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Biology of *Agathis unicolor* (Schrottky) and *Agathis gibbosa* (Say) (Hymenoptera: Braconidae), Primary Parasites of the Potato Tuberworm

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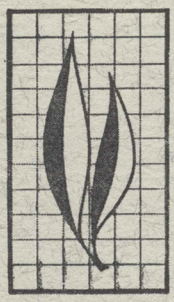

Studies were conducted on the biology, and on temperature and humidity responses, of *Agathis unicolor* (Schrottky), and exotic species. Results were compared with similar studies on the native species, *A. gibbosa* (Say), and their common host, the potato tuberworm, *Phthorimaea operculella* (Zeller). The two species of parasites were reared at several constant temperatures and humidities, and life-table data were obtained in each test environment. These data were used to calculate the intrinsic rate of natural increase, which was used as a bioclimatic index for each of the two species. The influence of several different constant temperatures and humidities on the parasites, and on host-parasite relationships, was evaluated on the basis of relative changes in the intrinsic rate of increase, developmental time, and the mean generation time.

The egg of *A. unicolor* is deposited in a ganglion of the ventral nerve cord of the host larva. Parasite larvae develop within the host body cavity and, after emergence, spin their silky-white cocoons inside the host cocoons. There are three larval instars, the first being both caudate and mandibulate, and the other two, hymenopteriform. The mean minimum developmental time from egg to adult emergence was 18 days at 26.7 C 50 ± 2 percent relative humidity (RH). Measurements and morphological descriptions of the immature stages are presented, and mating and ovipositional behavior of the adults are described. The optimum host density for maximum parasite progeny was 85 larvae per tuber. The biology of *A. unicolor* is similar to that of *A. gibbosa.*

(Continued inside back cover)

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Biology of *Agathis unicolor* (Schrottky) and *Agathis gibbosa* (Say) (Hymenoptera: Braconidae), Primary Parasites of the Potato Tuberworm[1]

INTRODUCTION

AGATHIS UNICOLOR (Schrottky) is native to South America. It is a primary parasite of the potato tuberworm, *Phthorimaea operculella* (Zeller), which is its only recorded host. *Agathis unicolor* was originally described *Orgilus unicolor* by Schrottky (1902). Muesebeck (1956) transferred it to the genus *Agathis*.

Agathis unicolor was received in quarantine at the Division of Biological Control, University of California, Riverside, in December, 1963, from Balcarce, Argentina. Following its release from quarantine and subsequent propagation in the insectary for several generations, *A. unicolor* was liberated in the principal potato-growing areas of southern California. Subsequent efforts to recover it were unsuccessful (Oatman and Platner, 1974). *Agathis unicolor* was shipped from California to the Commonwealth Institute of Biological Control (CIBC) Laboratory at Bangalore, India, from where it was later shipped to other Commonwealth countries, including Australia, Bermuda, New Zealand, and South Africa. In these countries, *A. unicolor* was released but never recovered (Simmonds, personal communication).

Physical factors can be important in limiting the establishment and success of introduced natural enemies. As attempts to establish *A. unicolor* in southern California were unsuccessful, studies were initiated on the effect of temperature and humidity on various phases of its biology, such as developmental rate, longevity, fecundity, progeny sex ratio, and the intrinsic rate of increase *r*. Because *r* is specific for a given condition, the limits of climatic tolerance as indicated by the different values of *r* can be established for the species by compiling these statistics into a life table. Used this way, the intrinsic rate of increase has been referred to as a bioclimatic index (Force and Messenger, 1964).

Agathis gibbosa (Say) is native to North America, and is a primary parasite of the potato tuberworm. As its biology had been previously studied (Qdębiyi and Oatman, 1972), only its temperature and humidity responses were investigated in this study. The responses of the two parasites to these physical factors were then compared to help determine which species has the most potential for control of the potato tuberworm.

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Further investigations on the potato tuberworm were unnecessary, as its responses to temperature and humidity were studied by Cardona (1971). However, for comparative purposes, similar studies with the two parasite species were conducted within the same range of temperature in which the host studies were conducted.

METHODS AND MATERIALS

Environmental conditions

Except for life-table studies, experiments were conducted in an insectary room at 26.7 C and 50 ± 2 percent R.H. Light was provided by 12 40-watt, cool-white fluorescent tubes, regulated by a time switch set to provide 12-hr photoperiod. The exchange of air in the room was supplied by an integral air-conditioning system. Variations in temperature and relative humidity were minimized by an electrical fan which provided constant air movement.

All life-table studies were conducted in constant temperature cabinets modified from apartment size refrigerators (Platner, Scriven, and Braniger, 1973). Humidity in the cabinets was regulated by varying the strength of an aqueous solution of sulphuric acid in plastic pans. By changing the acid solution weekly, the humidity was kept within 2 to 3 percent of the desired level. The photoperiod in the cabinets was maintained at 12-hr photoperiod. Plywood sheets (0.64 cm thick) were placed on metal racks in the cabinets for rearing and oviposition studies, as described in the general experimental setup.

Host culture

A stock culture of the potato tuberworm is maintained in the insectary of the Division of Biological Control, University of California, Riverside, using techniques developed by Platner and Oatman (1968). As *Agathis unicolor* and *A. gibbosa* are larval parasites, only host larvae were needed. Potato tuberworm egg sheets were removed daily from the stock culture, and the eggs were incubated in a 1-qt (0.94 liter) polystyrene container. The larvae thus obtained were used to infest potato (*Solanum tuberosum* 'White Rose') tubers for different experiments.

Parasite culture

A stock of *A. unicolor* has been maintained in the insectary since 1963. The initial culture of *A. gibbosa* was obtained in 1970 from parasitized potato tuberworm larvae in leaves of potato plants collected from untreated experimental plots on the University of California's Moreno Agricultural Experiment Station near Riverside.

Stock cultures of the two parasites were treated similarly throughout the study. There were two cages for each parasite culture. Each cage was 118 cm long, 42 cm wide, 53 cm high in front, and 61 cm high in the back. The slanted top of each cage was covered with glass, the back with muslin. The front of each cage was a wooden detachable door which contained two circular, 15 cm diameter openings. Each opening was provided with a white muslin sleeve to facilitate transfer of materials in and out of the cage. To maintain the cultures, potato tubers, which had been punctured by a mechanical device (Leong and Oatman, 1968) to ensure even and adequate host larval infestation, were infested with newly emerged potato tuberworm larvae and placed in the stock culture cages for oviposition by the parasites. After 24 to 48 hr, the tubers were removed and arranged horizontally on a ½ inch (1.27 cm) mesh wire tray inside the second cage. White sand was spread evenly over the bottom of the cage to facilitate pupa-

tion of the potato tuberworm larvae.

Parasite subcultures were held in wooden cages measuring 42 cm × 42 cm × 36 cm. Each cage had a glass top, lateral panels of muslin cloth, and a removable round section on the front and back to permit manipulation of materials within the cage without letting the parasites escape. Subcultures were initiated and maintained by methods similar to those described for stock cultures. Parasite cocoons were collected and isolated in gelatin capsules whenever newly emerged female parasites were needed.

General experimental setup

'White Rose' tubers were used, because, with this cultivar, potato tuberworm larvae feed shallowly beneath the skin and thus are more readily accessible to parasite oviposition. The tubers averaged 6 cm x 4.5 cm, and had fairly smooth surfaces. They were harvested from untreated, parasite-release plots at the Moreno Agricultural Experiment Station.

Potato tubers, punctured as previously described, were impaled lengthwise on nails which had been driven through ½ inch (1.3 cm) thick plywood. The nails protruded five cm to provide support for the tubers, leaving sufficient space between them and the surface of the plywood for the parasites to have access to entire tubers. Before the tubers were impaled, tops of 100 x 15 mm plastic Petri dishes, each with a ⅛-inch (0.32 cm) hole in the center, were inverted on the nails and pushed down until they rested on the plywood, to collect potato tuberworm larvae which emerged to pupate. These Petri dish collection units were supplied with white sand distributed evenly in the dish to facilitate pupation of larvae. After the tubers were impaled, they were infested with a given number of one-day-old potato tuberworm larvae which were transferred from 1-qt (0.94 liter), unvented, polystyrene emergence units, using a camel-hair brush (size 0000).

Infested tubers were covered with 1-pt (0.47 liter), clear polystyrene containers before and after exposure to parasites. These containers were vented on opposite sides with 5-cm holes covered with muslin. In place, the units were inverted with their rims pressed down firmly inside the Petri dishes.

Parasite oviposition units

For oviposition, adult parasites were confined to the tuber, using 1-qt (0.94 liter) polystyrene containers which were 11 cm in diameter at the top, 9 cm at the bottom, and 12 cm high. Each of these oviposition units (cages) was vented on opposite sides with a 5-cm diameter hole covered with organdy. A 3.8 cm hole and a 1.3 cm hole were cut through the bottom of each unit. The 3.8 cm opening was covered with 100-mesh brass screen through which honey was forced to supply food for the parasites. Water was supplied through a 2-dr (9.4 ml), cotton-stoppered glass vial inserted in the 1.3 cm opening. When in use, the unit was inverted so that the bottom served as the top of the oviposition cage, and the top, with its polyethylene lid in place, was the floor. Adult parasites were introduced into the oviposition unit through the 1.3 cm opening, either with a mouth aspirator or a gelatin capsule. The lid was then carefully removed before inverting the unit over the infested potato tuber to prevent the parasites from escaping. After oviposition, the units and the parasites were removed, and the holding cages placed over the tubers. The oviposition unit was also used in studies of the effect of food on the longevity of adult parasites, and for observations on their mating behavior.

Parasitization in relation to host age

To determine the age of the potato tuberworm larva most suitable for maximum parasitization, each of 10 potato tubers infested with 50 potato tuberworm larvae of a known age group was exposed to a newly emerged male and female parasite in an oviposition unit for 24 hours. Age groups ranged from 0 to 1 day to 9 to 10 days, and each group was replicated 10 times. The 9- to 10-day-old group was used as the control, and therefore was not exposed to parasites. After exposure, the parasites were discarded, and the tubers were held for adult emergence. The number of moths and parasites which emerged was recorded.

Parasitization in relation to host density

To determine the maximum host density for maximum parasite progeny production, potato tubers (average 6 cm x 4.5 cm) were infested with different densities of hosts, ranging from 40 to 115 potato tuberworm larvae per tuber. Infested tubers were held until the larvae reached the most suitable age for parasitization. Tubers were then exposed to a newly emerged male and female parasite in an oviposition unit for 24 hours. After exposure, tubers were isolated for adult parasite emergence, and the number of parasites and moths obtained was recorded.

Determination of duration of development

Potato tubers were infested with the optimal number of host larvae and held at 26.7 C until the larvae reached the most suitable age for parasite oviposition. Infested tubers were then spaced evenly on inverted wire trays inside modified subculture cages (36 cm x 30 cm x 27 cm), containing large numbers of parasites. Cages were immediately transferred to their respective temperature cabinets. After 12 hr of exposure, the parasites were discarded. One tuber was immediately removed, and host larvae were extracted by the heat extraction method (Platner, Greany, and Oatman, 1969). This procedure was repeated at 12, 18, and 24 hr, and daily thereafter until development was completed.

As the larvae were extracted, they were killed in 60 percent alcohol and dissected immediately in 0.9 percent saline solution to study developmental stages of the parasites. Parasite larvae in prepupal and pupal stages were recovered from cocoons of the host for study. Measurements of immature stages were made in the saline solution. The body form of the larvae was studied, and gross features were noted.

In all instances, some parasitized hosts were held in cabinets until the parasite progeny emerged. These were used in subsequent experiments on reproductive capacity and longevity of adult parasites.

Reproductive, longevity, and sex-ratio studies

Adult parasites, emerging under each test environment in the developmental studies, were placed in feeding and oviposition units and returned to their respective temperature cabinets. After 12 hours of feeding and mating, cohorts of 15 pairs per test environment, one male and one female per pair, were placed in separate oviposition units. Every 24 hours, each pair was provided with a potato tuber infested with the optimal number of host larvae at the optimal age for oviposition, and the number of initial cohorts still alive was recorded. This procedure was continued until all females in the cohort had died. Exposed tubers were held in the insectary room (previously described conditions) until the parasite progeny emerged. Dead adults were removed, counted, and sexed.

These data, and those obtained from the developmental experiments, were combined at each test environment to construct life tables from which the potential growth rates of the parasites were computed.

CONSTRUCTION OF LIFE TABLES

Life table studies were designed to provide data on the developmental time, longevity, and fecundity of *A. unicolor* and *A. gibbosa.* From these data, the intrinsic rate of natural increase of the two parasites was calculated at selected temperatures and humidities.

Life tables were constructed for each parasite at each test environment, using Birch's (1948) methods in which only female progeny were considered. The following data were assembled for each life table:

x = age intervals in days;

l_x = fraction of initial cohort still alive at the beginning of age x;

m_x = mean number of female offspring produced per female parent alive at age x;

l_xm_x = the product of the l_x and m_x columns for each age interval.

The initial number of eggs or newborn parasites was needed to calculate immature survival for the prereproductive period in the l_x column. However, *A. unicolor* and *A. gibbosa* deposit their eggs in the ganglia of the ventral nerve cord. When the eggs hatch, the larval stages develop within the body cavity of the host. Consequently, it was impossible to determine the initial number of eggs and the larval mortality of these parasites without destroying the parasite larvae during dissection of host larvae. These data were, therefore, obtained indirectly.

The mean number of parasite progeny produced at 26.7 C and 50 percent R.H. was considered as 100 percent prereproductive survival, and was entered into the life table as $l_x = 1.0$. To obtain the l_x values at other test environments, 10 potato tubers were infested and exposed to parasite oviposition for 12 hr. After exposure, the tubers were transferred to the different temperature cabinets and held there until parasite progeny emerged and died. The mean number of progeny obtained at each temperature was compared to that obtained at the reference temperature (26.7 C). Egg and larval mortality was only introduced into the life table (l_x column) in those cases where emergence was substantially lower than the number that theoretically should have emerged.

Superparasitism and variations in the progeny sex ratio are important factors in life-table studies (Messenger, 1964). Superparasitism occurred occasionally in *A. unicolor* and *A. gibbosa,* under high parasite density. However, when this occurred, only one parasite larva survived, other larvae being encapsulated in the posterior end of the body. When one parasite was confined to an infested tuber, as was true in all life-table studies, superparasitism was never observed. Therefore, the intrinsic rate of increase was calculated without regard to losses due to superparasitism.

The sex ratio of the progeny of both parasite species varied daily. Therefore, a sex-ratio correction factor (the proportion of females in the total progeny) was multiplied by the mean daily progeny to obtain the correct m_x values of the life-table (Force and Messenger, 1964).

The following statistics were computed from each life-table: (a) Gross

Reproductive Rate (GRR). This is the average number of female eggs produced per female parent without regard to the longevity of the parent, viz., the sum of the values in the m_x column. (b) Net Reproductive Rate (R_o). This is the average lifetime production of female progeny by an individual female in the cohort. This statistic considers the effect of cohort survival rate. It is computed as the sum of the l_xm_x column. (c) Intrinsic Rate of Natural Increase (r). It is defined as the maximum rate of increase of a population under specified environmental conditions where food and space are unlimited (Andrewartha and Birch, 1954). It is calculated from the equation:

$$\sum_{x=o}^{\infty} e^{-rx}\ l_xm_x = 1$$

The equation is only applicable when the population has reached a stable age distribution. Given a life-table of the kind described above, r is the only unknown. In this study, it was evaluated by iteration. As environmental factors were temperature and humidity, differences in r values were regarded as representing the effect of these factors on the potential growth rate of *A. unicolor* and *A. gibbosa*. (d) Finite Rate of Increase (λ). This is the number of times the population will multiply itself per unit of time: It gives r as a simple expression of an observed value, and is computed from the equation:

$$\lambda = e^r$$
$$= \text{antilog}_e r$$

(e) Generation Time (T). It is defined as the mean length of a generation (birth to weighted reproductive age in adult). It is computed from the equation:

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

RESULTS AND DISCUSSION

Agathis unicolor (Schrottky)

I. General biology

The life cycle of *Agathis unicolor* averaged 21 days (range, 18 to 24 days) at 26.7 C and 50 percent R.H. The mean minimum incubation period was 5 days; first-instar, 3 days; second-instar, 2 days; third-instar, 3 days; prepupa, 2 days; and pupa, 3 days. The adult male and female emerge on the same day.

The egg is laid in a ganglion of the ventral nerve cord. Similar behavior was reported for *A. Gibbosa* (Ọdẹbiyi and Oatman, 1972) and *A. lacticinctus* (Dondale, 1954). The thoracic ganglia and the last three abdominal ganglia are preferred oviposition sites.

After emerging from the eggs, the larvae float freely in the host haemocoel. Only one parasite larva develops to maturity in a single host larva. Superparasitism was occasionally observed under high parasite density and oviposition pressure, especially during the first 4 days of the adult female's life. Under such conditions, only one parasite larva developed beyond the third day of larval life; all others were found encapsulated in the posterior end of the host larva.

The parasitized host larva is active until the parasite larva reaches the early third-instar stage, when the host, after spinning its cocoon, becomes progressively sluggish, finally loses all power of locomotion, and eventually dies. At this point, the parasite larva cuts its way out of the host larva and feeds externally on the remains of the

host. By the time the parasite larva begins to spin its cocoon, only the head capsule of the host remains, usually being found at the posterior end of the cocoon.

Based on these observations, *A. unicolor,* like *A. gibbosa* (Qdębiyi and Oatman, 1972), is a primary, solitary, internal larval parasite of the potato tuberworm.

Host-parasite life cycles are well synchronized. Unparasitized host larvae developed to maturity, and adults emerged 3 to 4 days before parasite emergence. Thus, in nature, a new generation of host larvae would be available for oviposition when adults of *A. unicolor* emerge.

The egg

Because of its cryptic, internal placement, the egg is difficult to observe shortly after oviposition. The ovarian egg is smooth and translucent, bluntly rounded at one end and slightly tapered at the other. Based on 25 individuals, the mean length is 0.10 mm and the width, at the widest point, 0.02 mm.

At 96 hr after oviposition, the egg is more than three times larger than the ovarian egg, and the embryo is fully formed. Length of the 96-hour-old egg ranged from 0.24 to 0.44 mm, average 0.31 mm; width ranged from 0.18 to 0.27 mm, average 0.21 mm.

First-instar

The first-instar larva was found floating freely in the haemocoel 4.5 days after oviposition. The larva is translucent-white and has 13 body segments, ending in a caudal process. The cephalic structure, with its pair of sickle-shaped mandibles, is well sclerotized. Pairs of appendages are situated on the ventral side of each body segment, except the last, the caudal process; one pair each is situated on the second and third segments, and two pairs each are on the following nine segments.

The size of the first-instar larva varied considerably. Based on 25 individuals, length of the first-instar at eclosion ranged from 0.52 to 0.93 mm, average 0.72 mm; and width ranged from 0.12 to 0.17 mm, average 0.14 mm. Two days after eclosion, the late first-instar is more than twice as long as the early first-instar, ranging from 1.01 to 2.0 mm, average 1.50 mm. Width ranged from 0.17 to 0.29 mm, average 0.16. The caudal horn retrogresses progressively, finally becoming an anal vesicle in the second-instar.

Second-instar

The second-instar larva is creamy-white and is hymenopteriform. Its segmentation is similar to that of the first-instar, but the mandibulate, sclerotized head is no longer present. The caudal horn is reduced to a vesicle, and the paired ventral processes of the first-instar are lacking.

Based on 18 individuals, length ranged from 2.8 to 5.1 mm, average 3.7 mm; and width ranged from 0.5 to 1.1 mm, average 0.7 mm.

Third-instar

The third-instar appears one to two days after cocooning of the host. It is hymenopteriform, with 13 body segments and an anal vesicle. There are no body appendages, and the cephalic skeleton is heavily sclerotized. The mandibles have a minute, spine-like row of teeth on their inner margins. The antennal region, silk press, and labial and maxillary palpi are well developed.

The internal structures also are well developed. The respiratory system is similar to that of the second-instar, but nine pairs of spiracles are visible. The digestive tract consists of a slender oesophagus, a large, fat-filled midgut, and an anus.

Body length of 27 individuals ranged from 4.5 to 8.0 mm, average 6.2 mm;

width from 1.5 to 2.0 mm, average 1.7 mm.

The occurrence of three larval instars in *A. unicolor* was determined by Dyar's Law. Although variations occurred in the size of the first-instar, the width of the head capsule at the widest point is 0.18 mm; second-instar, 0.25 mm; and third-instar, 0.40 mm, based on 57, 15, and 22 individuals, respectively. The overall growth ratio is 1.48 mm. Three instars also occur in *A. gibbosa* (Ọdẹbiyi and Oatman, 1972).

Prepupa

The prepupal stage is a 1- to 2-day period between cessation of feeding and the transformation to the pupa. The mature prepupa is pale yellow, with dark red, crescent-shaped eyes. Three body segments are discernible. The length of 23 individuals ranged from 6.0 to 7.1 mm, average 6.4 mm.

Cocoon

The parasite cocoon is contained within the host cocoon, having been spun during the late third-instar. It is a silky-white, parchment-like structure, bluntly rounded at both ends. When the larva finishes spinning, it usually voids a dark red fluid (meconium) into the posterior end of its cocoon. Size of the parasite cocoon is determined by that of the host. The length of 25 individuals ranged from 7.0 to 8.2 mm, average 7.6 mm. The width ranged from 2.0 to 3.0 mm, average 2.4 mm.

Pupa

The pupa, which was formed after the discharge of the meconium described above, is creamy-yellow with a distinct head, thorax, and abdomen. The appendages are fully visible, somewhat translucent, and loosely appressed to the body. Pigmentation begins at the anterior part of the body and progressively proceeds posteriorly. The spherical, dark red eyes are completely formed, and there are three red ocelli. The mean length of 30 individuals was 6.4 mm, and the width, 1.9 mm.

The adult

Adults of *A. unicolor* are brown. The male has a more slender abdomen than does the female (Fig. 1), but the latter is readily distinguished from the male by the presence of a long ovipositor. Based on 50 individuals each, mean

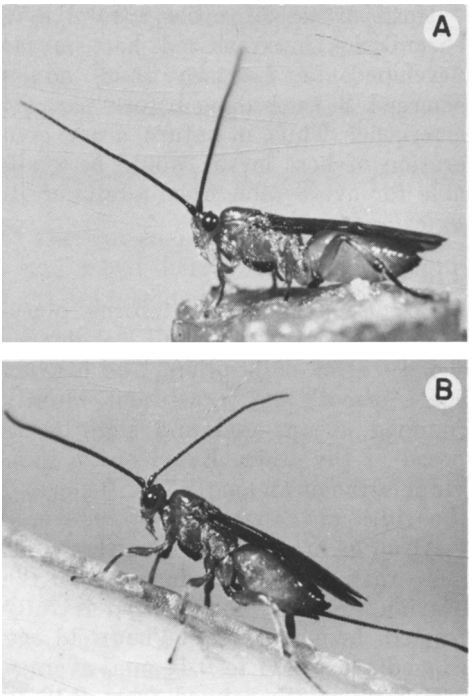

Fig. 1. Male (A) and female (B) of *A. unicolor*.

length of the male is 4.9 mm; female, 4.7 mm. Mean length of the ovipositor is 4.3 mm.

A detailed morphological description of the species was given by Schrottky (1902).

Emergence of the adult parasite is stimulated by light, occurring shortly after such exposure. After emergence, about 5 minutes is spent in cleaning and drying the body. If food is available, feeding occurs immediately. Mating can occur anytime after the period of cleaning.

Mating by the male is always preceded by a fanning of its wings. Successful copulation occurs only with receptive females. Both sexes remain quiet during copulation, which takes 50 to 90 seconds. Males mate several times, but females mate only once.

Preoviposition and parthenogenesis

To determine preoviposition time and parthenogenic reproduction, 10 mated and 10 unmated newly emerged females were each exposed to a potato tuber infested with 2- to 3-day-old potato tuberworm larvae. Every 6 hr, each female was transferred to a similarly infested tuber. The transfers were terminated after 48 hr. All tubers were held individually until the parasites emerged and died. The experiment was replicated 10 times.

Both mated and unmated females oviposited within 24 hr of emergence. Although all females oviposited within 12 to 24 hr, about 25 percent did not oviposit within 0 to 6 hr. To assure oviposition in subsequent experiments, females were always allowed a 24-hr preoviposition period.

The progeny of unmated females consisted entirely of males, whereas mated females produced both male and female progeny. *Agathis unicolor* is therefore arrhenotokous.

Oviposition behavior

Upon reception of appropriate stimuli, the female begins to search an infested potato tuber. She continuously taps the tuber with her antennae as she moves around. When contact is made with the extended frass of infesting larvae, the female stops and searches the area thoroughly. If appropriately stimulated, she raises her body with her hind legs, unsheaths the ovipositor, bends it at an acute angle, and begins to probe the tunnel. When contact is made with the host, the ovipositor is driven deeper, apparently to locate the preferred ovipositional site in the host. When the site is located, the female remains motionless while the egg is being laid. After oviposition, the ovipositor is withdrawn and briefly flexed, and then it may or may not be cleaned. The female then searches for additional hosts to parasitize.

Host larvae must be inside the potato tuber to elicit the ovipositional reaction. Potentially suitable hosts removed from the tuber were ignored by the female. Frass extruded by tunnelling host larvae apparently enhanced the oviposition reaction, although without frass suitable host larvae still elicited the ovipositional reaction, provided they were inside the tuber.

Effect of food on longevity

To study the effect of food on the longevity of adults of *A. unicolor*, newly emerged adults were kept without either honey or water or given water alone, honey alone, or water plus honey. Each test was conducted in an oviposition unit with 10 males and 10 females, and replicated 10 times. The mortality of each sex was recorded daily.

There was no significant difference (5 percent level) between longevity of male and female parasites under any of the conditions provided. There also was no significant difference between longevity recorded for water and that for complete starvation, being an average of 3 days for both sexes under both conditions. With honey, both sexes lived about twice as long as those provided water only, or those under complete starvation. When honey and water were provided, the mean longevity was 11.52 days for males and 12.06 days for females. As both sexes lived longest when provided with honey and water, these were provided to the adult parasites in subsequent experiments.

Parasitization in relation to host age

The most parasite progeny (216) and the highest percentage of parasitization (72.2) were obtained when 2- to 3-day-old potato tuberworm larvae were exposed. Potato tuberworm larvae less than 2 days old produce no, or relatively minute amounts of frass, which, as discussed previously, enhances oviposition. Females of *A. unicolor* spent more time searching for host larvae less than 2 days old than for older ones.

The suitability of host larvae more than 4 days old decreased rather rapidly, as indicated by the decline in the fecundity of the female parasite. This was probably partially due to the fact that older tuberworm larvae tunnel deeper into the tuber, making it more difficult for the parasite to contact them with its ovipositor.

As the data indicated that 2- to 3-day-old potato tuberworm larvae are most suitable for parasitization, they were used in subsequent studies involving *A. unicolor*. Cardona (1971) showed that 2- to 3-day-old potato tuberworm larvae are late first-instar.

Parasitization in relation to host density

The mean number of progeny ranged from 10.4 at a density of 115 host larvae per tuber to 26.8 at a density of 85 host larvae. At densities above and below 85, the number of parasite progeny produced generally decreased. At densities less than 85 host larvae per tuber, females spent more time in searching than in ovipositing, which probably was partially responsible for the reduced fecundity at low host densities. In the control (not exposed to parasites), the percentage of potato tuberworm moths emerging was 69.1, 68.0, and 61.8 at host densities of 85, 100, and 115, respectively. The percentage of moths and parasites emerging from exposed tubers was 63.5, 35.9, and 47.9, respectively, at the same host densities. A crowding effect apparently occurred at high host densities, resulting in some mortality of both parasitized and unparasitized host larvae. Accordingly, potato tubers each infested with 85, 2- and 3-day-old potato tuberworm larvae, were considered to be near the optimum and were used in subsequent experiments.

Parasitization in relation to parasite density

To determine if parasite densities affect the utilization of optimal host densities, females (one to five per oviposition unit) were exposed to a potato tuber infested with 85, 2- to 3-day-old larvae for 24 hours. Each test was replicated 10 times. Exposed tubers were held individually until parasites emerged and died.

Mean total number of progeny produced ranged from 30.2 at a parasite density of five females per infested tuber to 38.2 at a density of two females per tuber. There was no significant difference (1 percent level) between means produced at different parasite densities.

Based on these results, and to help prevent superparasitism, which was occasionally observed at high parasite densities, only one adult female was exposed to each potato tuber infested with the optimal number of optimal aged host larvae in subsequent experiments.

Female progeny production

To determine the fecundity, longevity, and reproductive period of female parasites, 10 unmated and 10 mated females were each exposed to a potato tuber infested with 85, 2- to 3-day-old potato tuberworm larvae for successive 24-hour periods until the female died. The exposed tubers were held individually for larval pupation and subsequent adult emergence. After the adults died, the number of moths and the number and sex of parasites were recorded.

Mean total progeny of unmated females was 296.0 (range, 166 to 414), and consisted entirely of males. Maximum mean daily progeny was 37.3, and was reached on the third day of oviposition (Fig. 2). The longevity of ovipositing virgin females ranged from 6 to 19 days, average 13.4 days. Their reproductive period ranged from 6 to 18 days, average 11.8 days. Most virgin females continued reproduction until 2 days before their death.

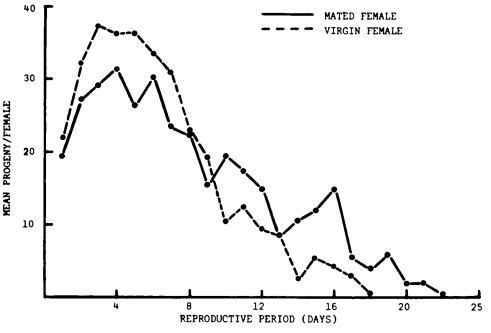

Fig. 2. Mean daily production of progeny by virgin and mated females of *A. unicolor*.

Mean total progeny of the mated females was 289 (range, 141 to 470), and consisted of both males and females. Maximum mean daily progeny was 31.5 on the fourth day of oviposition (Fig. 2). Longevity of mated females ranged from eight to 31 days, average 17.1 days; and their reproductive period ranged from 6 to 22 days, average 13.6 days. Most mated females laid eggs until 4 days before their death.

Although there was considerable variation in the fecundity, longevity, and reproductive period of individual virgin and mated females, there was no significant difference (1 percent level) in the mean total progeny produced by the two groups. The rate of reproduction of virgin females was higher than that of mated females during the first week of reproduction, but was lower shortly thereafter (Fig. 2).

II. Temperature studies

Temperature studies were conducted in constant temperature cabinets at 21.1, 23.9, 26.7, 29.4, 32.2, and 35.0 C, 50 percent R.H., and 12-hour photoperiod.

Effect of temperature on rate of development

Developmental time is the time between oviposition and emergence of the adult female. Results of the experiment on the effect of temperature on development, as reflected in the duration of the total life cycle, indicated that the time required for development decreased progressively with increase in temperature. Mean developmental time ranged from 16.0 days at 32.2 C to 34.1 days at 21.1 C. No development occurred beyond the prepupal stage at 35.0 C.

The rate of development was obtained by expressing the mean developmental time in terms of percentage development per day. An increase in the rate of development occurred with an increase in temperature. Within the range of 21.1 to 29.4 C, the rate of development increased about 1.5 percent for every 5.6 C rise in temperature. Although the highest rate of increase (6.25) was recorded at 32.2 C, the number of adults emerging at this temperature was the lowest.

When the rate of development (percentage development per day) was plotted against temperature, a straight line relationship was evident (Fig. 3). The coefficient of determination (r^2 = 0.958) was significant at the 1 percent level.

The immature survival was assumed to be 100 percent at 26.7 C, and was entered into the life table as l_x = 1.0. Based on this, no mortality occurred at 21.1, 23.9, or 26.7 C. At 32.2 C, the immature mortality was 27.5 percent;

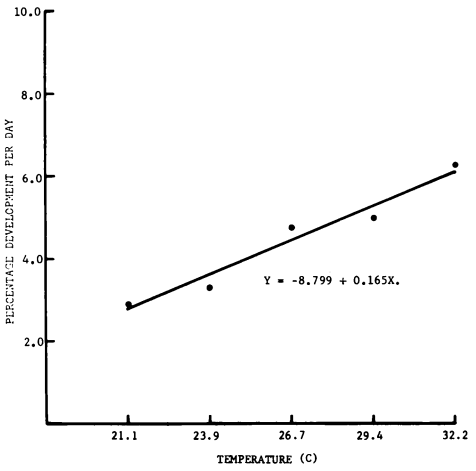

Fig. 3. Relationship between temperature and rate of development of *A. unicolor* from egg to adult emergence.

therefore, the initial l_x value was correspondingly adjusted. This agrees with the observation made previously concerning the rate of development and emergence of *A. unicolor* at this temperature. As development was incomplete at 35.0 C, immature mortality was 100 percent. Using the life cycle at 26.7 C, each of the immature stages from egg to late pupa was exposed to 35.0 C. Only pupal stages survived this temperature; no parasites emerged from material containing earlier stages. Thus, the upper limits of temperature at which complete development of *A. unicolor* occurred were between 32.2 and 35.0 C.

Effect of temperature on longevity

Longevity of the adult female of *A. unicolor* at several constant temperatures is shown in Fig. 4. Longevity decreased with an increase in temperature. The mean longevity ranged from 39.8 days at 21.1 C to 12.0 days at 32.2 C. Longevity at 26.7, 29.4, or 32.2 C, was significantly less (1 percent level) than that at 21.1 or 23.9 C. Within the range of 21.1 to 29.4 C, longevity decreased about 20 days for every 5.6 C increase in temperature.

The inverse relationship between temperature and longevity was again quite obvious, the survival rate being highest at lower temperatures (21.1, 23.9 C). At intermediate temperatures of 26.7 and 29.4 C, and especially at the higher temperature of 32.2 C, adult females were more active than at lower temperatures. Consequently, a higher rate of energy expenditure probably occurred at these temperatures. Senescence occurred more rapidly at 29.4 and 32.2 C than at lower temperatures. The time required to reach 50 percent mortality was 17.2, 13.6, and 12.0 days at 29.4 and 32.2 C, respectively, compared to 39.8 and 31.3 days at 21.1 and 23.9 C. The data thus seem to conform with the theory that, within the same species, longevity is inversely proportional to the intensity of life (Bodenheimer, 1958). Accordingly, survivorship curves at 26.7, 29.4, and 32.2 C were steeper than those at 21.1 and 23.9 C. All curves conformed very well with the curve of physiological longevity (Rockstein and Miguel, 1973), which is generally convex or rectangular in shape. According to Bodenheimer (1958), physiological longevity is the life duration which a normal individual may expect to live, under optimal conditions, until death due to senescence. In this type of curve the initial death rate is low; but, once initiated, it increases rapidly, so that most members of the population die within a short period of time. The slope in such a curve is quite

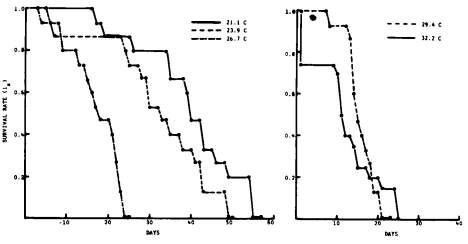

Fig. 4. Survivorship curves for adult females of *A. unicolor* at several constant temperatures, 50% RH, and 12-hour photoperiod.

steep. In terms of steepness, curves at 21.1 and 23.9 C seemed to depart somewhat from the general pattern because intervals between deaths of individuals were longer.

These curves do not necessarily represent the ecological life expectancy of *A. unicolor* in nature. This is because survivorship curves were derived in the laboratory under optimum conditions, where the population was protected from external mortality factors. Consequently, the death rate was probably underestimated.

Effect of temperature on reproduction

Fecundity is an inexact measure of the reproductive power of an insect. It is the total number of male and female progeny produced under a given set of conditions. In population studies, fecundity is expressed as the age-specific fecundity rate (m_x), which is defined as the mean number of female offspring produced in a given time unit by a female of a given age (Birch, 1948). Such a definition is used because population growth depends mainly on female members of the population. Therefore, the calculation of the age-specific fecundity rate depends mostly on the population sex ratio at any given condition. Consequently, temperature might affect the total fecundity and age-specific fecundity rate in a different way.

Effect of temperature on total fecundity

The effect of temperature on total fecundity is shown in Table 1. The highest mean progeny per female was 363.9 at 23.9 C. Within the range of 21.1 to 29.4 C, fecundity decreased gradually below and above 23.9 C, but dropped abruptly to 186.5 at 32.2 C. Considerable variation occurred in the reproductive performance among members of the cohort within this range of temperature. The coefficient of variation ranged from 31 percent at 23.9 C to 45 percent at 26.7 C. A Student-Newman-Keuls' (SNK) multiple range test (Sokal and Rohlf, 1969) conducted on the means revealed no significant difference at the 1 percent-level within this range of temperatures. The coefficient of variation was equally high at 32.2 C, but the mean total progeny was significantly different from all others at the 5 percent level. As discussed earlier, 32.2 C is near the upper thermal limit (35.0 C) for reproduction, hence the low fecundity.

The highest mean daily progeny production was 35.7 per female on the fifth day of reproduction at 29.4 C. Generally, females reached their peak reproduction within 4 to 5 days of oviposition at 26.7 to 32.2 C, and within 6 to 7 days at 21.1 and 23.9 C.

TABLE 1

EFFECT OF DIFFERENT CONSTANT TEMPERATURES ON REPRODUCTION OF *A. UNICOLOR* AT 50% RH AND 12-HOUR PHOTOPERIOD[a]

Temperature (C)	Mean total progeny/female[b]	Mean percent females in total progeny[b]	Reproductive period (days)	
			Range	Mean[c]
21.1	348.8a	21.76a	13–37	28.3a
23.9	363.9a	15.22a	19–33	24.8a
26.7	299.1a	13.13a	7–23	14.0b
29.4	304.9a	46.81b	4–21	11.8b
32.2	186.5b	23.63a	3–19	8.93b

[a] Based on cohort of 15 individuals at each temperature.
[b] Means followed by the same letter on the vertical line are not significantly different at the 5% level.
[c] Means followed by the same letter on the vertical line are not significantly different at the 1% level.

There was no significant difference between the mean reproductive periods at 21.1 and 23.9 C, but both were significantly different from means at 26.7 to 32.2 C. Death usually occurred 2 to 3 days after cessation of reproduction at 26.7 to 32.2 C, and after 7 to 11 days at lower temperatures.

Age-specific fecundity (m_x)

Calculation of the age-specific fecundity is based principally on the sex ratio. In *A. unicolor,* the progeny sex ratio varied daily. In such cases, the fecundity is customarily adjusted for the variation in sex ratio, because the latter affects the intrinsic rate of increase of the population (Force and Messenger, 1964). To adjust for the variation, a sex-ratio correction factor (proportion of females in total progeny) was calculated at each temperature. This factor was 0.2176, 0.1522, 0.1313, 0.4681, and 0.2363 at 21.1, 23.9, 26.7, 29.4, and 32.2 C, respectively. The sex-ratio correction factor multiplied by the daily mean progeny gives the m_x values in life tables. In Table 1, these factors are expressed as the percentage of females in the total progeny. The mean percentage of females at 29.4 C was significantly higher (5 percent level) than that at other temperatures (Table 1).

The age-specific fecundity rate of *A. unicolor* is shown in Fig. 5. The highest fecundity rate occurred between the sixth and seventh days of oviposition at 21.1 and 23.9 C, and between the fourth and fifth days at higher temperatures. The differences in the ages at which the peak fecundity occurs affects the population growth rate (Barlow, 1962). The fecundity rate within the first 10 days was higher than in the rest of the reproductive period, and largely determined the various values of the intrinsic rate of increase. The peak fecundity rate was 16.5 females per female per day at 29.4 C. Below and above this temperature, the peak fecundity rates varied from 4.4 females per day at 26.7 C to 6.3 females at 32.2 C.

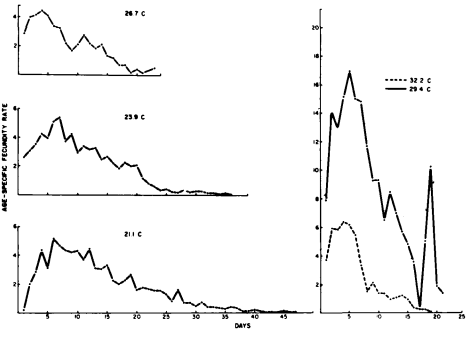

Fig. 5. Effect of several constant temperatures on age-specific fecundity rate of *A. unicolor* at 50% RH and 12-hour photoperiod.

Effect of temperature on population growth

The growth rate of a species population depends on the fecundity (m_x), longevity (l_x), and speed of development (the age at which reproduction begins). The effect of temperature on fecundity and longevity has been discussed. The remaining life table statistics were calculated for *A. unicolor* at each temperature, and the population growth statistics obtained were used as a bioclimatic index to evaluate the performance of the species at each temperature. These data are summarized in Table 2. The Gross Reproductive Rate (GRR) and the Net Reproductive Rate (R_o) reached their maximum values at 29.4 C. These statistics were substantially lower above and below 29.4 C, apparently reflecting variations in the sex ratio and survival rate at these temperatures. Curves of GRR and R_o are shown in Fig. 6. The differences between these two curves and that of the mean total progeny is a measure of the variations in the sex ratio and in the survival rate at the various constant temperatures. The curves of GRR and R_o are similar in configuration due to

TABLE 2

EFFECT OF CONSTANT TEMPERATURES ON POPULATION GROWTH STATISTICS OF *A. UNICOLOR* AT 50% RH AND 12-HOUR PHOTOPERIOD[a]

Temperature (C)	Gross reproductive rate (GRR) (female progeny/female)	Net reproductive rate (R_o) (female progeny/female)	Mean generation time (T) (days)	Intrinsic rate of natural increase (r)	Finite rate of increase (λ)
21.1	80.82	75.91	42.4	0.1020	1.107
23.9	69.89	61.82	36.2	0.1140	1.120
26.7	47.03	39.00	23.6	0.1552	1.168
29.4	181.02	148.72	24.4	0.2052	1.228
32.2	48.60	32.62	19.3	0.1805	1.197

[a] Based on cohort of 15 individuals at each temperature.

the similarity in the survival rates of parent females during most of the reproductive period, especially from 21.1 to 26.7 C.

Values calculated for the generation time (T) show that the mean length of the generation decreased as the temperature increased (Table 2).

The intrinsic rate of natural increase (r) is the best indicator of the response of a population to a given set of environmental conditions.

Like all measures of reproductive power (GRR, R_o) previously discussed, r had the highest value of 0.2052 at 29.4 C (Table 2). The r value at 32.2 C (0.1805) was not substantially different from that at 29.4 C because the generation time was shorter. At other temperatures where the generation time was longer and the net reproductive rate was smaller, r values were relatively smaller than at 29.4 C. At 29.4 and 32.2 C, peak fecundity was reached earlier in life than it was at lower temperatures (Fig. 6). Thus, r was apparently higher where a more rapid development and earlier attainment of maximum fecundity tended to occur. Barlow (1962) and Birch (1948) discussed this phenomenon in detail.

The reduction in the value of r at 32.2 C was apparently due to an unfavorable sex ratio, which was about 50 percent of that at 29.4 C (Table 1). Consequently, the net reproductive rate was correspondingly reduced.

Values calculated for the intrinsic rate of increase have three possible implications in relation to the actual population growth. When the r value is positive, population increases; when negative, population decreases; and, when r is zero, the population is stationary (birth and death rates are the same). For *A. unicolor*, this relationship was clearly revealed by the finite rate of increase, λ, which is the number of times the population will multiply itself per unit of time. As with r, λ has the highest value of 1.228 at 29.4 C (Table 2). This means that at 29.4 C, a population of *A. unicolor* can multiply itself 1.228 times per day, or will double every 3.36 days.

The positive values of r within the

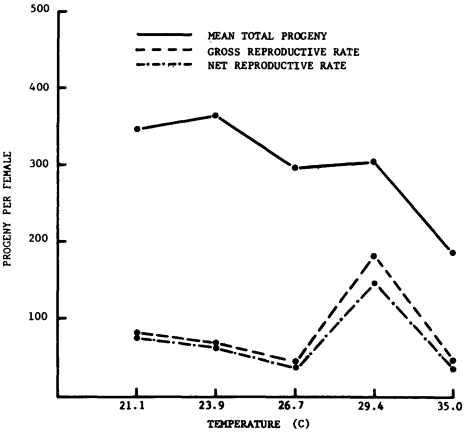

Fig. 6. Mean total progeny, Gross Reproductive Rate, and Net Reproductive Rate of *A. unicolor* at several constant temperatures, 50% RH, and 12-hour photoperiod.

range of 21.1 to 32.2 C, indicated that *A. unicolor* can survive and reproduce under these environmental conditions. As development was incomplete at 35.0 C, the r value was negative, with the upper thermal limit of reproduction being somewhere between 32.2 and 35.0 C. The temperature at which r is maximum is defined as the optimum condition, and was 29.4 C for *A. unicolor*. As environmental conditions at release sites in southern California are relatively mild, the inability to establish *A. unicolor* probably was not due to temperature.

To calculate the intrinsic rate of increase, unlimited food and space, and a stable age distribution within the population, are assumed. These conditions rarely, if ever, occur in nature. Additionally, r itself is specific for a particular time interval and set of age-specific fecundity and survival rates, which may not necessarily be optimal nor, more importantly, density-free. Therefore, the intrinsic rate of natural increase derived in this study may not be an accurate estimate of the rate of increase of the species in nature. Regardless of these limitations, a close correlation between a laboratory-derived rate of increase and the estimated rate of increase in the field was reported by Force and Messenger (1968), Lamb (1961), and Watson (1964), among others.

III. Humidity studies

The effect of humidity on the biology of *A. unicolor* was studied at 29.4 C, at which the intrinsic rate of natural increase was maximal. Experiments were conducted at 30 and 70 percent R.H., and results obtained were compared with results at 50 percent R.H. in previous studies. Experimental procedures were the same as those used in temperature studies. Parent females used were reared from egg to adult under their respective humidity regimes.

Effect of humidity on rate of development

There was no significant difference in mean developmental time or in the rate of development of *A. unicolor* at 30, 50, or 70 percent R.H. at 29.4 C. Andrewartha and Birch (1954) discussed the response of various organisms to different humidity regimes. According to their study, there was no law governing such responses; each organism seemed specific in its own response. *Agathis unicolor* would appear to belong to that group of organisms whose rate of development is apparently independent of humidity.

There was no significant difference in the interaction between temperature and humidity on development.

Effect of humidity on longevity

Data are shown in Table 3 and in Fig. 7 as the age-specific survival rate. The longevity was similar at all humidities tested at 29.4 C.

During early adult life, the survival rate of the parents was slightly higher at 70 percent R.H. than at other humidities (Fig. 7). Otherwise, survivorship curves were essentially similar, and conformed well to the curves of physiological longevity discussed earlier. In a combined analysis, the interaction between temperature and humidity on longevity did not reveal any significant differences. Andrewartha and Birch (1954) state that the relationship between humidity and survival rate is a function of the rate at which an insect gains or loses water, and the extent to which it can withstand desiccation. Although these factors were not measured in this experiment, there was no indication that humidity has any adverse effect on the survival rate of *A. unicolor* within the range of humidities studied.

TABLE 3

EFFECT OF SEVERAL RELATIVE HUMIDITIES ON THE REPRODUCTION AND LONGEVITY OF *A. UNICOLOR* AT A CONSTANT TEMPERATURE OF 29.4 C AND 12-HOUR PHOTOPERIOD[a]

Relative humidity (percent)	Mean total progeny	Mean number[b] females in total progeny (percent)	Mean reproductive[b] period (days)	Mean longevity[b] (days)
30	237.2a	26.53a	13.3a	14.3a
50	304.7a	46.81a	11.8a	13.0a
70	249.8a	13.95b	12.7a	14.3a

[a] Based on cohort of 15 individuals at each humidity level.
[b] Means followed by the same letter on the vertical line are not significantly different at the 1% level.

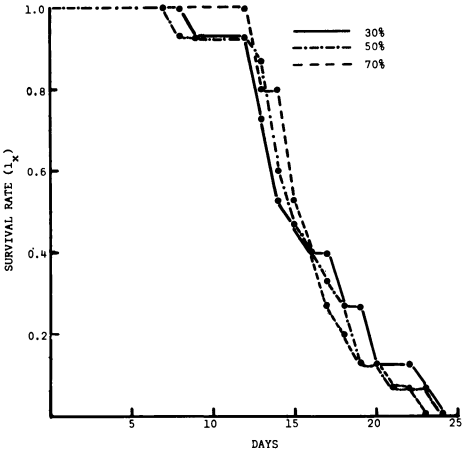

Fig. 7. Effect of several relative humidities on survival rate of *A. unicolor* at a constant temperature of 29.4 C and 12-hour photoperiod.

Effect of humidity on reproduction

The effect of humidity on reproduction at 29.4 C is also shown in Table 3. More progeny were produced at 50 percent R.H. than at either 30 or 70 percent R.H. However, none of the differences was significant at the 1 percent level.

There was no significant difference (1 percent level) between mean total females produced at 30 and at 50 percent R.H., but both means were significantly less than the mean total females produced at 70 percent R.H.

The mean reproductive period was similar at all three humidity levels, and ranged from about 12 days at 50 percent to 13 days at 30 percent R.H. Most females continued reproduction until 1 to 2 days before death.

The effect of humidity on the overall sex ratio is reflected in the age-specific fecundity rates (Fig. 8). The fecundity rate at 30 percent R.H. was higher than

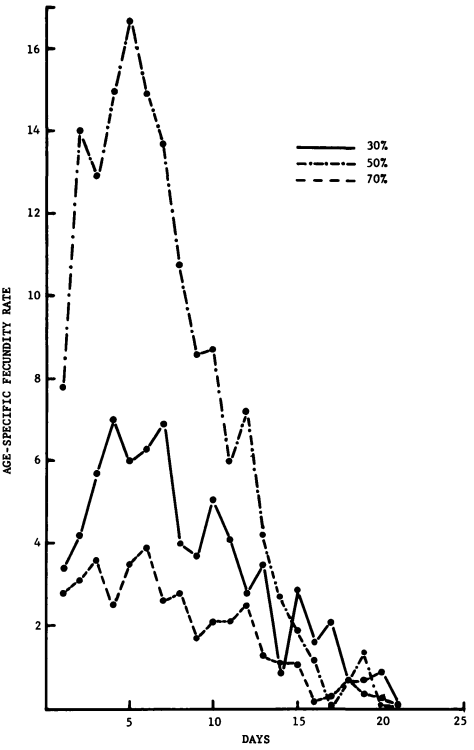

Fig. 8. Effect of several relative humidities on the age-specific fecundity rate of *A. unicolor* at a constant temperature of 29.4 C and 12-hour photoperiod.

TABLE 4

EFFECT OF SEVERAL RELATIVE HUMIDITIES ON THE GROWTH STATISTICS OF *A. UNICOLOR* AT A CONSTANT TEMPERAURE OF 29.4 C AND 12-HOUR PHOTOPERIOD[a]

Relative humidity (%)	Gross reproductive rate (GRR)	Net reproductive rate (R_o)	Mean generation time (T) (days)	Intrinsic rate of increase (r)	Finite rate of increase (λ)
30	73.56	62.86	23.7	0.1747	1.1908
50	181.02	148.72	24.4	0.2052	1.2277
70	38.82	35.09	24.5	0.1448	1.1558

[a] Based on cohort of 15 individuals at each humidity level.

that at 70 percent. The rate at 50 percent R.H. was the highest, and it remained relatively high for a greater part of the reproductive period.

Effect of humidity on population growth

Data on the effect of humidity at 29.4 C on various growth statistics which were summarized from life tables are shown in Table 4.

Both measures of reproductive power (GRR and R_o) reached their maximum values at 50 percent R.H. Although there were no significant differences in mean total progeny among the three humidity levels, differences in the corresponding GRR's and R_o's were substantial. This was because of the variation in the overall sex ratio which, according to Messenger (1964), causes exact proportional changes in the real fecundity (female progeny per female). For instance, at 30 percent R.H., the overall sex ratio declined to 33.2 percent of what it was at 50 percent R.H., and the corresponding net reproductive rate (R_o) declined 46.7 percent. At 70 percent R.H., the sex ratio and the R_o declined 62.2 and 66.4 percent, respectively. Although the generation times were essentially the same, the intrinsic rate of natural increase (r) increased from 0.1747 at 30 percent to 0.2052 at 50 percent, then decreased to 0.1448 at 70 percent R.H. Thus, differences in r values were probably due to variations in the sex ratio. Presently, there is no statistical method to judge the significance of different values of r.

Response of insects to humidity is difficult to analyze, and is apparently specific for each species. In this study, *A. unicolor* survived and reproduced within the range of 30 to 70 percent R.H., but was more favorably affected by 50 percent R.H.

Agathis gibbosa (Say)

I. General biology

The biology of *Agathis gibbosa* was previously studied by Ọdẹbiyi and Oatman (1972). Therefore, only the influences of temperature and humidity on the intrinsic rate of increase, and their effect on various components which determine population growth, were investigated in the present study. The biology of *A. gibbosa* is hereby summarized.

Agathis gibbosa is a primary, solitary, internal larval parasite of the potato tuberworm. The egg is deposited in a ganglion along the ventral nerve cord of the host larva. The parasite larva develops in the body cavity, emerging after the host larva spins its cocoon. It then feeds externally on the host larva for one or two days before spinning its own cocoon inside that of

the host. There are three instars, the first being mandibulate and the other two, hymenopteriform. At 26.7 C and 50 ± 2 percent R.H., total developmental time from egg to adult ranged from 16 to 22 days, with an average of 18 days. Mean minimum duration of each developmental stage was: egg, 3.5 days; first-instar, 3.5 days; second-instar, 1 day; third-instar, 3 days; prepupa, 2 days; and pupa, 3 days.

Adult emergence was stimulated by light, and copulation occurred within a few minutes to several hours later. Males mated several times, females only once. Unmated females produced only males; mated females produced both males and females. There is essentially no preoviposition period. Without food and water, adults died within 2.6 days; with both honey and water, males lived an average of 12.6 days, and females, 18 days.

Two- to 3-day-old potato tuberworm larvae were the most suitable for parasitization, and 100 potato tuberworm larvae per tuber was the optimum number of host larvae to be exposed to a single female parasite. Mated females had an average ovipositional period of 9 days, and produced an average of 288.5 adult progeny. The highest average daily production of progeny was 40.5, attained on the fourth day of reproduction. The longevity of mated females averaged 10.8 days, and the sex ratio (male to female) of their progeny averaged 1.9 to one.

II. Temperature studies

Experiments were conducted at 21.1, 23.9, 26.7, 29.4, 32.2, and 35.0 C, 50 percent R.H., and a 12-hour photoperiod. An analysis of variance was performed on all measurements of the reproductive period, longevity, and fecundity. When a significant "*F*" value was obtained, the Student-Newman-Keuls' (SNK) multiple range test was used for individual comparisons.

Effect of temperature on rate of development

The mean developmental time of *A. gibbosa* decreased with an increase in temperature, ranging from 39.2 days at 21.1 C to 13.0 days at 35.0 C. Reduction in developmental time with an increase in temperature was more pronounced at lower temperatures (21.1 to 26.7 C) than at higher temperatures (32.2 to 35.0 C). There was almost no difference between mean developmental time at 26.7 and that at 29.4 C; but, with further increases in temperature (32.2 to 35.0 C), an appreciable decrease was again recorded. A similar phenomenon was discussed by Bursell (1964).

The rate of development increased in a direct linear manner with temperature (Fig. 9). The coefficient of determination, r^2, was 0.959. The upper thermal limit for development was not determined, but a developmental test conducted at 37.8 C indicated that *A. gibbosa* could not develop at that temperature. As development occurred at 35.0 C, the upper thermal limit is between 35.0 and 37.8 C. This is an important difference between this species and *A. unicolor,* which could not develop at 35.0 C.

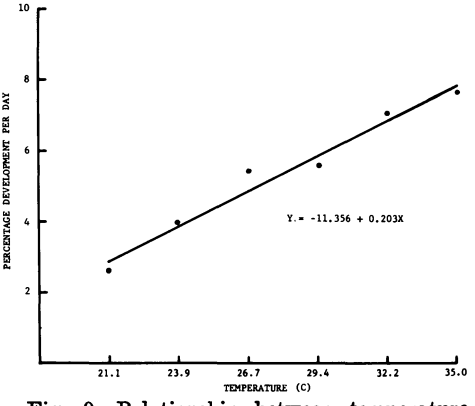

Fig. 9. Relationship between temperature and rate of development of *A. gibbosa* from egg to adult emergence.

TABLE 5

EFFECT OF DIFFERENT CONSTANT TEMPERATURES ON REPRODUCTION OF *A. GIBBOSA* AT 50% RH AND 12-HOUR PHOTOPERIOD[a]

Temperature (C)	Mean total progeny[b]	Mean females in total progeny (%)[b]	Reproductive period (days)		Mean longevity (days)
			Range	Mean[b]	
21.1	140.6b	46.79a	5–16	11.3d	13.0
23.9	203.3c	37.93a	5–17	10.7cd	11.1
26.7	144.1c	29.78a	3–14	9.1bc	10.1
29.4	119.7ab	24.28a	3–13	7.7ab	10.2
32.2	84.1b	28.76a	3–8	5.3a	6.1
35.0	48.86a	9.14b	2–9	4.4a	5.1

[a] Based on cohort of 15 individuals at each temperature.
[b] Means followed by the same letter on the vertical line are not significantly different at the 1 % level.

Immature mortality was calculated as previously described for *A. unicolor*. There was no mortality at 23.9 C. Mortality was 18.7, 15.4, 20.9, and 19.5 percent at 21.1, 29.4, 32.2, and 35.0 C, respectively. Based on these mortality values, the l_x values were correspondingly adjusted for each temperature.

Effect of temperature on longevity and reproduction

The influence of temperature on progeny production, sex ratio (percent females in total progeny), reproductive period, and longevity of *A. gibbosa* is shown in Table 5. Mean longevity decreased with an increase in temperature, ranging from about five days at 35.0 C to 13 days at 21.1 C. Adult females lived longer at 21.1 and 23.9 C than at other temperatures. There was considerable variation in heat tolerance among individual members of a cohort, for any given temperature.

The mean reproductive period had a similar inverse relationship with temperature. Most females continued to reproduce until 1 or 2 days prior to death.

Maximum mean total progeny was 203.3 at 23.9 C. Below and above this temperature, progeny production decreased. It was especially low at 32.2 and 35.0 C, because the reproductive period was relatively shorter at those temperatures. Statistically, sex ratios were of the same order of magnitude, except at 35.0 C where the ratio was significantly lower than at the other temperatures. The effect of variations in the sex ratio on the population growth rate and real fecundity was discussed earlier for *A. unicolor*.

Effect of temperature on population growth

Data from life tables on the effect of temperature on various growth statistics of *A. gibbosa* are shown in Table 6.

The gross reproductive rate (GRR) and the net reproductive rate (R_o) were higher at 21.1 and 23.9 C than at the other temperatures. The difference between GRR and R_o is a measure of the cohort survival rate. The highest real fecundity (R_o) was 77.26 at 23.9 C. However, in comparing two populations, R_o is not an adequate measure of population growth, unless the generation times are the same. Given the same R_o for two different populations under the same conditions, the one with a shorter generation time will have a higher growth rate.

Although R_o was maximal at 23.9 C, the intrinsic rate of increase was maximal at 32.2 C (Table 6). This was due to the shorter generation time at 32.2 C, about one-half that at 23.9 C. Conversely, longer generation time was re-

TABLE 6

EFFECT OF SEVERAL CONSTANT TEMPERATURES ON THE POPULATION GROWTH STATISTICS OF *A. GIBOSSA* AT 50% RH AND 12-HOUR PHOTOPERIOD[a]

Temperature (C)	Mean total progeny (progeny/female)	Gross reproductive rate (GRR) (female progeny/female)	Net reproductive rate (R_o) (female progeny/female)	Mean generation time (T) (days)	Intrinsic rate of natural increase (r)	Finite rate of increase (λ)
21.1	140.6	74.09	53.87	41.8	0.0953	1.0999
23.9	203.3	92.13	77.26	28.6	0.1520	1.1641
26.7	144.1	48.64	42.93	19.4	0.1942	1.2143
29.4	119.7	30.97	24.91	19.3	0.1665	1.1811
32.2	84.1	27.17	17.0	14.8	0.1944	1.2145
35.0	48.9	5.64	3.61	14.6	0.0876	1.0915

[a] Based on cohort of 15 individuals at each temperature.

sponsible for the lower rate of increase at the lower temperatures. The intrinsic rate of increase decreased at 35.0 C, where the generation time was the shortest. At this temperature, R_o was 3.61, about 20 percent of what it was at 32.2 C. Thus, the very small advantage gained in generation time at 35.0 C was apparently offset by a very low fecundity.

Because the intrinsic rate of increase was maximal at 32.2 C, this temperature was considered optimal for *A. gibbosa*. The intrinsic rate of natural increase was positive at all temperatures. Thus, *A. gibbosa* is capable of survival and reproduction at these temperatures. Although the intrinsic rates of increases obtained in these studies do not necessarily represent the real growth rate of the species in the field (because of limitations discussed earlier), as a bioclimatic index they appear to support field observations. *Agathis gibbosa* has been collected in the field throughout the year in southern California, where both extremes of experimental temperature occur. Its ability to exist and reproduce at 35.0 C gives it an advantage over *A. unicolor* and its potato tuberworm host, neither of which could develop at this temperature. However, a constant temperature of 35.0 C in potato-growing areas of southern California is highly unlikely.

III. Humidity studies

Experiments were conducted at 32.2 C, at which the intrinsic rate of natural increase was maximal. Relative humidities of 30 and 70 percent were used because, without sophisticated equipment, humidity control below and above this range is unattainable. Results were compared with those previously obtained at 50 percent R.H., the experimental procedures being similar.

Effect of humidity on rate of development

There was no significant difference in mean developmental time, or in rate of development, at 30, 50, or 70 percent R.H. The interaction between temperature and humidity was not significant. Thus, as in the case of *A. unicolor*, the rate of development of *A. gibbosa* is apparently independent of humidity.

The effect of humidity on longevity and reproduction is shown in Table 7. There was a tendency toward a decrease in longevity with an increase in humidity. This was perhaps because of excess accumulation of water in some organs, resulting in the interference of normal physiology (Andrewartha and Birch, 1954). The survival rate, and the inverse relationship between humidity

TABLE 7

EFFECT OF SEVERAL RELATIVE HUMIDITIES ON THE REPRODUCTION AND LONGEVITY OF *A. GIBBOSA* AT A CONSTANT TEMPERATURE OF 32.2 C AND 12-HOUR PHOTOPERIOD[a]

Relative humidity (%)	Mean total progeny[b]	Mean female in total progeny (%)	Mean reproductive period (days)[c]	Mean longevity (days)[c]
30	125.86a	18.33	6.9a	7.4a
50	84.10b	28.75	5.3a	6.1a
70	61.13c	36.52	4.5b	5.5a

[a] Based on cohort of 15 individuals at each humidity level.
[b] Means followed by the same letter on the vertical line are not significantly different at the 5% level.
[c] Means followed by the same letter on the vertical line are not significantly different at the 1% level.

and survival rate, are apparent in Fig. 10. Senescence was reached sooner at 70 percent than at 30 or 50 percent R.H. Survivorship curves were similar at all three humidities in the first week of life, but thereafter only the 30 percent and 50 percent curves were similar. Except for this change in survival rate late in life at 30 and 50 percent R.H., survivorship curves were similar to the curve of physiological longevity discussed earlier for *A. unicolor*. Again, the interaction between temperature and humidity was not significant.

Mean total progeny decreased, but the proportion of female progeny increased, as the R.H. varied from 30 percent to 70 percent (Table 7). Although variations in sex ratio affect the age-specific fecundity (Fig. 11), their overall effect on population growth can only be appraised along with the effect of generation time. Peak fecundity was reached within 2 days of oviposition at 50 and 70 percent R.H., but occurred at a later age at 30 percent R.H. (Fig. 11). The earlier the population reaches its maximum fecundity, the greater is

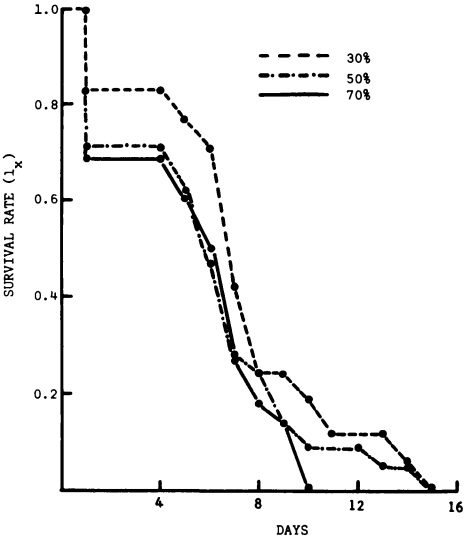

Fig. 10. Effect of several relative humidities on survival rate of *A. gibbosa* at a constant temperature of 32.2 C and 12-hour photoperiod.

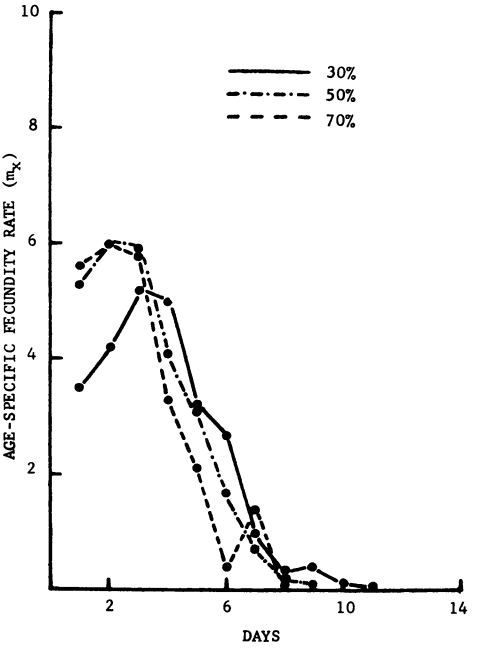

Fig. 11. Effect of several relative humidities on age-specific fecundity rate of *A. gibbosa* at a constant temperature of 32.2 C and 12-hour photoperiod.

TABLE 8

EFFECT OF SEVERAL RELATIVE HUMIDITIES ON THE GROWTH STATISTICS OF *A. GIBBOSA* AT A CONSTANT TEMPERATURE OF 32.2 C AND 12-HOUR PHOTOPERIOD[a]

Relative humidity (%)	Gross reproductive rate (GRR)	Net reproductive rate (R_o)	Mean generation time (T) (days)	Intrinsic rate of increase (r)	Finite rate of increase (λ)
30	25.49	19.20	19.14	0.1544	1.1669
50	27.17	17.0	14.8	0.1944	1.2145
70	24.49	15.30	17.44	0.1564	1.1692

[a] Based on cohort of 15 individuals at each humidity level.

its capacity to increase, because the survival rates of the parents are maximal during early adult life (Barlow, 1962).

Effect of humidity on population growth

The effect of humidity on population growth is shown in Table 8. The highest GRR and R_o were recorded at 30 percent R.H., but the generation time was longest (about 19 days) at this humidity. Consequently, the intrinsic rate of increase at 30 percent was the lowest. The intrinsic rate of increase was maximal at 50 percent R.H., because the generation time was the shortest.

The growth rate was positive throughout the range of humidities studied. Thus, *A. gibbosa* can survive and reproduce at a range of 30 to 70 percent R.H. The highest value of r was recorded at 50 percent R.H.

COMPARISON OF THE BIOLOGY OF THE TWO SPECIES OF PARASITES

Agathis gibbosa and *A. unicolor* are native to North and South America, respectively. Despite their apparent geographical isolation, they are similar in their biologies and general morphology of the immature stages.

Both are primary, solitary, endoparasites of larvae of the potato tuberworm. They deposit their eggs in the ganglia of the ventral nerve cord of the host larvae. Both have three larval instars: the first is caudate-mandibulate, and the other two are hymenopteriform. At most temperatures studied, adults of *A. gibbosa* emerged 2 to 3 days earlier than those of *A. unicolor*. In both species, unmated females produced only males, whereas mated females produced both males and females. There is essentially no preoviposition period.

The suitability of potato tuberworm larvae for oviposition at different ages is shown in Fig. 12. Maximum progeny production occurred with 2- to 3-day-old larvae, indicating that this age group is the most suitable for oviposition by both species. The data also reveal that 0- to 5-day-old host larvae are more suitable than older larvae.

Interspecific crossing

Because of their close biological similarities, cross breeding experiments were conducted at 26.7 C. As both species are arrhenotokous, production of female progeny would be a primary indication of successful crossing. Ten crosses and reciprocal crosses were set up: *A. gibbosa* males by *A. unicolor* females, and *A. unicolor* males by *A. gibbosa* females. No females were produced

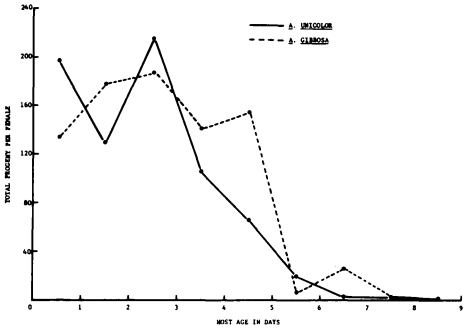

Fig. 12. Suitability of potato tuberworm larvae at different ages for oviposition by *A. unicolor* and *A. gibbosa*.

in any cross. The mating stimulus is apparently similar in both species, as males of one species attempted to mate with females of the other. However, copulation was observed only in the cross, *A. unicolor* males by *A. gibbosa* females. As males only were produced, it was additional evidence that *A. unicolor* and *A. gibbosa* are separate species.

Agathis gibbosa has a shorter developmental period than does *A. unicolor,* which is important when the population growth of both parasites is compared with that of their common host. More importantly, the choice of suitable hosts and ovipositional sites of both species are similar. This is an important prerequisite for possible competitive displacement (DeBach, 1964). As only one parasite larva develops to maturity in a host larva, larvae of both parasites cannot exist in a single host. In the field, *A. gibbosa* has the advantage of a shorter developmental time over *A. unicolor*. Thus, these two parasites are apparently ecological homologues, which may help explain why *A. unicolor* was not established on the potato tuberworm in southern California where *A. gibbosa* is an indigenous species.

COMPARISON OF THE TEMPERATURE RESPONSES OF THE TWO PARASITES AND THEIR HOST

Cardona (1971) studied temperature responses of the potato tuberworm and constructed life tables for it at 23.9, 26.7, 29.4, and 32.2 C. The potato tuberworm did not reproduce at 35.0 C. Data from his life tables were used in comparisons of *Agathis unicolor, A. gibbosa,* and their host.

Developmental and generation times

The effect of temperature on developmental times is indicated in Fig. 13. At all temperatures between 23.9 and 35.0 C, *A. gibbosa* had the shortest developmental time. Developmental curves of *A. unicolor* and the potato tuberworm were similar between 23.9 and 26.7 C; but thereafter, the curve for the potato tuberworm dropped, indicating a shorter developmental time than that for *A. unicolor*. In addition to having the longest developmental time, *A. unicolor* could not develop at 35.0 C. This is an important difference between the two parasites, as *A. gibbosa* developed and reproduced at 35.0 C. Thus, *A. unicolor* is less tolerant of high temperature than either *A. gibbosa* or the potato tuberworm.

The generation times of the two parasites and their host are shown in Fig. 14. Curves follow the same pattern as those of developmental time. Again, *A. gibbosa* had the shortest generation time and *A. unicolor* the longest. As *A. unicolor* could not develop, and the potato tuberworm could not reproduce, at 35.0 C, their curves of generation time terminated at 32.2 C.

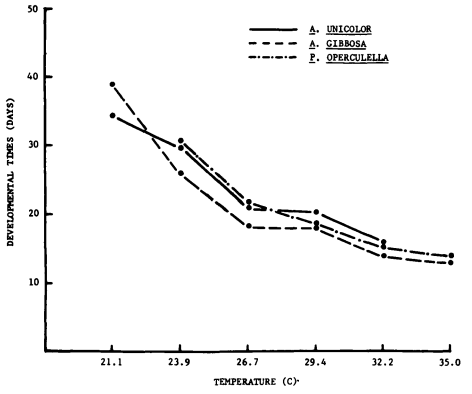

Fig. 13. Mean developmental time of *A. unicolor, A. gibbosa,* and the potato tuberworm at several constant temperatures, 50% RH, and 12-hour photoperiod.

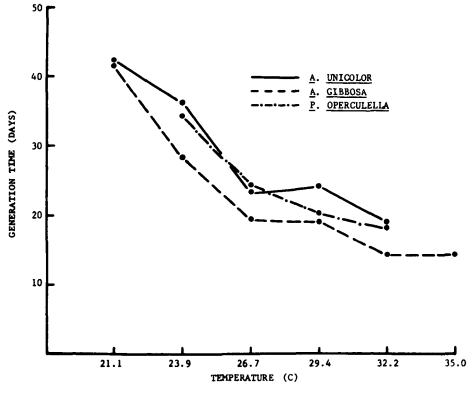

Fig. 14. Generation times of *A. unicolor, A. gibbosa,* and the potato tuberworm at several constant temperatures, 50% RH, and 12-hour photoperiod.

Fecundity and multiplication per generation

The fecundity of a female is the total male and female progeny produced at each temperature. When mean total progeny is corrected for sex-ratio variation and adjusted for cohort survival rate, the net reproductive rate (R_o) is obtained. In life-table studies, R_o is the real fecundity and represents the multiplication capacity per generation.

The two parasites reached maximum fecundity at 23.9 C, and their host at 26.7 C (Fig. 15). *Agathis unicolor* had the highest fecundity at all temperatures. However, total fecundity in itself is misleading, because only the female progeny per female, R_o, is important. Thus, based on the values of R_o, the apparent overall reproductive superiority (Fig. 15) of *A. unicolor* was negated except at 29.4 C (Fig. 16). Also, the temperatures at which peak fecundity occurred were no longer the same, remaining at 23.9 C for *A. gibbosa* but changing to 29.4 for *A. unicolor*. Although R_o is a measure of reproductive power, its usefulness in comparing populations under any given condition depends upon the generation times being equal. Thus, the intrinsic rate of natural increase becomes the preferred statistic when comparing responses of different populations under a given set of conditions.

The intrinsic rates of increase for the two parasites and their host are shown in Fig. 17. Only *A. gibbosa* reproduced and increased in numbers at 35.0 C, giving it a definite advantage over its host and *A. unicolor* at this temperature. Between 21.1 and 32.2 C, *A. unicolor* had a lower rate of increase than did the potato tuberworm, except at 29.4 C. At this temperature, its r was 0.205, and that of the potato tuberworm, 0.196. The corresponding generation times were 24.4 and 20.4 days, respectively. Thus, the slightly lower growth rate of the host at 29.4 C is probably offset by its shorter generation time. Theoretically, therefore, *A. unicolor* should be incapable of suppressing a population of potato tuberworms. *Agathis gibbosa* had a higher rate of increase than did the potato tuberworm between 23.9 and 26.7 C, falling below that of its host at 29.4 C, and reaching a slightly lower maximum at 32.2 C. The generation times of *A. gibbosa* were 19.3 and 14.8 days at 29.4 and 32.2 C, respectively, and those for the potato tuberworm were 20.5 and 18.5 days. Eventually, the shorter gen-

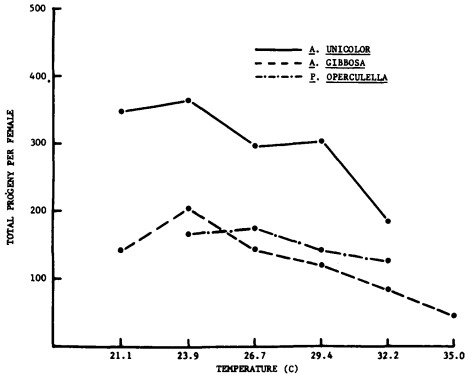

Fig. 15. Mean total progeny of *A. unicolor*, *A. gibbosa*, and the potato tuberworm at several constant temperatures, 50% RH, and 12-hour photoperiod.

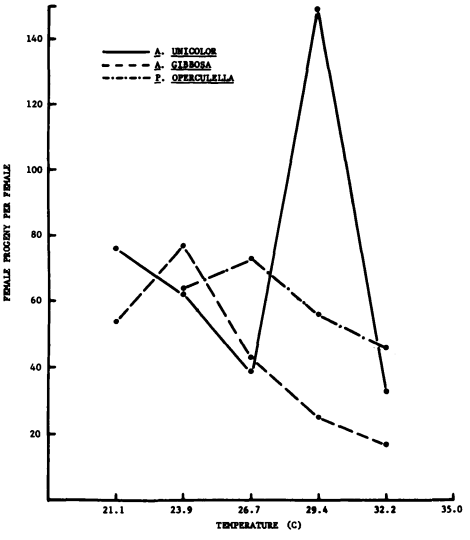

Fig. 16. Net Reproductive Rates of *A. unicolor*, *A. gibbosa*, and the potato tuberworm at several constant temperatures, 50% RH, and 12-hour photoperiod.

eration time of *A. gibbosa* would probably reduce the difference between the growth rate of *A. gibbosa* and its host. Thus, *A. gibbosa* has more potential than *A. unicolor* for suppressing a population of potato tuberworms. This conclusion may be oversimplified, however, as host-parasite interactions depend, among other things, on the initial host-parasite ratio (Burnett, 1960; Messenger, 1964). Besides, assumptions underlying the calculation of r are so stringent that they rarely, if ever, occur in nature. Therefore, the use of a laboratory-derived r to rate the effectiveness of parasites provides purely theoretical results, comparable at best, to those of a model. To be useful, in addition to r, other factors such as parasite searching ability, density-dependent modification of parasite fecundity, and additional external mortality factors which affect parasites, must be considered.

SUMMARY

The biology of *Agathis unicolor* was studied at 26.7 C, 50 ± 2 percent R.H., and 12-hour photoperiod, and compared with that of *A. gibbosa*. The effects of temperature and humidity on the biological attributes of the two species were compared with results of similar studies on the potato tuberworm, their common host.

The egg of *A. unicolor* is deposited in a ganglion of the ventral nerve cord of the potato tuberworm larva. There are three larval instars: the first being both caudate and mandibulate, and the other two, hymenopteriform. The mean minimum duration of each developmental stage was egg, 5 days; first-instar, 3 days; second-instar, 2 days; third-instar, 3 days; prepupa, 2 days; and pupa, 3 days. Total developmental time from egg to adult emergence ranged from 18 to 24 days.

Adult emergence was stimulated by light, and mating occurred within a few minutes to several hours after emergence. Adult females are arrhenotokous, and there is essentially no preoviposition period.

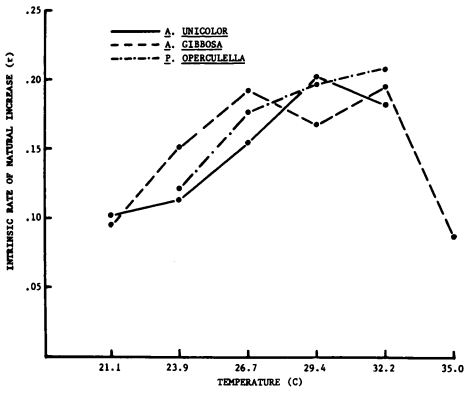

Fig. 17. Intrinsic rates of natural increase of *A. unicolor, A. gibbosa,* and the potato tuberworm at several constant temperatures, 50% RH, and 12-hour photoperiod.

Potato tuberworm larvae, 2 to 3 days old, were the most suitable for oviposition by the adult female. The most favorable host density for exposure to a single adult female parasite was 85 potato tuberworm larvae per potato tuber. The oviposition rate decreased with increasing parasite density per tuber.

The biology of *A. unicolor* and the morphology of its immature stages are similar to those of *A. gibbosa,* except the adults and immature stages are generally larger than those of *A. gibbosa.*

The effects of temperature and humidity on the two parasites were studied at 21.1, 23.9, 26.7, 29.4, 32.2, and 35.0 C, and at 30, 50, and 70 percent R.H. There was a linear relationship between temperature and speed of development of both species. *Agathis unicolor* could not develop beyond the prepupal stage at 35.0 C, whereas *A. gibbosa* developed and reproduced at this temperature. There was an inverse relationship between temperature and longevity for both species, and their corresponding survivorship curves conformed to the curve of physiological longevity. For both parasites, progeny production was highest at 21.1 C. The sex ratio of the two parasites varied both with temperature and age.

Life tables were constructed for each experimental condition, and the intrinsic rate of natural increase (r) was calculated for each species. The r values were used as a bioclimatic index for each parasite, because a population can survive only where its intrinsic rate of increase is greater than zero. *Agathis unicolor* survived and reproduced between 21.1 and 32.2 C, and the maximum value of r was recorded at 29.4 C. The upper thermal limit for survival was between 32.2 and 35.0 C. The highest rate of increase for *A. gibbosa* was obtained at 32.2 C, and it survived and reproduced at all temperatures tested, including 35.0 C.

Humidity experiments were conducted at the temperature where each parasite had the greatest rate of increase. In both species, developmental time and longevity were unaffected by humidity. Both parasites had the largest value of r at 50 percent R.H.

When the intrinsic rates of natural increase of both parasites were compared with that of their common host, *A. gibbosa* was the better parasite. At most temperatures studied, the rate of increase of *A. gibbosa* was higher than that of the host. In the few instances where its rate was lower, its generation time was shorter than that of the host. The rate of increase of *A. unicolor* was almost always lower than that of its host at all temperatures studied.

The biologies of the two parasites were sufficiently similar that they are probably ecological homologues.

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(Continued from inside front cover.)

Temperature and rate of development of both parasites were linearly related. However, at 35.0 C, *A. unicolor* could not develop beyond the prepupal stage. Longevity and reproductive periods were inversely related to temperature, and survivorship curves of both parasites conformed to the curves of physiological longevity.

On the basis of the intrinsic rate of natural increase, *A. unicolor* survived and reproduced from 21.1 to 32.2 C. *Agathis gibbosa* survived and reproduced from 21.1 to 35.5 C. Both parasites developed best at 50 percent relative humidity. Comparisons of the intrinsic rate of natural increase, developmental time, and mean generation time indicated that *A. gibbosa* would be better able to suppress populations of the host than *A. unicolor*.

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