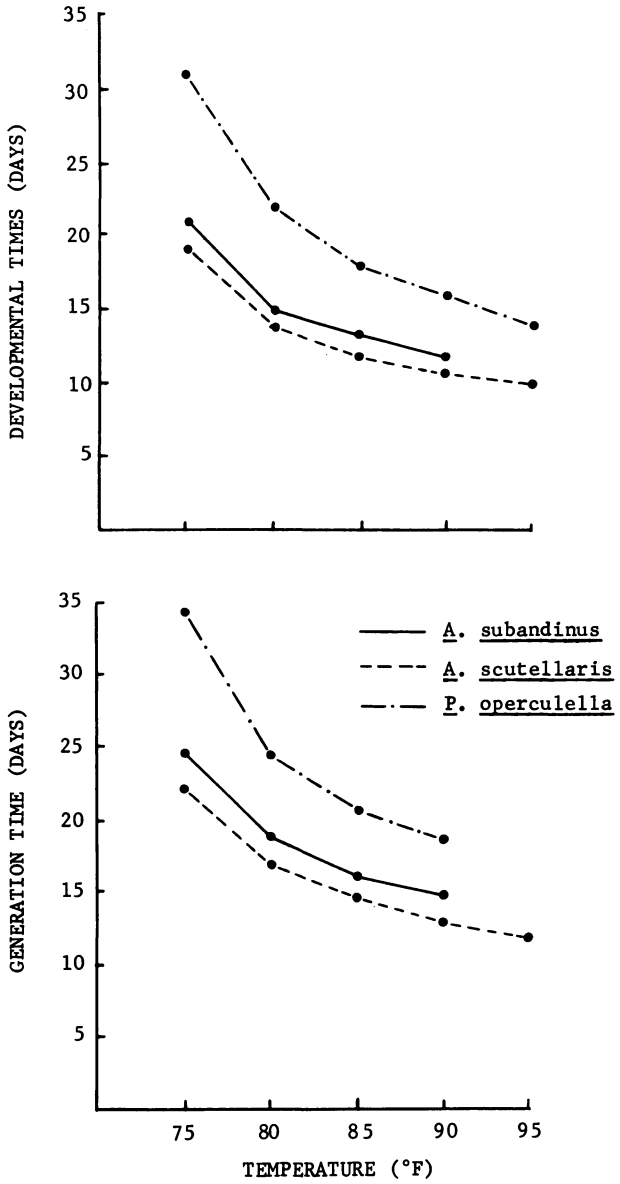

Fig. 18. Mean developmental (above) and generation (below) times of the potato tuberworm and two of its parasites at different constant temperatures, 50 per cent R.H. and 12-hour photoperiod.

on *A. subandinus,* survival of its females falling sharply as temperature increased. Although females of *A. scutellaris* lived fewer days than *A. subandinus,* they tolerated high temperatures better. The curve for the potato tuberworm indicates the small effect of temperature on its survival; longevity values remaining similar, especially between 80 and 95° F.

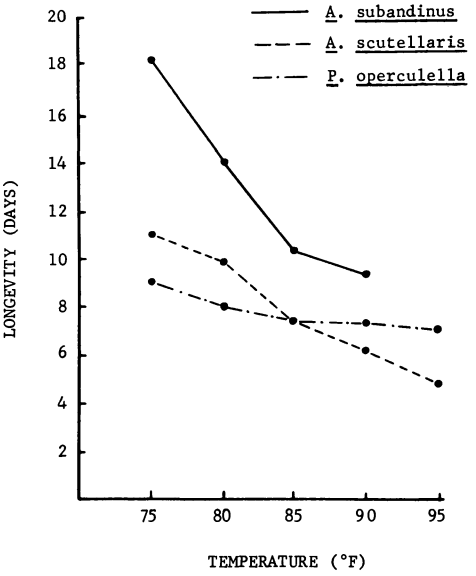

Fig. 19. Mean female longevities of potato tuberworm and two of its parasites at different constant temperatures, 50 per cent R.H., and 12-hour photoperiod.

Adult longevity alone can be a misleading statistic and, by itself, does not indicate the extent to which survivorship is favorable to the population. This is due to the fact that the capacity of the individual to produce the maximum of female progeny in the shortest possible time is more important than longevity, especially during the first days of life of the parent female. Progeny produced during the last days of life of the parent female contributes little to the value of the intrinsic rate of natural increase.

Progeny production and population growth

Characteristically, the two parasites and their hosts reached the peak of total progeny production at 80° F (fig. 20). Between 75 and 90° F, *A. subandinus* produced more total progeny than did *A. scutellaris* and the potato tuberworm. The curves for *A. scutellaris* and the host were very similar in this range of temperature. However, at temperatures above 90° F *A. scutellaris* was superior, being the only species capable of producing progeny at 95° F (fig. 20). *A. subandinus* did not develop at this temperature, and *P. operculella* did not reproduce as a consequence of male sterility.

The Net Reproductive Rates of the three species also peaked at 80° F (fig. 21). The Net Reproductive Rate is a better estimate of the reproductive ability of an organism because it includes survivorship and progeny sex ratios (Cole, 1954). For these reasons, the superiority of *A. scutellaris* over *A. subandinus* at high temperatures is better illustrated in figure 21. In this figure, the curve for Net Reproductive Rate of *A. subandinus* fell sharply between 85 and 90° F to such a level that, at the latter temperature, female progeny production was lower than that of *A. scutellaris*.

The over-all effect of temperature on population increase in terms of values of the intrinsic rate of natural increase is illustrated in figure 22. Potentials for growth of the parasites were higher than that of the host, mainly as a result of their shorter developmental periods (fig. 18) and, to a lesser extent, because of their higher reproductive rates (fig. 21). This suggests that, theoretically, both parasites should be able to supress populations of the host. This of course is an oversimplification and, as pointed out by Burnett (1960), depends on many factors, including the initial densities of host parasites.

The curves for *A. subandinus* and *A. scutellaris* were similar up to 80° F, with a slight advantage for *A. scutellaris* due to its shorter developmental periods (fig. 18). At 90° F, differences between the two parasite species became obvious (fig. 22). While the curve for *A. subandinus* fell sharply, that of *A. scutellaris* reached a peak at 90° F and remained high at 95° F, a temperature at which *A. subandinus* failed to

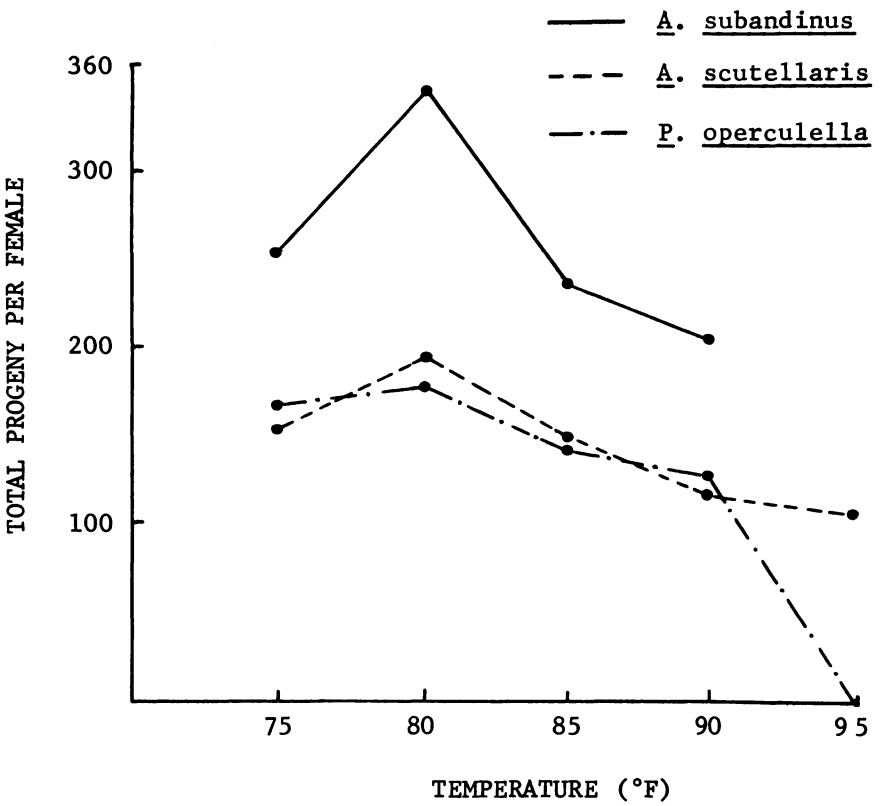

Fig. 20. Mean total progeny of potato tuberworm and two of its parasites at different constant temperatures, 50 per cent R.H., and 12-hour photoperiod.

develop. This indicates that *A. scutellaris* is better adapted to higher temperatures, not only because of better survival and lower developmental times, but also because its reproductive capacity at the upper thermal levels was higher. This species should have a competitive advantage at high temperatures.

To what extent the lesser adaptability of *A. subandinus* to high temperatures might help to explain its failure to become established in southern California, is a matter that requires further research. With the basic data provided in this study, additional research could be conducted to ascertain the competitive ability of both species. The results herein suggest that at high temperatures *A. subandinus* could not compete with a better adapted, already established species such as *A. scutellaris*. However, additional factors such as the searching capacity of each species, which is generally accepted as the single most important attribute of an effective parasite (DeBach, 1964), should be investigated. Furthermore, the presence of the tomato pinworm as an alternate host for *A. scutellaris* is probably an advantage for this species, especially during periods of scarcity of the potato tuberworm.

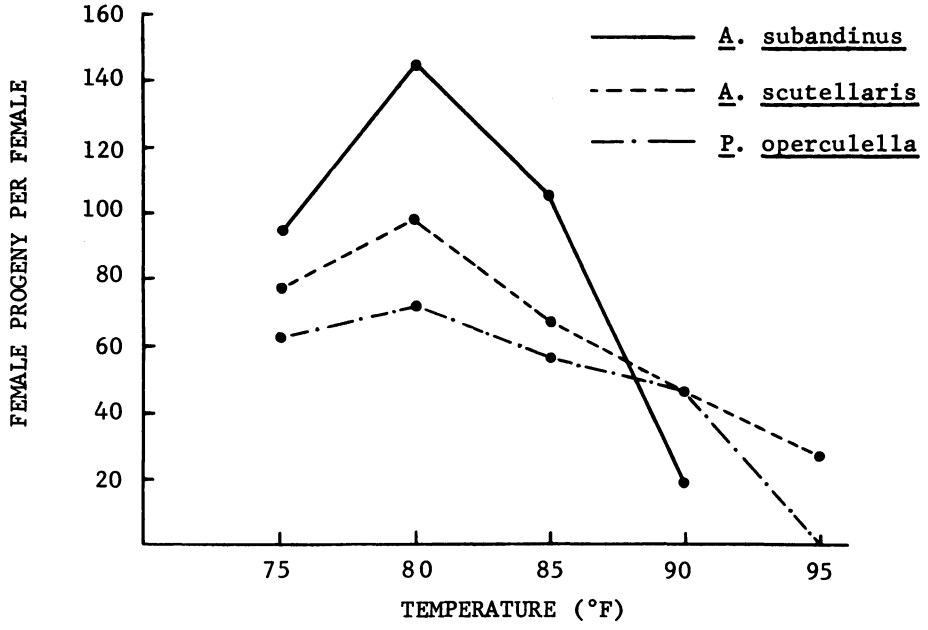

Fig. 21. Net Reproductive Rates of potato tuberworm and two of its parasites at different constant temperatures, 50 per cent R.H., and 12-hour photoperiod.

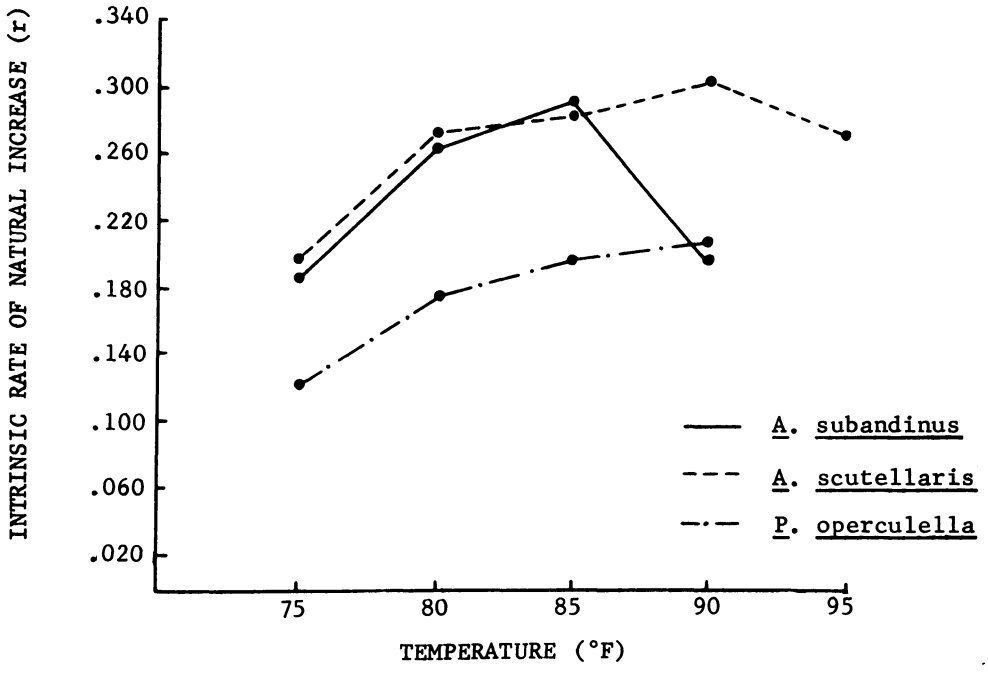

Fig. 22. Intrinsic rates of natural increase of potato tuberworm and two of its parasites at different constant temperatures, 50 per cent R.H., and 12-hour photoperiod.

SUMMARY

The biology and temperature and humidity responses of *A. subandinus* were studied and the temperature responses of this parasite were compared with those of *A. scutellaris* and their common host, the potato tuberworm.

At 80° F and 50 per cent R.H., the mean duration of the life cycle of *A. subandinus* was 15 days (range: 14 to 16 days). The mean duration of the developmental stages was as follows: egg, 20 to 24 hours; first instar larva, 4.5 days; second instar, 2.5 days; third instar, 2 days; prepupa, 0.5 days; and pupa, 4.5 days.

The egg was found floating free in the body cavity of the host larva. Though superparasitism may occur, no more than one late instar parasite larva was found in a host nor more than one parasite emerged from a cocoon. The parasite larva develops in the body cavity of the host and, when mature, emerges by cutting its way out along the lateral line, thus killing the host. Parasite females did not oviposit in host eggs or pupae. These observations indicate that *A. subandinus* is a primary, solitary, larval endoparasite of the potato tuberworm.

The immature stages of *A. subandinus* were described and their dimensions recorded. The head structures of the last instar larva were also described. The occurrence of three larval instars was ascertained by observations and measurements of the head capsules and mandibles. The first instar is of the mandibulate-caudate type and the other two are hymenopteriform.

After emergence from the host larva, the parasite larva spins a silver-white cocoon inside that of the host. Adult emergence was stimulated by light. The mating, feeding, and ovipositional behaviors of the adults were described.

There is essentially no preoviposition period in *A. subandinus* since both virgin and mated females produced progeny within the first 80 minutes of life. The progeny of virgin females consisted entirely of males, indicating that *A. subindinus* is an arrehnotokous species.

Potato tuberworm larvae, 2- to 3-days-old, were the most suitable for parasitization. The optimal host density was 100 larvae per tuber.

The effect of constant temperatures on the biology of *A. subandinus* was studied in a range from 60 to 95° F (50 per cent R.H., 12 hours photoperiod). The speed of development was directly and significantly related to temperature. A constant temperature of 95° F prevented development of the parasite beyond the first instar. Consequently, the upper thermal limit occurred somewhere between 90 and 95° F. By regression analysis the lower thermal limit for development was calculated as 52.3° F.

Longevity of the adult females was inversely related to temperature, but followed the pattern of the curve of physiological longevity. Maximum production of progeny occurred at 80° F and decreased at lower or higher temperatures. Extreme temperatures affected the progeny sex ratio, with an excess of males being produced at 60 and 90° F. The daily sex ratio also varied, older females producing more males than females. The mean reproductive period was inversely related to temperature.

Life tables were prepared for each environmental condition and the overall effect of physical factors on the parasite was determined by using the intrinsic rate of natural increase as a precise bioclimatic index. As determined by calculations of r, *A. subandinus* persisted and increased in numbers between 60° F and some temperature

between 90 and 95° F. The maximum value of r was obtained at 85° F, indicating that this temperature was optimal for this species.

The influence of relative humidity upon *A. subandinus* was studied at 80 and 85° F. Developmental rates and immature mortality were unaffected by humidity. High levels of humidity (70 per cent) adversely affected longevity, reproductive period, and progeny production. At both temperatures, progeny production was maximum at 50 per cent R.H. which was also optimum for population growth.

The biology of *A. scutellaris* was studied at temperatures between 75 and 95° F (50 per cent R.H., 12 hours photoperiod). This parasite developed and reproduced at 95° F, a temperature at which *A. subandinus* could not develop. The calculations of life tables and values of intrinsic rates of natural increase indicated that the optimal temperature for *A. scutellaris* was 90° F.

The potato tuberworm host was also studied at temperatures between 75 and 95° F (50 per cent R.H., 12-hour photoperiod). This species developed at 95° F but this high rearing temperature caused male sterility, thus preventing the production of progeny. Between 75 and 90° F, temperature did not have a significant effect (5 per cent level) on progeny production, sex ratios, longevity, or reproductive period. The calculations of r indicated that 90° F was the optimal temperature mainly as a result of shorter developmental periods at this temperature.

Comparisons of the temperature responses of the two parasites and their host revealed that the parasites have a higher power of increase than the host. The temperature comparisons also showed that *A. scutellaris* is much better adaptd eto high temperatures than is *A. subandinus*.

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This level of humidity was also optimal for population growth. *Apanteles scutellaris* developed and reproduced at 95°F, a temperature at which *A. subandinus* could not develop. The optimal temperature for *A. scutellaris* was 90°F. The potato tuberworm host developed at 95°F but this temperature caused male sterility, preventing production of progeny. The shortest developmental period of the potato tuberworm occurred at 90°F. Comparisons of the temperature responses of the two parasites and their host revealed that the parasites have a higher power of increase than the host, and that *A. scutellaris* is better adapted to high temperatures than is *A. subandinus*.

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