1980

Reproductive biology of the egg parasite Gryon parkeri (Fouts) (Hymenoptera: Scelionidae)

Richard Lee Lampman
College of William & Mary - Arts & Sciences

REPRODUCTIVE BIOLOGY OF THE EGG PARASITE *GRYON PARKERI* (FOUTS) (HYMENOPTERA : SCELIONIDAE)

A Thesis

Presented to

The Faculty of the Department of Biology

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Master of Arts

---

by

Richard Lee Lampman

1980

APPROVAL SHEET

This thesis is submitted in partial fulfillment of

the requirements for the degree of

Master of Arts

Richard Lee Sampson

Author

Approved, May 1980

Norman J. Fashing

Norman J. Fashing

Lawrence Wiseman

Lawrence Wiseman

Garnett K. Brooks Jr.

Garnett Brooks, Jr.

DEDICATION

To Scott Walker Kress

TABLE OF CONTENTS

ACKNOWLEDGMENTS

The author would like to express his gratitude to the members of his graduate committee at the College of William and Mary for their valuable critical comments on this paper and their great patience; Norman Fashing (chairman), Lawrence Wiseman, and Garnett Brooks. The author wishes to extend special thanks to Dr. Fashing who expressed a concern beyond that of mere professor.

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

The reproductive behavior of Gryon parkeri and the effect of three variables (temperature, feeding and species of host) on longevity and progeny production is described.

Monogamous females mate soon after emergence and oviposit almost immediately after mating. Pheromonal marking of the host by the female parasite prevents subsequent oviposition in parasitized eggs. The degree of restraint appears to vary with the age of the parasite as well as with the density of hosts and parasites. G. parkeri differs from several scelionid species by the conspicuous absence of male and female aggression. It is suggested aggression may have developed along inter- and intraspecific lines.

The longevity and fecundity for G. parkeri females is recorded at 24, 27, 30 and 33°C for fed and unfed wasps reared on L. kalmii and O. fasciatus. Mean total values, overall rate data (especially the intrinsic rates of increase), and graphic analysis of longevity and fecundity are utilized.

The greatest longevity occurs at 24°C and, in most cases, the highest number of offspring are produced at 27°C. Feeding not only lengthens life and increases the fecundity, but also buffers the change in longevity and total progeny production at certain temperatures. Although the difference between wasps reared on different hosts is small, G. parkeri reared on O. fasciatus generally lives longer, produces more offspring, and consistently has higher intrinsic rates of increase. The graphic analysis reveals initial progeny production for fed and unfed wasps parallel each other for the first days of oviposition of all test temperatures and species of hosts.

THE REPRODUCTIVE BIOLOGY *GRYON PARKERI*

FOREWORD

Gryon (=Hadronotus) parkeri (Fouts) is an egg parasite of the large and small milkweed bugs, Oncopeltus fasciatus Dallas and Lygaeus kalmii Stal, respectively. Milkweed bugs, especially O. fasciatus, are widely used as research animals and are geographically widespread (Feir, 1974), yet little is known about their parasites. G. parkeri was first described as a heteropterous egg parasite by Fouts (1920). Kenaga (1944) identified the large and small milkweed bugs as two hosts of G. parkeri. No other published study of the parasite has been made, however, Harrell (1975) recorded several general remarks on the biology of Gryon parkeri in an unpublished study at the College of William and Mary.

This paper investigates the reproductive biology of G. parkeri and is divided into two sections. The first presents observations on the reproductive behavior of G. parkeri, as well as a review of the literature on the reproductive behavior of the Scelionidae. The major emphasis in this review centers on family behavior norms as described by F. Wilson (1961). The second section is concerned with the population biology of G. parkeri; specifically the effect of three variables, temperature, food, and host species, on the longevity and fecundity of the wasps. Mean values for total longevity and fecundity, intrinsic

rates of increase and other related rate data, and the graphic analysis of life tables are used to describe the effect of the three variables on the reproductive success of Gryon parkeri.

PART I

THE REPRODUCTIVE BEHAVIOR OF *GRYON PARKERI*

AND A REVIEW OF THE SCELIONIDAE

INTRODUCTION

Scelionid wasps are generally solitary, arrhenotokous egg parasites that complete their development from egg to adult within the host egg. Only one wasp ecloses from each host egg. The majority of non-taxonomic literature on scelionids concerns parasites on the eggs of Hemiptera and Orthoptera, however, members of the family also parasitize eggs of Lepidoptera, Diptera, Arachnida, and occasionally Coleoptera and Neuroptera (Clausen, 1940). Two major interests in this family have centered on phoresy and the utilization of scelionids as biological control agents. Phoresy is the transport of an adult parasite on the body of the adult host in whose eggs the wasp oviposits. It implies more than an occasional incidental transport and is most common among the egg parasites of Orthoptera and Lepidoptera. Phoresy on hemipteran hosts is rare and the only reference for such behavior is by Schneider (1940). The best review of the literature on phoresy among scelionids is by Clausen (1976).

Scelionids have also been considered for the control of insect vectors of disease and crop pests. They have been investigated for the control of Triatoma spp., vectors of Chagas' disease (Sankaran and Hagaraja, 1975; Rabinovich, 1971; Costa Lima, 1928; Zeledon, 1957), the green vegetable bug, Nezara viridula (L.) (Cumber, 1951, 1953, 1964; Kamal, 1938; Noble, 1937), the armyworm, Spodoptera

littoralis Boisd. (Gerling, 1972; Schwartz and Gerling, 1974; Wojcik, et al., 1977), the pigeon pea coreid, Acanthomia tomentosicollis Stal (Taylor, 1975), and the black rice bug, Scotinophara lurida Burmeister (Hidaka, 1958). The best review on scelionids as control agents is by Safavi (1968) who worked with egg parasites of cereal bugs, Eurygaster and Aelia species.

A major problem in comparing the literature on any group of insects is the variability in experimental design among investigators. Since many aspects of hymenopteran biology vary with environmental conditions, direct comparisons were difficult. Reproductive behavior, however, is usually highly fixed and, even under varying conditions, is usually consistent. Wilson (1961) recognized the similarity in reproductive behavior among members of the family and compared various aspects of Asolcus (=Microphanurus) basalis (Wollaston) to the literature on other scelionids. This paper describes the reproductive behavior of Gryon parkeri and attempts to enhance Wilson's review.

METHODS AND MATERIALS

Gryon parkeri used in this study were descendants from cultures established January, 1975, and maintained on Oncopeltus fasciatus and Lygaeus kalmii eggs in several plexiglas stock colony cages. Stock colonies were kept at room temperature, 25°C to 20°C, with a photoperiod of 16L and 8D and a relative humidity of 40 to 65%. Milkweed bugs were given absorbent cotton as a substrate for oviposition, as well as weekly fed milkweed seeds, Asclepias species, and supplied cotton wick water vials. Wasps were provided no special supplement, yet were able to maintain their numbers without any apparent difficulty. Milkweed bugs and wasps, in various stages of development, were transferred monthly to clean cages. Although the egg parasites reduced milkweed bug populations in stock colonies, it was never to the extent the bugs could not replace themselves.

Large quantities of unparasitized eggs of a known age were necessary for observation of the wasp's ovipositional behavior. Mating cages for both species of milkweed bug were constantly maintained with four to eight mating pairs. The mating cages were either kept in wasp-free areas outside the laboratory, or covered with a fine nylon mesh to prevent contamination by the parasites. Since the literature suggests the two host species reach maximum reproductive rates at different temperatures

(Dingle and Caldwell, 1971), O. fasciatus mating cages were maintained at temperatures between 24°C and 28°C and L. kalmii cages between 28°C and 33°C. The cages and cotton were daily examined for parasites. If any wasps were found in a mating cage, the entire contents were placed in a stock colony cage, and the mating cage was cleaned and reconstituted. This procedure eliminated the possibility of unknowingly introducing parasitized eggs to test female wasps. Approximately one-half of the clutches were placed intact in vials and the other half were teased apart with a camel's hair brush. These eggs were then distributed among plastic vials, approximately sixty eggs per vial, and examined for any damage due to transfer. This supplied large quantities of eggs and egg masses that were one day or less in age.

G. parkeri from both species of milkweed bug eggs were utilized in the study of reproductive behavior, since previous pilot studies indicated there was no difference in behavior between wasps that emerged from different hosts. After the wasps were gassed with carbon dioxide for approximately ten to sixty seconds and sexed under a stereomicroscope, females were transferred to observation vials. When the wasps revived, approximately ten to twenty seconds after gassing, they were examined for aberrant behavior. Any wasps that appeared damaged due to transfer were removed and replaced. Several hundred vials with unparasitized eggs and various densities of females were observed in order to ascertain oviposition behavior and female-female

interactions. Intact egg clutches were primarily used to determine female competition patterns. Separation of eggs allowed individual eggs to be "tagged," thus facilitating the investigation of discrimination of parasitized and unparasitized eggs by females. The separated eggs also allowed unobstructed observation of oviposition behavior.

After host-parasite interactions were observed in each vial, the vials were placed in constant temperature incubators at 27°C or 30°C. These vials were subsequently used to observe development and emergence behavior. After emergence, the behavior associated with courtship and mating was recorded. The vials with egg masses were especially closely examined to ascertain if there were any male dominance patterns prior to and after female emergence. The density of males was increased in some vials, in order to facilitate male-male interactions as well as increase the number of matings.

OBSERVATIONS ON THE REPRODUCTIVE BEHAVIOR OF G. PARKERI

Physical Description of the Parasite

G. parkeri emerge from the milkweed bug eggs as functional adults. They have a shiny, jet-black body, approximately 1.2 mm long by 0.5 mm wide (n=50). The legs are a translucent light brown and the wings, which fold flat over the body, are covered with fine hairs that give them a smoky appearance. The antennae of both sexes are twelve-segmented; however, there is sexual dimorphism. The male's antennae are simple (filiform) shaped and the female's are club (clavate) shaped. There is no apparent difference in body shape and size between males and females.

General Biology of the Hosts

O. fasciatus, the large milkweed bug, has been widely used as a research animal for physiological, behavioral, and ecological studies. The best reviews of its biology are by Feir (1974) and Sauer and Feir (1973). L. kalmii, the small milkweed bug, has not been as widely investigated and the literature on its biology is relatively incomplete. The only major study of L. kalmii's general biology is by Simanton and Andre (1936). Caldwell (1969) reviews the current literature on the small milkweed bug and compares flight behavior of O. fasciatus and L. kalmii. A brief review of the biology of the two milkweed bugs suggests they have many common characteristics.

The ranges of the two milkweed bugs almost totally overlap, extending from Canada to Central America and from the east to the west coasts (Slater, 1964). Both species are commonly found together on the same host plant (Asclepias species). Although O. fasciatus can overwinter in parts of California (Andre, 1934) and southwestern United States (Blatchley, 1926), it does not overwinter above the fortieth parallel (Essig, 1929). Dingle (1965; 1966; 1967; 1968A; 1968B) has recorded several migratory tendencies for O. fasciatus in the laboratory and proposes the species migrates from subtropical regions into the majority of the northern United States. L. kalmii, on the other hand, overwinters in a dormant state over the majority of its range (Blatchley, 1926; Dingle, 1968b).

Milkweed bugs oviposit on or near the seed pods of milkweed plants (Sauer and Feir, 1973). Eggs of both species are "lygaeid" type - ovoid with prominent chorial processes at one end. O. fasciatus eggs are slightly larger than L. kalmii eggs; 1.41 mm long by 0.63 mm wide and 1.21 mm long by 0.56 mm wide, respectively (Andre, 1934; Simanton and Andre, 1936). At 29.5°C, the first instar emerges from the egg within 3.5 to 4 days after oviposition for both species (Simanton and Andre, 1936; Andre, 1934) and passes through five paurometabolous stages prior to adult eclosion.

Changes in Parasitized and Unparasitized Bug Eggs and Parasite Eclosion

Parasite eggs and instars were not dissected from the host; however, changes in egg (host) color due to instar development were

recorded. Since the developmental times of wasp and host vary with temperature, changes are described for only one temperature, 27°C. Both parasitized and unparasitized eggs are straw-colored and no difference between them is discernable for the first two days after parasitism. By the third day, parasitized eggs are a light chocolate brown and unparasitized eggs have an orangish-red color. On the fourth day a white well-developed wasp larva can be seen through the clearning chorion. In contrast, unparasitized eggs exhibit bug larvae with distinctly pigmented red eyes on the fourth day. On the fifth or sixth day after parasitism, a white pupa forms which progressively darkens until it is jet black on the eighth or ninth day. Unparasitized eggs hatch on day five or six after oviposition.

Most G. parkeri males emerge on day 11 at 27°C and females begin emerging a day later. There is no discernible difference in developmental time due to the two different milkweed bug hosts. Male and female G. parkeri exhibit sporadic movement of the head and legs approximately one day prior to eclosion. On the day of emergence, the wasp rotates its head from side to side, with mandibles open, until one of the mandibles punctures the egg chorion. They use their mandibles to chew a cap around the punctured end until they can force their body through the opening. Approximately 70 percent (n = 1,000) of the wasps were oriented with their head toward the chorial egg processes. Once the chorion is punctured, emergence behavior usually takes one-half to one hour.

Both males and females usually preen their antennae, wings, and limbs for several minutes immediately after eclosion. Since males emerge prior to females, they wander over the eggs, tapping them with their antennae. If a male encounters an egg with an emerging female, he remains near it, moving back and forth in an agitated fashion and constantly taps the egg with his antennae. Males rarely display such agitated behavior if the emerging wasp is a male. Females, immediately after eclosion, avoid male contact and leave the egg mass for a brief period. If approached during the preening period which lasts two to ten minutes, the female is unreceptive. After this period, the female usually takes a stationary post near the egg mass until a male approaches.

Courtship and Mating Behavior

Mating behavior can be divided into a brief courtship followed by copulation. At the beginning of courtship, a male approaches a receptive female from any direction; however, it is not until antennal contact that the male recognizes the female. After contact, the female starts to move away, but the male usually chases and rapidly mounts her. He clasps the female around the abdomen and leans forward, using his antennae to palpate and beat down her antennae. Male palpation stimulates a receptive female to lower her antennae, cease movement, and extend her ovipositor. The initial antennal movement by the female in response to palpation is an important stimulus to elicit the extension of the male's curved aedeagus. The male leans backward after the female stops all movement and flexes his sex organ in the direction of the

female's ovipositor. Usually after several jabs, the male and female sex organs couple and copulation begins.

The female remains motionless as the male jabs his aedeagus back and forth within the ovipositor sheath. Copulation lasts five to fifteen seconds and is terminated when the female resumes movement and withdraws her ovipositor. The majority of females run away so rapidly that the male is dislodged from the female's back. If a female begins to move immediately after coupling, the male leans forward and beats her antennae down again until she once again ceases movement. After mating, the female becomes unreceptive to any further mating attempts. Although males often chased females after mating, no recoupling was ever observed. After several seconds of pursuit, the male abandons the chase and resumes search behavior for other females.

Several aspects of G. parkeri's behavior were further scrutinized. These included male-male interactions, prior to and during female eclosion, antennal recognition of females by males, unreceptivity of mated females, and mating capacity of males. After males emerge and preen, they remain near or on the parasitized eggs. Males never attempt to acquire dominance over an egg mass or a specific egg, nor do any try to drive another male away from the egg mass. No aggressive stances, biting, or beating of wings were observed in male-male interactions. Generally, males demonstrate a mutual avoidance on and off egg masses. Males often came very close or made brief contact with other males, however, they moved away in an agitated and hurried

manner. Males never mounted or palpated the antennae of other males. Males also seldom group on or off the egg mass, therefore, further reducing male-male contact. Male behavior around separated eggs or on an egg mass differed if a female was emerging from a host egg. During this time, males often crawl over each other while palpating eggs. When the number of males was increased such that there were more than five males per vial, "ganging" behavior was noted. Males run agitatedly over each other and attempt to juxtaposition themselves closer to the emerging female by force. Avoidance behavior appears to be suspended by the drive to mate. Ganging was rare when additional males were not added. Occasionally, when one male was mating another male would attempt to mount the female at the same time. No aggressive behavior ensued and the mating male ignored the other male and continued normal mating behavior.

The male-male avoidance and male-female chase behavior indicate males probably recognize sex by antennal perception of a surface pheromone. Male attraction to eggs with emerging females might be due to the sudden release of this pheromone when the chorion is punctured by the female. Males tend to become more excited on the parasitized egg mass when females are emerging. The presence of a pheromone is also suggested by males often scrutinizing the empty egg cases of recently emerged females and the ganging of males around emerging females. Harrell (1975) also concluded olfaction was important in sex recognition. He noted that males mount and palpate dead females, but not dead

males. Harrell noted that males show little interest in females that have been dead seven days or longer. Although Harrell records males extending their aedeagus in mating attempts with dead females, in this study, from approximately one hundred observations, it was found extension of the sex organ for dead females was extremely rare. Also males appear unable to distinguish between virgin and mated females and mount almost any moving female encountered.

Careful observation of mating attempts revealed a return stimulus from the female is important to elicit extension of the male's aedeagus. However, the required stimulus does not always mean the female is receptive. This is best exemplified by observations on the behavior of unreceptive females. Females, after mating, normally begin search behavior for hosts, however, if deprived they eventually take up a resting position. These resting females, if contacted by males, either run away or maintain a motionless stance. Males show a much greater interest in females that run away. Often a male mounts a moving unreceptive female, however, she never stops body movement nor extends her ovipositor in response to palpation. However, the activity of the female's antennae and her body movements does appear to stimulate the male to extend his aedeagus. Typically, when the male leans back to flex his aedeagus toward the female's abdomen, he is dislodged by the female's running movements.

Many of the resting females react to males by remaining motionless. Without antennal or body movement, males usually

show no interest after initial contact, or only briefly mount the females. As long as the female remains motionless, the male most often dismounts without extending his aedeagus. All observations suggest movement is a necessary stimulus for the male to begin mating movements. The exact stimulus required is probably female body movement, followed by antennal movement.

The initial indication that females are monogamous was the marked decrease in number of matings with time in the observation vials. With each consecutive day fewer matings were observed in each vial. This suggests females are not only monogamous, but the majority of matings occur within the first day after female eclosion. Two studies were initiated to support these conclusions. First, five females that were known to have mated were transferred to vials with approximately ten males. In five replicates, each observed for one hour, only one remating was recorded. Five females that had oviposited for two days were placed in the same situation and none remated. This indicates females do not have a tendency to remate after partial depletion of their sperm supply. All indications are that females normally mate only once.

The second study had ten vials each with ten females in various stages of eclosion (prior to emergence, but after the chorion had been punctured). Two newly emerged males were transferred to each vial for twenty-four hours, then sacrificed. The females were individually transferred to vials with ten to twenty host eggs less than one day old. After two days, the females were removed and the parasitized eggs kept at 27°C until adults emerged.

Only ten out of the hundred females produced only males or no progeny at all. Since virgin females produce only males, the majority of the females in the test were mated in the twenty-four hour period they were exposed to males.

Although females are monogamous, there is ample evidence that males have a high mating capacity. In many cases, there were five to fifteen times more females taken from observation vials that laid fertilized eggs (females) than there were males in the vials to mate with. The maximum number of females mated by one male was twenty, although it is likely the maximum mating capacity is much higher, however it wasn't studied in detail here. Ten replicates were conducted in which one male was placed in a vial with ten unwanted females. Almost immediately after mating each male would chase and mount another female. The minimum number of females mated by one male was three, with six of the ten replicates having all females mated. The success of the matings were verified by providing each female unparasitized host eggs in which to oviposit. Males are probably only necessary for a limited time after female eclosion and low numbers of males can successfully inseminate large numbers of females.

Oviposition and Marking Behavior

In observation vials, females begin examining eggs almost immediately after mating. They appear to wander randomly around the vial until they contact an egg. On initial contact, a female palpates the egg with the club end of her antennae. Close examination of the club reveals it has a curved surface that

closely matches the curvature of the host eggs. In uncrowded vials (those with one to two females), each female palpates the surface of several different eggs before ovipositioning in one. This is not rejection behavior, since females eventually do parasitize the majority of eggs previously investigated. The degree of inspection is highly variable, even for females with the same genetic and environmental background. It ranges from the inspection of two or three eggs to almost all the eggs in a test vial or egg mass (approximately fifty eggs). Inspection behavior was observed in vials containing both separated eggs and whole egg masses. It is possible the female is assessing the quantity and quality of eggs prior to oviposition.

When a female is ready to eviposit, she palpates the entire exposed surface of the egg. If it is shriveled or has an irregular surface (such as damage due to transfer), the female rejects the egg and moves to the next one. With the appropriate stimulus from the egg, the female turns and backs up to the egg coat, placing the tip of her abdomen against the surface. She then inserts her ovipositor through the chorion. Females rarely, if ever, oviposit through the cap formed by the chorial processes. At 27°C, a single oviposition lasts two to ten minutes for females less than three days old and up to an hour for females older than this. During oviposition each female remains motionless, with her antennae bowed and still. After the egg is deposited, the female resumes antennal movement and pulls her abdomen away, withdrawing her ovipositor. After withdrawal, she backs up to the egg, wiping her

ovipositor across the egg surface several times, usually behind the point of insertion. This marking behavior probably labels the egg surface with a pheromone to prevent superparasitism of the same egg. After marking an egg, the female draws her ovipositor in, turns, and starts the investigation of a new egg. Resting periods from one to ten minutes are common after five to ten successful ovipositions.

The behavior associated with oviposition, marking, and resting was recorded for virgin females and older females. Virgin females are generally reluctant to initiate oviposition behavior. Of twenty unmated females placed for one day in vials containing sixty eggs each, only four oviposited. The number of eggs laid by each of the four did equal the number of eggs laid by mated females. All offspring were males; a verification that these females were unmated. Of twenty mated females exposed to the same conditions, eighteen oviposited. Oviposition is not independent of mating condition at the 5% level of significance using the G-statistic 2 x 2 test of independence (Sokal and Rohlf, 1969). The behavior exhibited by an ovipositing unmated female is the same as that described for mated ones. The effect of age on reproductive behavior was also examined briefly. Inspection time, individual host oviposition time, and the resting period all increase in time as females get older. Older females at 27°C (unfed wasps greater than three days old) take longer and parasitize less eggs than they did when younger. Also older females often failed to mark eggs or marked an egg adjacent to the one in which they oviposited.

Although mismarking of eggs is more common among old females, young females occasionally mismark eggs also. The amount of care spent in marking eggs decreases with the age of the female.

Comparison of Crowded and Uncrowded Conditions

Crowded conditions (greater than five females per vial) were used to provoke maximum female-female interactions. The previously described inspection, oviposition, marking, and resting behavior were based on observations under uncrowded conditions. Under high female densities in vials with separated eggs, parasitism appears somewhat inhibited. Female contact is high as they walk around the vial searching for hosts. Agressive behavior was not observed; however, contacting female typically rapidly change direction to avoid prolonged contact, much as was observed for males. This behavior often results in females coming very close to hosts and then turning away due to avoidance of another female. Inspection behavior is also often abandoned upon contact with other females. High female contact, in vials where the eggs are scattered randomly, increases the wandering search time and decreases the time females spend investigating hosts and ovipositing. Throughout this study, maximum parasitism was obtained by using one female per vial.

The behavior differed in crowded vials with complete egg masses from that noted for separated eggs. Instead of a high amount of interaction, females divide up among the egg masses, thereby reducing overall interactions. Aggressive behavior was never involved in the female dispersal. Apparently females move from egg mass to egg mass such that contact with other females is

minimal. Egg masses (approximately three or four per vial) could accommodate two or three females on each. Contact prior to oviposition usually results in females moving to opposite areas on the same clutch. However, once oviposition begins, females ignore each other. Females often oviposit side by side and will even walk over each other while investigating an egg. Two females were observed ovipositing in the same egg at the same time. As long as the density on an egg mass is low (less than three females) and oviposition begins prior to contact, avoidance behavior appears to be suspended by the drive to lay eggs. Inspection, oviposition, and marking behavior were normal under these conditions.

Densities of females in vials with egg masses were experimentally increased until there was an average of five or six females for each egg mass in a vial. At this point, female interactions once again inhibit oviposition. Very few females got a chance to start oviposition before another female interrupted her. This inhibition was similar to that observed for vials with separated eggs. Females, even if they oviposited, spent much less time in oviposition and often failed to mark eggs after parasitism. The time spent investigating eggs prior to oviposition was also reduced. On these crowded egg masses, double or triple parasitisms of the same egg were common.

Stock colonies containing bugs and wasps were used to determine the number of females on egg masses. Fifty clutches with ovipositing wasps were isolated from these cages and the number of females on each recorded. These observations were made during a

time of peak population growth and the density of male and female parasites was extremely high. Twenty-nine of the clutches had only one female; fifteen had two; and six had three or more ovipositing females. The majority of egg masses had one female under crowded conditions. This may have been due to the somewhat hidden nature of the hosts and/or the avoidance behavior previously described. In stock colony cages, milkweed bug females generally lay their eggs just below the cotton surface. A female parasite walking across the surface of the substrate might not immediately find the hosts. Dispersal due to mutual avoidance may not only reduce the number of females on each egg mass, but may also increase the number of "searchers", as well as the search area.

In crowded and uncrowded conditions, on individual eggs or on egg masses, females that are ovipositing tend to ignore interruptions of any sort. As noted earlier, once females insert their ovipositor they ignore the presence of other searching females. This behavior can best be demonstrated by introducing a male into a vial with a previously mated female. Males tend to inhibit females ready to oviposit by constant mating attempts; however, females ignore males once they start to oviposit. Even if a male mounts a female and palpates her antennae, she remains motionless during the egg laying period. Even when prodded with dissecting needles, females rarely move unless pried from the host.

Discriminatory Oviposition and Superparasitism

Throughout the investigation of G. parkeri's reproductive behavior, there was a relatively low number of reparasitisms,

except by other females and females in crowded conditions. Marking behavior, as described in the previous section, is probably the basis for this discriminatory oviposition. Wilson (1961) noted similar behavior for the scelionid, Asolcus basalis. He found that females seldom insert their ovipositors in host eggs that have been marked. G. parkeri females also usually reject eggs that have been marked by a previous female or by herself. Several brief studies were conducted to investigate the ability of females to distinguish between parasitized and unparasitized eggs, the importance of marking to discrimination, conditions under which superparasitism is observed, and the consequence of superparasitism.

Ten known marked parasitized and unmarked unparasitized eggs were transferred to a vial containing a mated female, less than two days old. The eggs were distributed in the vial such that parasitized and unparasitized eggs were side by side. The parasitized eggs were labelled with a marking pencil on the bottom of the plastic vial. After one hour of observation under a binocular microscope, the female had parasitized eight of the unparasitized eggs and only one of the parasitized eggs. A 2 x 2 test of independence using the G-statistic suggests parasitism of a host is not independent of whether the host is parasitized or not at the 5% level of significance. In another experiment, twenty eggs were exposed to a female and each egg she oviposited in was labelled. In one hour, she parasitized twelve eggs, and only one was parasitized twice. All unparasitized eggs and the female were then

removed. The female was reintroduced to the eggs after a thirty minute separation. After one hour she reparasitized two of the twelve parasitized eggs. The female was then replaced with a new female, also mated and less than two days old. An hour of observation revealed she parasitized only three of the eggs. The results of these experiments are by no means conclusive, however, they do strongly suggest females have an ability to distinguish parasitized and unparasitized eggs. From the occasional mistakes observed, it appears either the discrimination or the ability to restrain oviposition is not perfect.

The next aspect investigated was the importance of marking to the discrimination observed above. Alcohol rinses, to rid the surface of the eggs of any pheromone, proved to be inappropriate. Females rejected both parasitized and unparasitized eggs that had been exposed to alcohol. The alternative was to remove females from vials after oviposition, but prior to marking. Eighteen parasitized but unmarked eggs were obtained by this method. Nine of these eggs were placed in each of two vials with one mated female. After one hour of observation, one female parasitized five and the other, six of the eggs. The same females were each exposed to nine parasitized and marked eggs for one hour. They parasitized two eggs and one egg, respectively. Testing the data using the G-statistic in a 2 x 2 test of independence, parasitism is not independent of marking at the 5% level of significance. The evidence suggests wiping the ovipositor over the surface of the egg is important for discrimination.

Parasitism of a host egg more than once was most often noted in crowded conditions and among older females. Earlier observations indicate that marking and inspection time is reduced when female contact is high. Older females (greater than three days old at 27°C in the unfed condition) also tend to mark and inspect eggs less thoroughly. They were occasionally observed not to mark eggs at all. This may be the basis for the greater number of superparasitisms among these two groups. With regard to age, females lay the majority of their eggs within the first days after eclosion (see Part II) which coincides with the period of peak discrimination. In addition to crowded conditions and among older females, superparasitism occasionally is a mistake made by an ovipositing female that parasitizes a different egg than the one investigated. The occurrence of such mistakes is relatively rare and was observed only fifteen times out of several hundred observations of females less than three days old.

During the investigation of superparasitism, eggs that were parasitized more than once were separated and placed in vials at 27°C. A maximum of one larva develops to the adult stage per host egg, and eggs parasitized more than three times produced no wasps. Superparasitism in uncrowded conditions is not advantageous for G. parkeri, since it results in a loss of gametes.

Host Egg Suitability and Parasite Preference

There were no observations that suggest G. parkeri prefer eggs of one milkweed bug species over the other, and developmental time of wasp larvae did not differ between the two hosts. Throughout

this paper, all experiments were conducted with fresh (less than one day old) eggs, unless otherwise mentioned. Parsite development is most successful if oviposition is in freshly laid hosts. Harrell (1975) notes, at 30°C, parasitism of eggs less than three days old results in the development of wasps; however, parasitism of eggs greater than three days old results in the continued development of the bug first instar. He recorded high mortality for both wasps and bugs in three day old eggs. My observations support the conclusion that once development of the host is visible through the chorion, the success of a wasp developing from a newly laid egg is minimal. Clausen (1940), in a brief review of the family, notes there are several species that prefer freshly laid host eggs for oviposition.

Although G. parkeri females develop more successfully in fresh host eggs, there is a question as to whether they prefer eggs of a specific condition, since he observed several females ovipositing in eggs with visible bug first instars or wasp larvae. Even though I observed the same behavior, it was only when females were given no choice or were in crowded conditions. Females exposed to fresh hosts and less suitable ones usually parasitize the fresh eggs first. They reject eggs with developing wasps or bugs several times before ovipositing. This suggests G. parkeri females have a preference for fresh hosts, but will oviposit in less suitable ones if no other are available.

REVIEW AND DISCUSSION OF SCELIONID REPRODUCTIVE BEHAVIOR

One of the best studied aspects of the Scelionidae is their reproductive behavior. Gordh and DeBach (1978) utilize four species of the Scelionidae as representatives of the superfamily Proctotrupoidea in a brief review of sexual behavior among parasitic Hymenoptera. The most complete review of scelionid reproductive behavior is by Wilson (1961). He divides the reproductive behavior of the scelionid, Asolcus basalis, into eight categories. For each category, he lists several references which describe similar behavior in other scelionids. Wilson's intent was to suggest that some of the behavior seen in A. basalis is evident within the entire family, whereas other aspects are only evident in groups within the family. Unfortunately, at least one author (Eberhard, 1975) has taken all eight characteristics of A. basalis as the family norm. Although most of Wilson's behavioral characteristics do apply to the majority of scelionids studied, there is ample evidence that at least two characteristics, both dealing with aggressive behavior, may not be as widespread as suggested. This review includes several recent investigations and attempts to establish whether the characteristics seen in A. basalis truly represent the family norm.

The eight characteristics Wilson observed in A. basalis are discussed individually. It should be noted that Wilson listed references that showed similar, but not necessarily the same, behavior. His review, therefore, can be misleading, since the

characteristics, as worded, apply specifically to A. basalis. In this paper Wilson's characteristics are written as they appeared in his paper and, if necessary, reworded to encompass more members of the family. In many cases, Wilson's categories are divided into subsections, since he often combined distinctly separate characteristics into one category. Some sections are also augmented with related behavior Wilson did not mention. Throughout this review, references to Gryon parkeri are based on observations made in this study.

I. Immediate fertilization of each female on emergence. As Wilson suggested, this category should include species where mating occurs immediately at emergence, as well as species that mate within a few hours after emergence. This implies the female emerges from the host egg as a fully reproductive individual with little or no pre-mating period. Another trait closely associated with this characteristic, not mentioned by Wilson, is the ability to oviposit fertilized eggs on the first day of emergence, therefore, implying a short preovipositional period. It is assumed from the diploid-haploid sex determination of most of these hymenopterans that any reference in the literature to oviposition of fertilized eggs within a few hours after emergence, implies early mating of the females.

Early mating and early ability to parasitize for scelionids is seen in Gryon parkeri, G. triatomae Masner and G. linschcostei Masner (Sankaran and Nagaraja, 1975), G. flavipes (Ashmead) (Rothschild, 1970), G. ajax (Girault) (Schell, 1943), G. gnidus Nixon (Taylor, 1975), Asolcus basalis (=Microphanurus megacephalus)

(Wollaston) (Noble, 1937; Kamal, 1938; Wilson, 1961), Aholcus (=Asolcus?) euphrotiscidis Mani (Narjanan, Subba, and Chacko, 1959), Telenomus remus Nixon (Schwartz and Gerling, 1974), Telenomus gifuensis Ashmead (Hidaka, 1958), Telenomus nawai Ashmead (Pemberton, 1933A), Telenomus ullyetti Nixon (Jones, 1947), Telenomus fariai Lima (Lima, 1928), Trissolcus bodkini, Phanuropsis semiflaventris Girault (Eberhard, 1975), Idris sp. (Bradoo, 1972), Scelio calopteni Riley (Pickford, 1964), and Scelio pembertoni Timberlake (Pemberton, 1933b). The literature indicates scelionid females mate within the first few hours after emergence, and typically oviposit diploid eggs within the first twenty-four to forty-eight hours after emergence.

II. High mating capacity of the male; the fertilization of nearly all females by one male. These two characteristics are not dependent upon each other. Fertilization of females by only one male in A. basalis is the result of male aggression leading to the possession of a parasitized egg mass by a single male. Male aggression does not occur in all scelionids; therefore, it is difficult to justify this as a general trait. However, there is usually a preponderence of females, thus making the number of males per egg clutch relatively low. Therefore, even in the absence of aggression, the majority of females are mated by a small number of males. The fertilization of nearly all females by one male will be only briefly discussed in this category, since its cause is more closely related to male aggression and female preponderence.

This category is divided into three subsections: high mating capacity of males, mating capacity of females, and the dominance of mating by one male. Although Wilson did not mention the capacity of females, it is included here because female mating capacities have important biological implications.

A. High mating capacity of the male. The ability of scelionid males to mate more than once is a widespread phenomenon. In all papers where the mating capacity of males is mentioned, it has been reported as high. Wilson (1961) records one A. basalis male effectively mating with as many as fifty-six females. One male of E. benefica, Trissolcus bodkini, and P. semiflaviventris have been recorded as mating with approximately ten females; however, the maximum number of matings possible by one male was not tested (McCollach and Yuasa, 1915; Eberhard, 1975). One Gryon parkeri male mated with as many as twenty females. In most cases, the exact mating capacities are not mentioned. High mating capacity has been recorded for G. ajax (Schell, 1943), Telenomus ullyetti (Jones, 1937), T. fariai (Dreyfus and Breuer, 1944), T. remus (Schwartz and Gerling, 1974), Telenomus sp. (Kulshreshtha, et al., 1967) and Idris sp. (Bradoo, 1972). The extraordinary mating capacity of males allows the majority of eggs oviposited in a clutch to be female without decreasing the likelihood of a female being mated. This increases the number of females in the environment searching for hosts.

B. Female mating capacity. Wilson and the majority of other authors make little mention concerning the mating capacity of females. This is somewhat surprising since it has an impact on experimental designs and population studies. An experiment, designed to study a scelionid's fecundity, could be affected by whether single-mated females or constant male companionship was used. If a female needed to mate after depletion of sperm or if she required more than one mating to obtain an optimal sperm supply, then using a single-mated female would yield a lower fecundity than the female actually has. However, if the female only needs to mate once, then the constant presence of males could possibly be a hindrance to oviposition. G. parkeri exhibited a decreased oviposition rate when males were left in test vials. The male's persistent, but usually fruitless, mating attempts decreased the female's inspection and oviposition. Obviously, the experiment must be designed to meet the female's specific needs. Population effects of female mating capacity include the behavior of males, the effectiveness of female dispersal, and the genetics of the species. If females require subsequent matings after depletion of sperm, then males necessarily have to follow the females in their dispersal, in order to be present on unparasitized egg masses. For G. parkeri in stock colony cages, males were never found on unparasitized egg masses in the cotton substrate. Other literature on scelionids does not indicate males were present on field unparasitized clutches. Closely associated with this, is behavior associated with female dispersal. For G. parkeri, it is

noted that mated females avoid further male contact. Their dispersal and search would be inhibited by males on or near the unparasitized hosts. The presence of the male during female search and inspection behavior has not been adequately addressed by any author. Besides the presence and interference of the male, there is a genetic question associated with female mating capacity. Since the first interaction with a male is typically a sibling from the same egg mass, single matings with these males would tend to lead to a great deal of inbreeding. Unfortunately, these questions cannot be answered, since data on female mating capacity is generally lacking.

Species that are recorded to mate only once and resist copulatory attempts or avoid male contact thereafter include Gryon parkeri, Trissolcus bodkini, Phanuropsis semiflaviventris (Eberhaard, 1975), and Idris sp. (Bradoo, 1972). Females of Eumicrosa benefica (McColloch and Yuasa, 1914) and Telenomus remus (Schwarz and Gerling, 1974) are reported to mate more than once. One problem in observing female mating behavior is the common unsuccessful mounting attempts by a male. G. parkeri females often were mounted more than once, however, the female always failed to extend her ovipositor to complete coupling. Considering the small size of scelionids, mounting behavior can easily be mistaken for successful mating, unless the observations are made under a dissecting microscope or by following the progeny production of each female. Therefore, the species for which multiple matings are recorded are suspect unless coupling or the production of females (in arrhenotokous species) is recorded.

C. The fertilization of nearly all females by one male. Wilson inappropriately connected the high mating capacity of males with the mating of most females by one male. High mating capacity does imply that only a few males are necessary to fertilize a large number of females, but it doesn't imply only one male. If, as Wilson observed for A. basalis, male dominance leads to one male mating most females, then this characteristic belongs with the aggression category. If it is the result of only a low number of females and not aggression then it belongs with the category on the preponderence of females. In this review, mating by one male and mating by few males are separated into the above mentioned categories. It can be noted the genus Asolcus exhibits a high order of aggressive possession of an egg mass by one male and subsequently the fertilization of most females is by one male (Safavi, 1963; Hokyo and Kiritani, 1966). On the other hand, Gryon parkeri exhibits no male aggression and mating depends on whether a male contacts receptive females. Observations on G. parkeri do not suggest that one male has any more success than another, yet, because of the highly skewed sex-ratio in favor of females, most females in a clutch are fertilized by two to four males. For a more detailed discussion, refer to the respective categories on aggression and female preponderence.

III. Diurnal periodicity of adult emergence and the emergence of males before females. By grouping these two characteristics together, Wilson implies that diurnal periodicity is related to the early emergence of males. In fact, this has not been established

for scelionids. In this review the two characteristics are considered separately.

A. Diurnal periodicity of adult emergence. The variable environmental conditions (especially temperature) and methods of surveying for parasite emergence used by different researchers make it impossible to directly compare species. However, it may not be as important to know the exact conditions as it is to know when the major changes in these conditions occur. Wilson (1961) suggests that varying temperature is the most important stimulus in controlling the time of emergence. Early morning emergence, associated with a rise in temperature, has been observed in Asolcus basalis (Wilson, 1961), Eumicrosa benefica (McColloch and Yuasa, 1915), Teleonomus gifuensis (Hidaka, 1958), and Scelio pembertoni (Pemberton, 1933). Scelionids reared under varying temperature regimes tend to display emergence behavior in response to the early morning temperature rise. This was not the case, however, for Phanuropsis semiflaviventris in which seventy percent of adult emergence was recorded during the night (Eberhard, 1975). The relationship between photoperiod and temperature periodicity has not been investigated. Idris sp. (Bradoo, 1972), Gryon parkeri, and Gryon gnidus (Taylor, 1975) are recorded as emerging both day and night. Of the three, G. parkeri and G. gnidus were reared under constant temperature regimes. In their case, the absence of diurnal periodicity could be due to the absence of rearing temperature periodicity. At present, the data is too incomplete to make a general statement about diurnal emergence among scelionids, although it appears temperature may have a substantial effect.

B. Emergence of males before females. Sexual periodicity of emergence is suggested for the majority of scelionid species studied. Emergence of males before females has been recorded in Gryon parkeri, G. flavipes (Rothschild, 1970), Idris sp. (Bradoo, 1972), Trissolcus spp. (Safavi, 1968), Telenomus bodkini, P. semiflaviventris (Eberhard, 1975), Telenomus nawai (Pemberton, 1933A), Telenomus gifuensis (Hidaka, 1958), Telenomus remus (Schwartz and Gerling, 1974), Telenomus remus (Schwartz and Gerling, 1974), Telenomus nakagawi and A. mitsukurii (Hokyo, et al., 1966), A. basalis (Wilson, 1961), Microphanurus semistriatus Nees (Zomorrodi, 1959), and Scelio pembertoni (Pemberton, 1933B). Early emergence of males is probably due to two factors; earlier oviposition and shorter developmental times for males. Safavi (1968) recorded the first egg laid by Trissolcus spp. was invariably male. Cumber (1964) and Hokyo, et al. (1966) found this was true for A. basalis and A. mitsukurii and that males of these species also develop slightly faster than females. Gryon parkeri males are generally, though not always, laid first and have shorter incubation periods. Since females of many species of scelionids remain on or near the egg clutch from which the emerge for only a short period of time, early male emergence increases the likelihood of fertilization prior to dispersal and the subsequent unreceptivity of females. In aggressive species, like A. basalis, early male emergence allows time for them to establish dominance over a clutch.

IV. and V. Marking of the host egg after parasitism; female ability to discriminate between parasitized and unparasitized eggs

and to exercise restraint in oviposition. These characteristics are widespread among scelionids and most authors attribute discriminatory ability to the marking of the parasitized eggs. It is for this reason the two categories are considered together here, even though Wilson discussed them separately. An important aspect associated with this behavior is the result of the breakdown of discrimination which results in superparasitism. Observations of superparasitism, conditions under which it occurs, and its consequence on the development of the parasite are discussed in the section on superparasitism.

A. Marking, discrimination, and restraint. Wilson (1961) attempted to clarify the literature on discrimination behavior by statistically testing to determine if marking and reparasitism are random. Most studies base the ability to discriminate parasitized eggs simply on whether superparasitism is observed. If an egg was parasitized more than once, it was generally concluded that the parasites were unable to distinguish and restrain oviposition. Even the literature on A. basalis, the species studied by Wilson, varies on the subject of discriminatory ability. Kamal (1937) reported discrimination exists for A. basalis, but "promiscuous" oviposition is widespread. Noble (1937) stated A. basalis lacks the ability to discriminate, since it is observed to superparasitize eggs under crowded conditions. They fail to incorporate their experimental designs in their papers. Cumber (1964) noted A. basalis, when alone on an egg mass, exhibits a high order of discrimination

and restraint. Wilson demonstrated statistically that marking and parasitism were not random events, hence the females discriminate between parasitized and unparasitized eggs. Gryon parkeri and A. basalis exercise a great deal of restraint under uncrowded conditions, but much less so when densities are high (Wilson, 1961). Therefore in testing discrimination various conditions must be utilized. Although G. parkeri's marking and discriminatory ability were not vigorously tested for non-randomness, careful observation of the parasite, under crowded and uncrowded conditions, and its response to previously parasitized eggs, confirms its ability to distinguish parasitized eggs.

Morrill (1907) reported marking for Telenomus ashmeadi consists of distinct lines scraped upon the surface of the host egg chorion. Most authors since Morrill have described marking behavior as a weaving of the ovipositor across the surface of the egg, presumably leaving an exudate that has pheromonal properties. Physical marking of the surface is no longer considered necessary (Wilson, 1961). Salt (1935, 1937) and Laing (1937) have demonstrated for a Trichogramma sp. that host suitability in hymenopterans can be determined by antennal palpitation of eggs. Cumber (1964), Safavi (1968), and Hokyo and Kiritani (1966) record that Asolcus, Trissolcus, and Telenomus species perceive marking by the olfactory sense (antennae).

The marking of host eggs, plus the ability to recognize the mark as witnessed by at least partial discrimination of oviposition, is noted for Gryon parkeri, A. basalis (Wilson, 1961), A. mitsukurii

and Telenomus nakagawai (Hokyo and Kiritani, 1966), Microphanurs panei (Lever, 1933), Telenomus cosmopeplae Gahan (Balduf, 1926), Telenomus ashmeadi Morill (Morrill, 1907), Telenomus farai (Lima, 1928), Telenomus ullyetti (Jones, 1937), Telenomus sphingis Ashmead (Rabb and Bradley, 1970), Asolcus (=Trissolous) grandis Thomson, Trissolcus viktorovi Kozlov, and Trissolcus djadetschko Rjachovskij (Buleza, 1971), Trissolcus bodkini (Eberhard, 1975), and Trissocus simoni Mayr (Voukassovitch, 1925). Although marking is not specifically mentioned, antennal palpation, recognition, and discrimination are recorded for G. gnidus (Taylor, 1975), G. flavipes (Rothchild, 1970), G. ajax (Schell, 1943), and Telenomus gifuensis (Hidaka, 1958). Bradoo (1972) reported that a species of Idris does not mark eggs, but is able to discriminate between parasitized and unparasitized eggs by sense organs at the distal end of the female. Scelionids that show no marking, no recognition, and no discrimination include Telenomus remus (Gerling, 1972) and Phanuropsis semiflaviventris (Eberhard, 1975). Both T. remus and P. semiflaviventris readily oviposit more than one parasite per host egg. Eumicrosa benefica is also recorded to lack discriminatory oviposition (McColloch and Yuasa, 1915), however it is unclear whether this is only under crowded conditions or at all densities.

The recognition of parasitized and unparasitized eggs and the discrimination of oviposition are widespread among the species Ascolcus, Trissolcus, Telenomus, and Gryon. Although the majority of scelionids exhibit some type of marking and discrimination, there is at least one specie that appears to discriminate without

marking, as well as at least two species that lack both marking and discrimination.

B. Superparasitism among scelionids. As Salt (1936) noted for Trichogramma evanescens, recognition of a marked egg does not always result in discriminatory oviposition. He found that under crowded conditions recognition was perfect, but restraint broke down. Wilson (1961) noted that although recognition and discrimination are of a high order for A. basalis it does not preclude occasional multiple parasitisms. Superparasitism has also been recorded for the scelionids Microphanurus painei (Lever, 1933), Microphanurus sp. (Chatterji and Rahalkar, 1958), Telenomus nawai (Pemberton, 1933A), Eumicrosa benefica (McColloch, 1915), Trissolcus bodkini, Phanuropsis semiflaviventris (Eberhard, 1975), Gryon parkeri, Gryon ajax (Schell, 1943), Gryon flavipes (Rothschild, 1970), Telenomus remus (Schwartz and Gerling, 1974) Aholcus euprotiscidis (Narayanan et al., 1958), Trissolcus sp. (Safavi, 1968), Scelio fulgidus (Noble, 1938), Scelio calopteni (Pickford, 1964), and Scelio pembertoni (Pemberton, 1933B). In the aforementioned species, superparasitism is primarily observed under crowded conditions.

Wilson (1961) did not discuss the consequence of superparasitism in scelionids, but as noted for Gryon parkeri, usually one adult emerges from each superparasitized egg. For G. parkeri there appears to be a limit to the number of parasites a host can have before all parasite development is arrested. There is no mention in the literature if such a phenomenon occurs among other scelionids.

Several authors report larval competition in a superparasitized egg results in the survival of the fastest developing larvae (McColloch and Yuasa, 1915; Pemberton, 1933B; Lever, 1933; Noble, 1937; Kamal, 1937; Narayanan et al., 1958; Pickford, 1964; Safavi, 1968). Gerling (1972) notes that when Telenomus remus larvae meet in a superparasitized egg, one inserts its mandibles into the other. He also recorded that several larvae usually survive, and the one that completes its development and exhausts the food supply first is the one that successfully emerges as an adult. Since the early emergence of males is in part due to their faster development (Section III B), males often are the emerging sex from superparasitized eggs. Schwartz and Gerling (1974) also found increased female density on hosts results in a shift in sex ratio in favor of males for Telenomus remus. They attribute this rise to an increase in the amount of observed superparasitisms. Viktorov (1968) also found an increased number of males emerging from egg masses having three or four ovipositing females over those with one female. He also noted that females taken from these crowded vials continued to oviposit higher numbers of unfertilized eggs, even isolated from the other females. Therefore, the number of males can increase in the next generation as the result of high female contact experienced by the ovipositing females. Presumably, by increasing the number of males oviposited when female contact is high on an egg mass, the next generation of ovipositing females is reduced. This decreases the future overall parasitism capability

of that parasitized egg mass and may maintain a host-parasite balance.

The majority of scelionids tend to avoid superparasitism to varying degrees, but when it does occur, typically only one larva develops to the adult stage, if any develop at all. In uncrowded conditions, the parasitism of an egg more than once is probably a waste of gametes. The recognition of parasitized eggs, usually by a mark or pheromone left by the ovipositor, and the discriminatory oviposition prevent such a waste. Under crowded conditions, the increase in unfertilized eggs oviposited may be adaptive.

VI. Numerical preponderance of females. Mated scelionid females oviposit more fertilized eggs than unfertilized, and most records demonstrate that female preponderance is the norm. The relationship of the number of males to the total number of females. Recorded sex ratios are Gryon parkeri 1:6.3, G. gnidus 1:2 (Taylor, 1975), G. ajax 1:5 (Schell, 1943), G. flavipes 1:1.9 (Rothschild, 1970), Telenomus ullyetti 1:2.5 (Jones, 1935 from Wilson, 1961), Telenomus gifuensis 1:4 (Hidaka, 1958), Scelio calopteni 1:14 (Pickford, 1964), Trissolcus bodkini 1:3.2 and Phanuropsis semiflaviventris 1:4.3 (Eberhard, 1975), A. basalis 1:5 (Wilson, 1961), Telenomus fariai 1:4.3-1:5.7 (Zeledon, 1957), Telenomus ashmeadi 1:5.7 (Morrill, 1907), Telenomus nawai 1:1.3 (Pemberton, 1933A), Telenomus remus 1:1.5-1:2.3 (Schwartz and Gerling, 1974), Microphanurus sp. 1:1.2 (Chatterji and Rahalkar, 1958), A. mitsukurii 1:3.0 and Telenomus nakagawai 1:49 (Hokyo et al., 1966), Scelio

fulgidus 1:1.5-1:6.1 (Noble, 1938), Scelio pembertoni 1:1.4-1:4.0 (Pemberton, 1933B), and Idris sp. 1:10.1 (Bradoo, 1972). The mean sex-ratio appears to be 1:6.1 (± 9.6).

The above figures clearly support the conclusion that females are in preponderance, however, they cannot be directly compared nor can they be regarded as non-fluctuating. Flanders (1952) believes the proportion of males to females varies for parasitic Hymenoptera due to environmental changes effecting the spermatheca. Besides environmental fluctuations, superparasitism and high female density on egg masses can increase the proportion of males. Another problem encountered when dealing with the proportion of males to females is oviposition of all males by unmated females. This can rapidly change the proportions of the sexes. Parthenogenic reproduction depends, in part, on the number of females that are unmated and the readiness of unmated females to oviposit. Unmated females of G. parkeri and G. gnidus (Egwuatu and Taylor, 1977) are reluctant to oviposit, whereas A. basalis (Cumber, 1964) and S. pembertoni (Pemberton, 1933B) females readily oviposit when unmated. McColloch and Yuasa (1915), Pemberton (1933B), Noble (1938), Schell (1943), Hidaka (1958), Taylor (1975), and Eberhard (1975) all report that field-collected all-male egg masses are rare, suggesting that most females in nature are mated, or that unmated females are reluctant to oviposit. It is generally recognized that, although parthenogenic production of females (thelytoky) may be possible, sexual reproduction is by far more prevalent in this family.

A basic problem with overall sex-ratios is that they give little indication of the pattern of daily progeny production by individual females. There are two trends in daily production, observed in G. parkeri (see Part II), that are probably common for the majority of scelionids. First, the greatest number of offspring are laid within one to three days after the onset of oviposition for newly emerged females. Egwuatu and Taylor (1977) report that 83% of G. gnidus's eggs are deposited within the first and second day after eclosion. Hokyo et al. (1966) found the oviposition rate of A. mitsukurii and Telenomus nakagawai decreases abruptly after the second day of oviposition. Schwartz and Gerling (1974) observed the highest number of progeny was produced by Telenomus remus on the first day after female eclosion and oviposition sharply declined thereafter. This pattern is probably an adaptation to the parasite-host complex. Upon contact with hosts, it would be beneficial for the wasps to lay eggs at a maximum rate in order to establish themselves as rapidly as possible. It could also possibly be due to hosts being only rarely found.

The second aspect is the daily change in the proportion of the sexes. As female production decreases with the age of the female in G. parkeri, the percentage of males in the total population increases (see Part II). Schwartz and Gerling (1974) observed that the percentage of Telenomus remus females begins to decrease after the fourth day of oviposition. Nagel and Pimental (1964) noted a similar oviposition pattern in Nasonia vitripennis

(Walker) (Hymenoptera:Pteromalidae). They state that the increase in proportion of males oviposited as females become older is due to the depletion of sperm in the spermatheca, therefore increasing the percentage of eggs oviposited without being fertilized. This may be the reason for a few older G. parkeri females laying only males.

The number of males in each clutch is usually less than the number of females; therefore there are only a few males to fertilize most of the females. The male's high mating capacity allows scelionids to maximize the number of females in each clutch without describing their probability of being mated. This would also increase the searching capacity of the species. G. parkeri and Telenomus remus (Schwartz and Gerling, 1974) are two non-aggressive species that have most emerging females mated by one to four males. As will be discussed in the next section, aggression reduces the number of males on the egg mass such that one male may mate with the majority of females.

VII and VIII. Aggressiveness of the ovipositing female; male aggression leading to the possession of an egg mass by one male. Although Wilson separated these two categories, they are considered together in this paper since they both deal with other members of the same sex aggressively being driven away.

A. Problems in categorizing aggression. Aggressive behavior among males and females is well established for most Asolcus species and absent for many Gryon species. However, there are several

problems categorizing aggression, even among these two genera. First, aggression follows a continuum and, among the Scelionidae, it ranges from highly aggressive males and females, as in A. mitsukurii (Hokyo, et al., 1966) and Telenomus gifuensis (Hidaka, 1958), to non-aggressive males and females, as in Telenomus remus (Schwartz and Gerling, 1974) and G. parkeri. If only the extremes were discussed, many scelionid species, including A. basalis, would be left out. In this paper, aggressive species are those that exhibit, at some time, chase, fighting, or an aggressive stance in an attempt to exclude a member of the same sex from an egg mass or individual egg. Conversely, non-aggressive species are those in which members of the same sex co-exist on an egg mass or individual egg. Non-aggressive species can mutually avoid contact as long as it does not result in one male gaining a mating advantage over another male or one female having an oviposition advantage. For example, females are considered non-aggressive in this paper if an author records more than one female ovipositing on the egg mass without any excluding behavior. Using this distinction, A. basalis females are considered to exhibit a low level of female aggression, since Wilson (1961) observed as many as ten females ovipositing on a single egg mass. Aggression seems to be elicited in A. basalis by the failure to find unparasitized hosts, at which time the majority of eggs have already been parasitized. This also indicates individual aggression may change with density of suitable hosts.

Another difficulty in categorizing aggression is its presence in one sex and not the other. For example, Trissolcus bodkini and

P. semiflaviventris have aggressive males and non-aggressive females (Eberhard, 1975). When aggression is recorded for one sex, it cannot be automatically assumed to be present in the other sex. In many cases there is no specific mention of aggression or description of intrasexual coexistence. Therefore, several species cannot be properly categorized at present. Another problem which obscures the labelling process is contradictory statements by authors. For example, Rothschild (1970) described G. flavipes males as aggressive, yet he seemingly bases this on one observation of a female emerging when the number of males was unusually high. Although the males attacked one another, none appeared to be excluded from the egg mass. This closely resembles the occasional ganging behavior noted for G. parkeri. Since males did group on the egg mass, the behavior of G. flavipes must at most be considered a low level of male aggression. It is evident that categorizing aggression must be based on the author's classification as well as on his recorded behavioral observations. Unfortunately, the two do not always agree.

Finally, aggression is related, in part, to the amount of contact, which in turn is dependent on the density of the wasps on the egg mass as well as the size of the clutch. Wilson (1961), by using partial egg masses approximately one-third to one-fourth the normal clutch size, may have been eliciting abnormal aggressive behavior in his studies. Parasite densities and clutch sizes utilized for behavioral observations are seldom outlined in detail.

B. Distribution of male and female aggression among scelionids. A. mitsukurii (Hokyo, et al., 1966), Telenomus

gifuensis (Hidaka, 1958), and A. basalis (Wilson, 1961) exhibit aggressive behavior in both sexes. For all three species, males emerge prior to females, and one male gains dominance over the egg mass, although dominance can change through time (Wilson, 1961). The order in which the species are listed approximately reflects the degree of female aggression. A. mitsukurii and Telenomus gifuensis females tolerate no other females on the unparasitized egg mass (Hokyo et al., 1966; Hidaka, 1958). A.basalis, on the other hand, does not exhibit female aggression until the egg mass is almost completely parasitized (Wilson, 1961).

Microphanurus painei Ferr. (Lever, 1933), Telenomus cosmpeplae (Balduf, 1926), and Trissolcus simoni (Voussakovitch, 1925) are reported to also have aggressive female behavior. Lever (1933) observed M. painei females biting each other's wings prior to oviposition, however, he also notes they show a marked disregard to the presence of other individuals while ovipositing, even when walked over by another female. On the other hand, the latter two species become agitated when other females are present and often prematurely stop ovipositing (Balduf, 1926; Voussakovitch, 1925). M. painei, therefore, suspends aggression once oviposition begins. The presence or absence of male aggression is unrecorded for these species.

Two species that exhibit male chasing or fighting leading to the exclusion of other males from the parasitized egg mass are Trissolcus bodkini and P. semiflaviventris (Eberhard, 1975). As

discussed earlier, G. flavipes is recorded to demonstrate male aggression under crowded conditions, but it is much less severe than the aggressive behavior of the two species mentioned above (Rothschild, 1970). Safavi (1963), working with an Asolcus sp., found that males aggressively establish dominance prior to female emergence. In the case of Trissolcus bodkini, P. semiflaviventris, and G. flavipes, the female of the species does not exhibit aggression.

Telenomus remus (Schwartz and Gerling, 1974) and G. parkeri are two species that have both non-aggressive males and females. Although males generally avoid contact with each other off the egg mass, they are often observed side by side or examining the same egg on a parasitized egg mass without fighting or chasing each other. Females also coexist and oviposit on unparasitized egg masses at the same time. G. parkeri females avoid contact much as the males do, however contact seldom results in the exclusion of a female from the egg mass. It is interesting to note that G. parkeri, even without aggression, usually has only one female per egg mass in stock colonies. Scelionids that exhibit only female non-aggressiveness include Trissolcus bodkini and P. semiflaviventris (Eberhard, 1975). G. gnidus (Taylor, 1975), E. benefica (McColloch and Yuasa, 1915), and Telenomus nawai (Pemberton, 1933A) are recorded as lacking female aggression on egg masses, however, the male behavior for the two species is not recorded. The absence of female aggression, although not specifically mentioned, may be implied for Microphanurus sp. in which two females were observed ovipositing in the same egg (Chatterji and Rahalkar, 1958).

The literature indicates all scelionids are not aggressive. By utilizing the biologies of non-aggressive and aggressive species, several explanations of the presence and absence of aggression in different species can be tentatively examined. It is likely that more than one explanation will fit the entire group, since the ecology and nature of parasite-host complex among the Scelionidae does differ.

C. Theories of male aggression. Wilson (1961) interpreted male aggression as a method of increasing the number of males in the general environment thus providing males to mate with those females off the egg mass that are unmated or willing to mate again. Eberhard (1975) also suggests that aggressiveness in males emerging before females increases the number of males around the egg mass, therefore females do not have to hunt for mates. He contends this maximizes female search time since they mate on or near the parasitized egg mass and can immediately disperse. Unfortunately for this line of reasoning, the males of two non-aggressive species, Telenomus remus (Schwartz and Gerling, 1974) and G. parkeri, also remain near the parasitized egg mass. The absence of aggression among males in no way appears to reduce the number of females that mate nor would it probably decrease the amount of search time for females. Safavi (1963) and Hokyo and Kiritani (1966) alternately suggest that male aggression among Asolcus species may have developed in order to maximize the insemination of the majority of females by one male. Schwartz and Gerling (1974) consider this

a means of selecting the most "fit" males, hence "ensuring the best breeding stock for the propagation of the species". This does not explain why male aggression is absent in G. parkeri and Telenomus remus males. Schwartz and Gerling (1974) suggest the lack of aggression among males in the Telenomus remus-Spodoptera littoralis Boisd. complex provides a greater distribution of gametes since females mate more than once. For G. parkeri it is possible, but unlikely, that, due to the female monogamy, intrasexual competition occurs during the few seconds prior to copulation. This is unlikely however since mating appears to be based on random contact of males and females and competition is often totally absent. Hamilton (1967) suggests pugnacity of males is selected for in order to increase outbreeding. This idea cannot be adequately discussed here since there is little or no data as to where males go when driven off an egg mass.

A possible explanation which none of the previous authors considered, is the development of male aggression along interspecific lines that were carried over to intraspecific interactions. Aggressiveness among males appears high for those species visiting hosts that can be utilized by more than one scelionid. In those cases where different species of the Scelionidae oviposits in identical or adjacent egg masses of the same host, selection may have increased aggressive behavior between males as a method of one species excluding the males of another. Presumably, this would help maintain the integrity of the different species by preventing cross-fertilization and increasing the number of

successful matings by reducing the amount of intrasexual interference during female eclosion. Once such behavior was established it may have been maintained intraspecifically for any of the previously mentioned reasons. Behavior which suggests this explanation was recorded by Eberhard (1975) for Trissolcus bodkini and P. semiflaviventris, two species which exhibit male aggression only. Eberhard noted that the two species occasionally emerge from the same egg mass or adjacent egg masses of the pentatomid Antitechus tipterus Ruckes and vigorously attempt to exclude each other from the area around the eggs. He noted Trissolcus bodkini males appear to be slightly better fighters than P. semiflaviventris. When the two species are isolated on different parasitized egg masses, both also exhibit intraspecific male aggression. Interestingly, the more interpsecific aggressive species, Trissolcus bodkini, is also the less tolerant of conspecifics. A. basalis, A. mitsukurii, and Telenomus gifuensis which exhibit a high order of male aggression also oviposit in primary or alternative hosts that are utilized by several other scelionids (Wilson, 1961; Hidaka, 1958; Hokyo et al., 1966). In fact, A. mitsukurii and Telenomus gifuensis share four possible hosts in which they may have interacted in the evolution of male aggression (Hokyo et al., 1966). Conversely, non-aggressive males would be expected for species ovipositing in hosts seldom visited by other scelionids. Such is the case for G. flavipes and G. parkeri which are the only common egg parasites of Leptocorisa oratus (Fabricius) and L. kalmii and O. fasciatus, respectively

(Rothschild, 1970; Feir, 1974). The literature suggests there is a relationship between interspecific contact and the presence of male aggression intraspecifically.

D. Theories on female aggression. Wilson (1961) suggests female aggression on an unparasitized egg mass reduces the time wasted investigating parasitized eggs and increases the overall search time for the species. However, a high order of marking and discriminatory ability would also result in the same type of dispersal. For example, G. parkeri females recognize conspecific markings and generally avoid further oviposition in the parasitized eggs without aggression. In this case establishing and maintaining dominance might increase the amount of time required to parasitize an egg mass. Wilson also believes aggressive behavior is due to hosts being in aggregates and only available for a short time. G. parkeri and Telenomus remus, both of which have non-aggressive females, also parasitize hosts in aggregates that are available for a short period; therefore this does not explain the presence of aggression in some species and its absence in others. It might be suggested that aggression allows the "fittest" female to oviposit in an egg mass, much as Schwartz and Gerling (1974) suggested for males: however, none of the authors pursue this line. Presumably this is because occupation of an egg mass by a scelionid female appears to be random and not related to fitness. Hokyo and Kiritani (1966) and Hidaka (1958) imply the first A. mitsukurii or Telenomus gifuensis female to occupy an egg mass is usually the one that will

dominate it, but not necessarily the fittest. Hokyo and Kiritani (1966) and Wilson (1961) also observed that dominance can change, particularly if a female attempts to usurp the egg mass when the dominant female is busy ovipositing. It could be argued alternatively that the first females to find the egg mass are the most fit and dominance changes when more fit females approach the egg mass. At this time, fitness of the ovipositing female cannot be ruled out as a possible explanation of female aggression.

Two other explanations of female aggression emphasize the importance of the relative size of the host egg mass and the amount of female-female interspecific interaction. Hokyo and Kiritani (1966) and Hokyo et al. (1966) have demonstrated that species which parasitize small egg masses are generally more aggressive than those which parasitize large egg masses. For example, Hokyo and Kiritani (1966) note Telenomus gifuensis females parasitize egg masses that are approximately one-fourth their potential fecundity. Furthermore, although the aggressive female of A. mitsukurii can realize their entire potential on N. viridula, the majority of its alternative hosts have much smaller egg mass sizes. Hokyo and Kiritani also have shown the ovipositional behavior of A. mitsukurii is better adapted to small egg masses than large ones. They also believe the absence of agression in Telenomus nakagawai females is because they parasitize the large egg clutches of N. viridula and N. antennata. Cumber (1964) noted that an Asolcus species which parasitizes small pentatomid egg masses, but not those of N. viridula, is more aggressive than A. basalis which attacks all of these

species but is more successful on the large egg masses of N. viridula. Hokyo and Kiritani (1966) stress it is the size of the egg mass in relation to the parasite's fecundity as well as the size of alternative host egg masses that may be important. Presumably intraspecific contact on small egg masses would be high therefore, leading to female aggressive behavior. Schwartz and Gerling (1974) suggest that this explains the lack of aggression among Telenomus remus females. In this parasite-host complex there is an overabundance of eggs in a clutch relative to the parasite's fecundity. They suggest the progeny of several females can develop successfully on one egg mass, and aggressive behavior would reduce the degree of parasitism of the egg clutches if only one female dominated it. G. flavipes and G. gnidus females lack female aggression, however they appear to parasitize small egg masses. Closer inspection reveals these two parasites are recorded as having very low fecundities, therefore the small egg mass size may be large in relation to the parasite's potential fecundity (Rothschild, 1970; Taylor, 1975).

It is also possible reduced egg mass size increases the amount of intersexual interaction. Since superparasitism is more common under crowded conditions, and high female contact increases the number of males oviposited (Schwartz and Gerling 1974; Viktorov, 1968), the success of the species would be severely limited unless there were a means of preventing the frequent build-up of males. Aggression on small egg masses reduce the amount of contact during

active oviposition. On the other hand, large egg masses would allow cohabitation by several females until the egg mass is almost completely parasitized. Indeed, A. basalis females coexist on an unparasitized egg mass until it is nearly completely parasitized (Wilson, 1961). Aggression, therefore, may have been selected as a means of preventing the constant increase of males for species visiting small egg clutches. On large egg masses the interference would be somewhat less and the discriminatory ability would suffice in preventing superparasitism.

Gryon parkeri has non-aggressive females, yet its initial potential fecundity is about equal to or greater than the maximum egg mass size (see Part II). The size of the egg mass, therefore, does not seem to explain the absence of aggression for this species. The second possible explanation of female aggression is along the lines of interspecific interaction, much as was discussed for male aggression. Hokyo and Kiritani (1966) observed intraspecific interference among A. mitsukurii and Telnomus nakagawai females is less severe than interspecific interference. This suggests species that visit many different hosts or visit hosts that are parasitized by many different scelionids may have developed a strong aggressive tendency to exclude females of other species. As implied for male aggression, the exclusion behavior may have been maintained in intraspecific interactions. Hokyo et al. (1966) compare the hosts of two aggressive female species, Telenomus gifuensis and A. mitsukurii, to the relatively non-aggressive females of T. nakagawai. The aggressive species tend to be polyphagous, visiting the egg

masses of many pentatomids, whereas the non-aggressive Telenomus nakagawai is oligophagous, visiting only a few hosts. Although A. basalis, as mentioned earlier, principally visits the large egg masses of N. viridula, it is able to parasitize the eggs of several other species with small egg masses (Kamal, 1947; Cumber, 1964). These two factors combined may explain why A. basalis exhibits a lesser degree of female aggression than A. mitsukurii and Telenomus gifuensis. As expected from this hypothesis, the non-aggressive females of G. flavipes (Rothschild, 1970), G. gnidus (Taylor, 1975), Telenomus nawai (Pemberton, 1933A), T. nakagawai (Hokyo et al., 1966), and G. parkeri are highly host specific and/or visit hosts that are seldom visited by other scelionids.

It is likely the presence and absence of female aggression is related to the host clutch size and amount of interspecific contact; however, it may not fit for some species. For example, in the case of Trissolcus bodkini and P. semiflaviventris, Eberhard (1975) believes the defensive behavior of the adult host maintains selection against aggressive behavior of female parasites. In this host-parasite complex, aggressive behavior between females would give adult hosts more time to kick the wasps from the egg mass. Female aggression would also decrease the number of wasps the bug would have to guard against (Eberhard, 1975). Even though the host clutch size is small and at least two species of scelionids interact on the same host clutches, the behavior of the adult host selects against the development of female aggressiveness. However, this would have no effect on male aggression and, indeed, males of both species are aggressive.

Finally, Wilson (1961) and Hokyo and Kiritani (1966) believe host finding and discriminatory abilities may be related to aggression. They believe aggression raises the host finding efficiency by dispersing females when host finding ability is poor. Unfortunately, host finding ability is virtually unstudied for scelionids. It is also possible to approach host finding ability from the opposite veiwpoint. Namely, if host finding ability is good, aggression may have developed in order to disperse females to prevent crowding. Therefore if searching and finding ability are poor, fewer wasps would find egg masses, hence there would be reduced intrasexual contact. Another aspect often mentioned, but seldom documented, is the level of host discrimination. It seems unlikely that the ability, although present for most scelionids, is of the same degree. Possibly, if the ability to recognize and restrain oviposition is high intraspecifically, aggression would be less necessary to disperse females. Alternatively, if these abilities are present, but in a much less developed state, aggression could possibly help prevent superparasitism. As mentioned earlier, the presence and absence of aggression within the family is probably due to a combination of the previously discussed explanations.

CONCLUSIONS

The reproductive behavior of Gryon parkeri, an egg parasite of the large and small milkweed bugs, has been described and compared to other members of the Scelionidae. Monogamous females mate soon after emergence and almost immediately begin to search for eggs in which to oviposit. Female use pheromonal markings left by the ovipositor and sensed by the antennae, to distinguish and restrain oviposition in parasitized eggs. Superparasitism is typically observed under crowded conditions and among older females. Usually only one larva develops to the adult stage per egg. Males emerge prior to females and are able to mate several times. Overall sex ratios and daily fecundities reveal there is a preponderence of females produced in uncrowded conditions. G. parkeri differs most notably from the behavior of A. basalis and several other scelionid discussed by Wilson (1961), in its lack of aggressive behavior in males and females. Comparing aggressive and non-aggressive groups suggests aggression may have developed along intraspecific and interspecific lines.

PART II

THE EFFECT OF TEMPERATURE, FEEDING, AND SPECIES OF HOST ON THE REPRODUCTIVE BIOLOGY OF *GRYON PARKERI* (FOUTS)

INTRODUCTION

Survivorship and reproductive potential of the family Scelionidae have not been as thoroughly investigated and categorized as their reproductive behavior (see Part I). It is difficult to compare the few recorded longevities and fecundities, since experimental conditions, especially temperature and feeding, vary between investigations. In the genus Gryon, fed and mated females of G. gnidus live 8 to 27 days at 30°C (Taylor, 1975), whereas fed G. ajax adults live up to 12 days at temperatures ranging between 24° to 29° C, and as long as 35 to 42 days for unfed adults at 7°C (Schell, 1943). Clausen (1940) suggests scelionids have a reproductive capability between 50 to 200 eggs per female; however, the literature indicates Gryon species may have much lower fecundities. G. ajax, G. flavipes, and G. gnidus have recorded total fecundities ranging between 10 to 30 offspring per female (Schell, 1943; Rothschild, 1970; Taylor, 1975).

Eventhough detailed studies are limited, there are several trends in longevity and fecundity suggested by the literature on scelionids. Usually within their range of temperature tolerance, scelionid developmental time and adult longevity increase with decreasing temperature and vice versa (McColloch and Yuasa, 1915; Hodson, 1939; Noble, 1937; Egwuatu and Taylor, 1975). Egg parasites also tend to live longer when fed honey than when given water or left unfed (McColloch and Yuasa, 1914; Pemberton, 1933B; Hidaka,

1958; Hokyo, et al, 1966; Bradoo, 1972). It is generally assumed unfed conditions reveal minimum longevities and fecundities (Jubb and Watson, 1971). From the review of sex ratios in Part I, scelionids tend to produce more females than males; however, sex-ratios do not reveal absolute numbers of males and females produced per female.

Kenaga (1944) noted it takes between 14 to 16 days for Gryon parkeri to develop from the egg stage to adult at temperatures ranging from 18.3 to 32.3°C. Besides this reference, little else is found in the literature concerning the egg parasite's biology. This paper is concerned with the effect of three variables on longevity and fecundity of G. parkeri. The variables include four temperatures (24, 27, 30, and 33°C), two feeding conditions (dilute honey-fed wasps and unfed wasps), and two species of host (wasps reared from and on L. kalmii and O. fasciatus eggs). Mean total values for longevity and progeny production are combined with daily survivorship and reproductive rates to analyze the potentials of G. parkeri. The intrinsic rate of increase (r_m) is emphasized among the overall rates, since it combines survivorship and female production into one population statistic.

METHODS AND MATERIALS

Experimental Design and Materials

Constant temperature incubators, which varied no more than plus or minus one-half degree Centigrade, were programmed for 24, 27, 30, and 33°C which spans the temperature ranges of the two hosts (Dingle and Caldwell, 1971). The relative humidity in the incubators ranged between 40 to 60% and the photoperiod was maintained at 16 hours light and 8 hours dark. Hosts and parasites were reared and distributed among plastic vials as described in the Methods and Materials section of Part I. At each temperature there were four experimental groups; fed G. parkeri reared on L. kalmii, unfed G. parkeri reared on L. kalmii, fed G. parkeri reared on O. fasciatus, and unfed G. parkeri reared on O. fasciatus. Female G. parkeri were exposed to males from several minutes up to eighteen hours prior to being isolated in the test vials. The fed groups were daily supplied dilute-honey soaked filter paper (15 to 20% honey solution), whereas the unfed groups were given no added supplement. From the first day of eclosion until their death, females were transferred every 24 hours to vials containing unparasitized eggs less than one day old. Throughout their life, wasps were always supplied with more host eggs than they could parasitize. Due to variation in host production in mating cages and the number of replicates conducted at one time, it was not always possible to

use equal numbers of host for every 24 hour period. Generally, 60 to 70 separated eggs were supplied for the first three days of an experimental run, and 30 to 40 eggs for each day thereafter until death. The age of females used in an experiment was standardized at each temperature. Female G. parkeri that emerged 18 days after oviposition were used at 24°C; 12 days at 27°C; 11 days at 30°C; and 9 days at 33°C. This was usually the first day of female eclosion at each temperature. Adult wasps greater than one day old were never used to start an experimental run.

The parents of test wasps were "preconditioned", that is, at least two generations of wasps were reared under the specific test conditions prior to data collection. Since it is unknown whether G. parkeri females develop a preference for one species of host after being reared on that species for several generations, they were provided the same hosts to oviposit in as the ones from which they were reared. As a result of this method, variation in the data between species may be due to the species of host the test wasp was reared from and/or the species of host test wasps were provided. Since there appears to be little difference in choosing between hosts, the major emphasis on differences in the data due to host species is placed on the pre-experimental run rearing condition of the female (that is, the diet of the experimental wasp larvae).

An unexpected difficulty, encountered in the experimental design, was widespread cannibalism exhibited by milkweed bugs

emerging from unparasitized eggs in test vials. First instar nymphs of L. kalmii and O. fasciatus readily suck out the entire contents of any unhatched eggs, whether they contain milkweed bug or parasite larvae. Since host eclosion occurs 6 to 13 days prior to parasite eclosion over the 24 to 33°C temperature range, it is possible for milkweed bugs to destroy all parasitized eggs in a test vial. Exposing unparasitized eggs to temperatures below 5°C, carbon dioxide or alcohol prior to an experiment was ineffective in killing bug embryos without rendering the eggs unsuitable for parasitism; therefore, the method used in this study was to remove or destroy the unparasitized eggs once bug first instars were visible through the chorion. This method successfully curtails cannibalism.

Data Collection and Statistical Tests

Test females were individually followed throughout an experiment to determine daily survivorship and reproductive rates. Longevity was measured as the total number of days females lived from eclosion to adult death. Longevity was not measured for males and unmated females. All test vials were kept until adult wasps emerged, at which time they were counted and sexed. The vials were closely scrutinized to determine if any visible G. parkeri larvae failed to develop to eclosion. This allowed daily records of progeny production which were summed to determine total male and female production for each test female. This method can underestimate true fecundity, however, it is probably accurate in the case of G. parkeri for two reasons. First, over the 24 to 33°C

temperature range, the apparent larval mortality was less than 1% (n = 200 for wasps reared on either species of host at each temperature). Second, the experimental design provided an overabundance of eggs which elicited maximum parasitism rates and minimum superparsitism. Since parsitized eggs were not dissected, larval survivorship is probably slightly overestimated and fecundity slightly underestimated. The error in these measurements is believed to be minor.

The mean total values for adult longevity, number of males, number of females, and total number of progeny (males plus females) were analyzed by three-way ANOVA's and a posteriori tests (Student-Newman-Keuls and Duncan's). The three-way ANOVA's were all Model I, therefore mean squares were tested over residual mean squares (error variances). A three-way ANOVA tests main effects (temperature, feeding and species of host) and interactions between main effects. Analysis of significant interactions was facilitated by using two-way tables which are included in Appendices to this paper. (The two-way tables are further explained in a preface to the Appendix.)

The data, as recorded in linear scale, was significantly heteroskedastic and, therefore, was transformed to logs before testing. Although this did not make all variances homogeneous, it did shift them closer to homogeneity. All statistical tests were done at the College of William and Mary Computer Center using the Statistical Package for the Social Sciences (SPSS programs).

Each table in the text gives the mean total values, the test treatments, the number of replicates, 95% Confidence Intervals for the means, and the standard errors. The best indication of variation around the means is the assymmetrical confidence intervals. Each table is followed by an ANOVA table for a three-way ANOVA and a table listing a posteriori test results.

Methods of Determining Rate Data

Values for mean survivorship (l_x) and mean female production (m_x) were used to calculate the intrinsic rate of increase (r_m) for each test group. A pivotal age (x) of one day was chosen for determining r_m. The r_m values were generated by a Fortran IV computer program based on Birch's (1948) exact method; solving the equation $e^{-rx} l_x m_x = 1$. This program also generated the net reproductive rate (R_o) which refers to the number of times the population will multiply per generation, and the mean length of a generation (T) which refers to the mean time between birth of a female and birth of her offspring. The finite rate of increase (λ), which is the number of times a population will multiply per pivotal time interval, in this case per day, and the doubling time, which is the amount of time it takes a population to double in number, were calculated from the r_m values.

In this study, methods for determining l_x and m_x as outlined by Birch (1948) were modified. Since morality rates were extremely low for larval stages, the survival rate at emergence was designated 1.0. Therefore it is assumed the number of emerging adults wasps

is an accurate estimate of fertility. Also, m_x's were determined for a specific pivotal age group by dividing the daily number of emerged females from all test females by the number of replicates. Birch (1948) and Cole (1954) suggest that the number of progeny, male plus female, produced each age interval should be multiplied by a fixed sex-ratio to determine m_x. However, overall sex-ratios for hymenopterans can vary greatly with changes in environmental factors. Some hymenopterans also exhibit daily fluctuations in sex-ratio (see Part I). Nagel and Pimentel (1964) found that the pteromalid, Nasonia vitripennis Walker, can have daily sex-ratios that never approach their overall mean sex-ratio. Schwartz and Gerling (1974) found the daily sex-ratios of the scelionid Telenomus remus change with increasing age of the ovipositing female, therefore the use of a fixed overall sex-ratio poses inherent problems when calculating r_m values for many hymenopterans. If the rate and proportion of male and female production varies greatly through time, a fixed sex-ratio can greatly over- or under-estimate m_x's at a specific pivotal age. This is particularly troublesome to the calculation of r_m, since Birch (1948) emphasized early age-specific fecundities are often most important to the accurate determination of r_m. Since preliminary studies indicated G. parkeri has a varying sex-ratio with the age of the ovipositing females, a fixed sex-ratio was not used. By determining the mean number of females produced by each test female for each day, the definition of m_x is not violated and an accurate estimate of daily production is made.

RESULTS AND DISCUSSION

Mean Total Values

Longevity

The mean length of time from eclosion to death for mated G. parkeri females is given in Table 1. Length of life of adult females is not synonymous with the period of active parasitism, since many wasps cease to oviposit prior to death. Table 4 combines standardized developmental times for each temperature with adult longevities in order to estimate generation lengths (total longevity). To avoid redundancy, means for total longevity are not discussed since they essentially follow the same patterns as means for adult longevity.

Main Effects. Table 2 reveals temperature, feeding and species of host all have a significant effect on adult longevity. Longevity decreases with an increase in temperature for fed and unfed wasps reared on either species of host (Table 1). If means are rounded to whole days, change in longevity due to temperature is almost linear in the unfed condition for females reared on either species of host (6, 5, 4, and 3 days for G. parkeri reared on L. kalmii and O. fasciatus). The middle temperatures, 27 and 30°C, have almost equal effects on longevity in the fed condition for wasps reared on either species of host. Wasps fed a dilute honey solution live approximately three to four times longer than unfed wasps and the greatest

TABLE 1. Adult Longevity

No. of Replicates N	Temperature °C	Mean	95% Confidence Interval for Mean	Standard Error
		Fed *G. parkeri* reared on *L. kalmii*		
22	24	28.1	26.0-30.4	1.0482
24	27	19.0	17.3-20.8	1.0454
23	30	16.3	15.0-17.8	1.0416
28	33	10.8	9.8-11.9	1.0486
		Unfed *G. parkeri* reared on *L. kalmii*		
17	24	6.4	6.0-6.9	1.0337
19	27	4.9	4.5-5.4	1.0406
29	30	3.7	3.5-3.9	1.0275
25	33	3.1	2.9-3.3	1.0123
		Fed *G. parkeri* reared on *O. fasciatus*		
25	24	27.7	25.1-30.6	1.0495
20	27	19.0	17.2-21.0	1.0500
21	30	18.9	16.2-22.1	1.0780
28	33	13.5	12.5-14.5	1.0371
		Unfed *G. parkeri* reared on *O. fasciatus*		
21	24	6.1	5.5-6.6	1.0440
16	27	5.3	5.0-5.7	1.0301
20	30	4.2	3.8-4.6	1.0481
25	33	3.3	3.1-3.5	1.0285

TABLE 2. Three-way ANOVA for adult longevity*

	Sum of Squares	DF	Mean Square	FS	Significance of FS
Source of Variation					
Temp	5.307	3	1.769	229.876	0.0**
Feeding	33.686	1	33.686	4377.598	0.0
Species	0.114	1	0.114	14.789	0.0
Two-Way Interactions					
Temp x Species	0.100	3	0.033	4.338	0.005
Temp x Feeding	0.134	3	0.045	5.784	0.001
Species x Feeding	0.007	1	0.007	0.878	0.349 NS
Three-Way Interaction					
Temp x Species x Feeding	0.027	3	0.009	1.186	0.315 NS
Explained	40.395	15	2.693	349.963	
Residual	2.670	347	0.008		

*ANOVA tables test data in the logarithmic scale.

**Any significance of FS written as 0.0 means the probability is less than 0.001.

TABLE 3. *A posteriori* tests for adult longevity

Fixed treatment	Test Treatment	Probability
Fed *G. parkeri* reared on *L. kalmii*	Four temperatures (24, 27, 30, and 33°C)	24 27 30 33*
Unfed *G. parkeri* reared on *L. kalmii*	"	24 27 30 33
Fed *G. parkeri* reared on *O. fasciatus*	"	24 27 30 33
Unfed *G. parkeri* reared on *O. fasciatus*	"	24 27 30 33
G. parkeri reared on *L. kalmii* at 24°C	Fed wasps versus unfed wasps	$p < .001$ +
G. parkeri reared on *L. kalmii* at 27°C	"	$p < .001$ +
G. parkeri reared on *L. kalmii* at 30°C	"	$p < .001$ +
G. parkeri reared on *L. kalmii* at 33°C	"	$p < .001$ +
G. parkeri reared on *O. fasciatus* at 24°C	"	$p < .001$ +
G. parkeri reared on *O. fasciatus* at 27°C	"	$p < .001$ +
G. parkeri reared on *O. fasciatus* at 30°C	"	$p < .001$ +
G. parkeri reared on *O. fasciatus* at 33°C	"	$p < .001$ +
Fed wasps at 24°C	*L. kalmii* reared wasps versus *O. fasciatus* reared wasps	$p = 0.843$ NS
Fed wasps at 27°C		$p = 0.943$ NS
Fed wasps at 30°C		$p = 0.082$ NS
Fed wasps at 33°C	"	$p < 0.001$ +
Unfed wasps at 24°C	"	$p = 0.330$ NS
Unfed wasps at 27°C	"	$p = 0.128$ NS
Unfed wasps at 30°C	"	$p = 0.012$ +
Unfed wasps at 33°C	"	$p = 0.070$ NS

*The four temperature means were compared by Student-Newman-Keuls and Duncan's Multiple Ranges Test. Means that are not connected by a line are significantly different at the 5% level.

+ indicates the two means were significantly different at the 5% level.

TABLE 4. Total longevity (days from oviposition to adult death)

No. of Replicates N	Temperature °C	Mean	95% Confidence Interval for Mean	Standard Error
		Fed *G. parkeri* reared on *L. kalmii*		
22	24	46.2	44.1-48.5	1.0231
24	27	31.1	29.4-32.9	1.0271
23	30	27.4	26.1-28.8	1.0242
28	33	20.0	18.9-21.1	1.0264
		Unfed *G. parkeri* reared on *L. kalmii*		
17	24	24.5	24.0-24.9	1.0088
19	27	17.0	16.6-17.4	1.0118
29	30	14.7	14.5-14.9	1.0029
25	33	12.1	11.9-12.3	1.0072
		Fed *G. parkeri* reared on *O. fasciatus*		
25	24	46.0	43.4-48.8	1.0292
20	27	31.2	29.3-33.1	1.0290
21	30	30.3	27.8-33.2	1.0435
28	33	22.6	21.6-23.6	1.0221
		Unfed *G. parkeri* reared on *O. fasciatus*		
21	24	24.2	23.6-24.8	1.0120
16	27	17.4	17.0-17.7	1.0090
20	30	15.3	14.9-15.7	1.0127
25	33	12.4	12.2-12.6	1.0079

difference between fed and unfed wasps occur at 24°C. The absolute difference between G. parkeri reared on L. kalmii eggs and O. fasciatus eggs is small at the lower temperatures and becomes slightly more distinct at higher temperatures. At all temperatures and feeding conditions, except 24°C, wasps reared on O. fasciatus eggs have slightly greater longevities.

A posteriori tests (Table 3) reveal adult longevity is significantly different between each temperature for fed and unfed G. parkeri reared on L. kalmii and unfed G. parkeri reared on O. fasciatus. Fed wasps reared on O. fasciatus eggs did not have a significant difference between longevities at 27 and 30°C. Feeding, therefore, has a tendency to moderate change in longevity due to temperature. Fed wasps live significantly longer than unfed wasps over the various combinations of test conditions. The dilute-honey solution probably not only provides an additional energy source, but also acts as a source of water, thereby slowing dessication. Adult longevities of wasps reared on L. kalmii and O. fasciatus were significantly different at two temperatures, 33°C for fed wasps and 30°C for unfed wasps. In both cases O. fasciatus reared females lived longer than L. kalmii reared females.

Interactions. All interactions discussed in this paper have much less effect on the data than the main effects, except in the case of temperature X feeding for the total number of males produced per female. For this reason, the analysis of the main effects is not seriously impaired by ignoring those significant

interactions with minor effects on the data. In this paper all significant interactions are briefly analyzed for their effect on the data.

Table 2 indicates temperatures X feeding and temperature X species have significant interactions for adult longevity. This means the effect of temperature on adult longevity is dependent on whether test females are fed or on which species of host they were reared. Other interactions of the main effects were not significant.

The two-way table for temperature and feeding in Appendix 1 indicates the interaction is due to a relative change in the magnitude of the means. Although means for fed individuals are always greater than those for unfed, there is an alternation in the signs of interaction components calculated for each cell in the two-way table. The alternation of signs occurs between values at conservative temperatures. The difference between consecutive means in columns of the two-way table reveals fed wasps exhibit the least amount of change between the middle temperatures, 27 and 30°C, whereas unfed wasps have the greatest difference between thse temperatures. The "buffering" of change in longevity between these two temperatures is probably due to the honey solution acting as a source of energy and moisture. The honey solution moderates the increased activity and water loss caused by the increase in temperature. The reduced values at 33°C suggests G. parkeri females are near the upper limit of their temperature tolerance.

The temperature and species of host interaction suggests the effect of temperature on adult longevity is dependent on which

species of host the wasps were reared. The temperature and host species two-way table in Appendix 1 reveals there is a shift in magnitudes between G. parkeri reared on L. kalmii and O. fasciatus at 24°C. However, interaction components reveal there is a relative change in magnitudes between values at consecutive temperatures. The difference between row values in the two-way table indicates G. parkeri reared on L. kalmii and O. fasciatus eggs are more similar at 24 and 27°C than at 30 and 33°C. Column differences in the two-way table indicate L. kalmii reared wasps have the largest magnitude of change between 24 and 27°C and O. fasciatus reared wasps between 20 and 33°C. As discussed in the Methods and Materials of Part II, variation between wasps reared on different hosts can be due to the females being reared on a specific host during the experiment or test females being reared from a specific host prior to an experimental run. At present, the only known difference between the eggs of the two hosts is size; O. fasciatus eggs are longer and wider and, therefore, they have a greater volume than L. kalmii eggs (Andre, 1934; Simanthon and Andre, 1936). Although unstudied, it is conceivable there might be chemical differences in the composition of the eggs of the two milkweed bugs. Possibly, the difference in larval diets (species of host), although not affecting larval survivorship, results in G. parkeri reared on O. fasciatus being more fit. The difference between species of host that causes the wasps to react more similar at lower temperatures than at the higher temperatures is not known. Regardless of the cause, the deviation

between wasps reared on either species is small. The greatest difference between adult longevities of females reared on L. kalmii and O. fasciatus eggs is approximately three days in the fed condition (Table 1).

Number of Females

Total number of female progeny per female is given in Table 5. Progeny production is often considered one of the major parameters measured for a parasite. Female production is especially important since sex-ratios indicate females are in a higher proportion than males (see Part I). The total number of females produced by each female represents the next generation of reproductives. As will be discussed later, initial rates of female production may be more important in understanding the success of the parasite than total values.

Main Effects and Interactions. Table 6 reveals temperature, feeding and species of host have a significant effect on the total number of females. None of the main effects have a significant interaction, therefore, the main effects act independently on the number of females. The peak number of females occurs at 27°C with the second highest number of 24°C for fed and unfed G. parkeri reared on O. fasciatus eggs and unfed G. parkeri reared on L. kalmii eggs. Fed G. parkeri reared on L. kalmii reach a peak at 24°C with the second highest number at 27°C. The total number of females indicates 24 and 27°C are the optimal temperatures for maximum overall female production. Graphic and rate analysis will reveal there is a greater

TABLE 5. Total number of females

No. of Replicates N	Temperature °C	Mean	95% Confidence Interval for mean	Standard Error
		Fed *G. parkeri* reared on *L. kalmii*		
22	24	113.2	103.2-124.1	1.0454
24	27	107.4	101.5-113.6	1.0278
23	30	90.6	81.0-101.4	1.0556
28	33	45.7	39.2-53.2	1.0772
		Unfed *G. parkeri* reared on *L. kalmii*		
17	24	48.1	41.4-55.9	1.0732
19	27	54.6	47.0-63.4	1.0737
29	30	41.0	35.3-47.6	1.0755
25	33	24.2	20.1-29.1	1.0942
		Fed *G. parkeri* reared on *O. fasciatus*		
25	24	119.9	109.5-131.2	1.0447
20	27	127.1	115.6-139.7	1.0464
21	30	109.3	96.8-123.5	1.0602
28	33	61.0	52.4-71.0	1.0767
		Unfed *G. parkeri* reared on *O. fasciatus*		
21	24	53.0	45.6-61.6	1.0752
16	27	72.3	65.1-80.3	1.0505
20	30	46.1	37.2-57.1	1.1081
25	33	27.9	24.0-32.5	1.0757

TABLE 6. Three-Way ANOVA for total number of females*

	Sum of Squares	DF	Mean Square	FS	Significance of FS
Source of Variation					
Temp	7.567	3	2.522	126.446	0.0**
Feeding	9.563	1	9.563	479.418	0.0
Species	0.487	1	0.487	24.403	0.0
Two-Way Interactions					
Temp x Species	0.059	3	0.020	0.993	0.396 NS
Temp x Feeding	0.117	3	0.039	1.951	0.121 NS
Species x Feeding	0.003	1	0.003	0.154	0.695 NS
Three-Way Interaction					
Temp x Species x Feeding	0.042	3	0.014	0.694	0.556 NS
Explained	18.143	15	1.210	60.637	
Residual	6.921	347	0.020		

*ANOVA tables test data in the logarithmic scale.

**Any significance of FS written as 0.0 means the probability is less than 0.001.

difference in the effect of the two temperatures than suggested by the mean total values.

The most dramatic change in number of females occurs in the fed condition between 30 and 33°C for wasps reared on either species of host. In the unfed condition, the total number of females at 33°C is less than 30 for wasps reared on either species of milkweed bug. This, coupled with the reduced longevities at 33°C (Table 2), indicates this temperature is near the upper limit. Fed wasps reared from either species of host produced approximately two times the number of females in the unfed condition. G. parkeri reared on O. fasciatus always produced more females than those reared on L. kalmii.

Results of a posteriori testing are presented in Table 7. The total number of females at 33°C is significantly lower than at all other temperatures for fed and unfed wasps reared on either species of host. Although the highest number of females usually occurs at 27°C, the peak is only significantly separated from the means at other temperatures for unfed wasps reared on O. fasciatus eggs. In the fed condition for wasps reared on either species of host, the total number of females at 24 and 27°C are not significantly separated. In the unfed condition for wasps reared on L. kalmii eggs, means at 24 and 27°C, and 24 and 30°C are not significantly different. This indicates optimal temperature conditions for maximum female production is between 24 to 27°C. In Table 5, it is also evident fed wasps always produced significantly greater numbers

TABLE 7. *A posteriori* tests for total number of females

Fixed Treatment	Test Treatment	Probability
Fed *G. parkeri* reared on *L. kalmii*	Four temperatures (24, 27, 30, and 33°C)	24 27 30 33*
Unfed *G. parkeri* reared on *L. kalmii*		24 27 30 33
Fed *G. parkeri* reared on *O. fasciatus*	"	24 27 30 33
Unfed *G. parkeri* reared on *O. fasciatus*	"	24 27 30 33
G. parkeri reared on *L. kalmii* at 24°C	Fed wasps versus unfed wasps	$p < .001$ +
G. parkeri reared on *L. kalmii* at 27°C	"	$p < .001$ +
G. parkeri reared on *L. kalmii* at 30°C	"	$p < .001$ +
G. parkeri reared on *L. kalmii* at 33°C	"	$p < .001$ +
G. parkeri reared on *O. fasciatus* at 24°C	"	$p < .001$ +
G. parkeri reared on *O. fasciatus* at 27°C	"	$p < .001$ +
G. parkeri reared on *O. fasciatus* at 30°C	"	$p < .001$ +
G. parkeri reared on *O. fasciatus* at 33°C	"	$p < .001$ +
Fed wasps at 24°C	*L. kalmii* reared wasps versus *O. fasciatus* reared wasps	$p = 0.362$ NS
Fed wasps at 27°C		$p = 0.002$ +
Fed wasps at 30°C		$p = 0.023$ +
Fed wasps at 33°C	"	$p = 0.008$ +
Unfed wasps at 24°C	"	$p = 0.352$ NS
Unfed wasps at 27°C	"	$p = 0.004$ +
Unfed wasps at 30°C	"	$p = 0.342$ NS
Unfed wasps at 33°C	"	$p = 0.218$ NS

*The four temperature means were compared by Student-Newman-Keuls and Duncan's Multiple Ranges Test. Means that are not connected by a line are significantly different at the 5% level.

+ indicates the two means were significantly different at the 5% level.

of females regardless of species of host. The honey solution allows G. parkeri females to lay more eggs and live longer than unfed wasps. It is not known whether the increased number of females in the fed conditions is the result of subsequent formation of ovarian eggs after the first oviposition. Wasps reared on the two species of host differed significantly at 27, 30, 33°C in the fed condition and at 27°C in the unfed condition. In all cases where a significant difference occured, O. fasciatus reared wasps produced more females. This suggests feeding may slightly increase the difference between females reared on the two species of bugs.

Total Number of Males

The total number of males produced per female is given in Table 8. As mentioned in Part I, scelionid sex-ratios suggest males make up a smaller proportion of the total population than females. The biology of G. parkeri indicates males are important for a short period of time, and only a relatively few males are needed to fertilize large numbers of females. Therefore, it is not surprising the number of males is substantially less than the number of females. The values in Table 8 range from 23 to 26% of the total number of progeny for fed conditions and 9 to 15% for unfed conditions.

Main Effects. Table 9 reveals temperature and feeding have significant effects on total number of males. The number of males was not significantly affected by species of host ($p = .076$), unlike the total number of females (Table 6). However, since the probability is only slightly above the 5% level, it is possible a larger sample

TABLE 8. Total number of males

No. of Replicates N	Temperature °C	Mean	95% Confidence Interval for Mean	Standard Error
		Fed *G. parkeri* reared on *L. kalmii*		
22	24	28.6	23.5-34.8	1.0988
24	27	29.2	25.7-33.1	1.0627
23	30	27.4	22.6-33.3	1.0982
28	33	10.0	8.0-12.3	1.1105
		Unfed *G. parkeri* reared on *L. kalmii*		
17	24	6.3	4.8-8.4	1.1421
19	27	7.5	6.0-9.4	1.1148
29	30	5.5	4.6-6.6	1.0940
25	33	3.4	2.7-4.4	1.1275
		Fed *G. parkeri* reared on *O. fasciatus*		
25	24	26.0	21.4-31.6	1.0995
20	27	31.7	23.8-42.2	1.1471
21	30	26.6	20.7-34.3	1.1282
28	33	11.8	10.1-13.7	1.0760
		Unfed *G. parkeri* reared on *O. fasciatus*		
21	24	5.4	4.0-7.1	1.1439
16	27	9.3	7.5-11.6	1.1099
20	30	6.5	5.6-7.7	1.0797
24	33	4.8	3.6-6.6	1.1604

TABLE 9. Three-way ANOVA for total number of males*

	Sum of Squares	DF	Mean Square	FS	Significance of FS
Source of Variation					
Temp	7.894	3	2.631	53.024	0.0**
Feeding	29.600	1	29.600	596.485	0.0
Species	0.157	1	0.157	3.173	0.076 NS
Two-Way Interactions					
Temp x Species	0.318	3	0.106	2.133	0.096 NS
Temp x Feeding	0.976	3	0.325	6.555	0.0
Species x Feeding	0.056	1	0.056	1.134	0.288 NS
Three-Way Interactions					
Temp x Species x Feeding	0.045	3	0.015	0.302	0.824 NS
Explained	39.415	15	2.628	52.952	
Residual	17.219	347	0.050		

*ANOVA tables test data in the logarithmic scale.

**Any significance of FS written as 0.0 means the probability is less than 0.001.

size would reveal a significant difference. The values in Table 8 indicate unfed G. parkeri reared on O. fasciatus produced higher total numbers of males at 27, 30 and 33°C. In the fed condition, the upper limits of the confidence intervals are greater for G. parkeri reared on O. fasciatus at 27, 30 and 33°C.

Over the 24 to 33°C temperature range, there is a slight peak in the number of males for all test groups at 27°C, corresponding to the peak number of females usually found at the same temperature. Also, as was observed for the number of females, the number of males at 24, 47 and 30°C are similar. The smaller number of males occurs at 33°C and is approximately one-half the number at 30°C. The trends in total number of males due to temperature loosely follows the trends in number of females. The ability of a male to mate several times means the total number of males does not have to vary proportionally to the change in total number of females. The number of males produced by fed females ranges between three to five times the number by unfed females for wasps reared on either species of host. The least amount of difference between fed and unfed male production occurs at 33°C. There are only slight differences in male production between wasps reared on different milkweed bugs, as discussed previously. The largest difference was 2.6 males at 24°C for fed G. parkeri.

The a posteriori results for the number of males are given in Table 10. They indicate there is no significant difference between means at 24, 27 and 30°C for fed and unfed wasps reared on L. kalmii eggs and fed wasps reared on O. fasciatus eggs. Unfed O. fasciatus

TABLE 10. *A posteriori* tests for total number of males

Fixed Treatment	Test Treatment	Probability
Fed *G. parkeri* reared on *L. kalmii*	Four temperatures (24, 27, 30, and 33°C)	24 27 30 33*
Unfed *G. parkeri* reared on *L. kalmii*		24 27 30 33
Fed *G. parkeri* reared on *O. fasciatus*	"	24 27 30 33
Unfed *G. parkeri* reared on *O. fasciatus*	"	24 27 30 33
G. parkeri reared on *L. kalmii* at 24°C	Fed wasps versus unfed wasps	$p < .001$ +
G. parkeri reared on *L. kalmii* at 27°C	"	$p < .001$ +
G. parkeri reared on *L. kalmii* at 30°C	"	$p < .001$ +
G. parkeri reared on *L. kalmii* at 33°C	"	$p < .001$ +
G. parkeri reared on *O. fasciatus* at 24°C	"	$p < .001$ +
G. parkeri reared on *O. fasciatus* at 27°C	"	$p < .001$ +
G. parkeri reared on *O. fasciatus* at 30°C	"	$p < .001$ +
G. parkeri reared on *O. fasciatus* at 33°C	"	$p < .001$ +
Fed wasps at 24°C	*L. kalmii* reared wasps versus *O. fasciatus* reared wasps	$p = 0.480$ NS
Fed wasps at 27°C		$p = 0.566$ NS
Fed wasps at 30°C		$p = 0.851$ NS
Fed wasps at 33°C	"	$p = 0.194$ NS
Unfed wasps at 24°C	"	$p = 0.399$ NS
Unfed wasps at 27°C	"	$p = 0.160$ NS
Unfed wasps at 30°C	"	$p = 0.173$ NS
Unfed wasps at 33°C	"	$p = 0.084$ NS

*The four temperature means were compared by Student-Newman-Keuls and Duncan's Multiple Ranges Test. Means that are not connected by a line are significantly different at the 5% level.

+ indicates the two means were significantly different at the 5% level.

reared wasps exhibit no significant difference between means at 27 and 30°C and between 24, 30 and 33°C. The number of males is significantly lower at 33°C than at the other temperatures, except for unfed O. fasciatus reared wasps. Therefore, the optimal temperature for male production ranges between 24 to 30°C. Fed wasps, for all combinations of temperature and host rearing conditions, always had greater number of males than unfed wasps. There were no significant differences between wasps reared on different species of host. Of the three main effects, species of host has the least effect on the number of males as well as the number of females.

Interactions. The only significant interaction for the number of males is between temperature and feeding ($p < .001$) (Table 9). This indicates the number of males produced at a specific temperature is dependent on the feeding condition. The two-way table for temperature and feeding in Appendix 4 reveals the values for fed groups are all greater than the values for unfed groups. Interaction components, calculated for each value in the two-way table, exhibit an alternation in sign between values at consecutive temperatures. Therefore, the significance of the interaction is probably due to relative changes in means between the two variables. The value at 27°C in the unfed column is separated from the values at 30 and 24°C by a higher magnitude than the values in the fed column. The greatest change in the fed column is between 30 and 33°C, and in the unfed, between 27°C and 24°C.

Feeding moderates the degree of change in the number of males over 24 to 30°C, just as it moderates adult longevity over 27 to 30°C. The main effects of temperature and feeding, however, exhibit greater change in the variates than this interaction. The interaction does have a greater effect on the data than the main effect of species of host.

Total Number of Progeny (Males Plus Females)

The total number of progeny produced per female is given in Table 11. The total number of offspring is often measured for insects because it measures overall reproductive capacity, disregarding the sex of the offspring. Many authors consider the optimal conditions for parasitism as those where the greatest number of offspring are recorded. Total fecundity does not, however, reveal temporal patterns in progeny production. It is possible that the highest fecundity may occur at a different temperature than the highest initial rate. This will be discussed in more detail in a later section of this paper.

Another reason for analyzing the total number of progeny is to determine how patterns in the total numbers are affected by the majority and minority segments of the population (females and males, respectively).

Main Effects. Table 12 reveals that temperature, feeding and species of host have significant effects on the total number of progeny. A peak number of offspring occurs at 27°C for all test groups except fed wasps reared on L. kalmii eggs. This follows the

TABLE 11. Total number of progeny

No. of Replicates N	Temperature °C	Mean	95% Confidence Interval for Mean	Standard Error
		Fed *G. parkeri* reared on *L. kalmii*		
22	24	142.8	128.4-158.7	1.0522
24	27	137.8	131.1-144.9	1.0245
23	30	119.3	105.8-134.6	1.0597
24	33	56.2	48.1-65.7	1.0792
		Unfed *G. parkeri* reared on *L. kalmii*		
17	24	55.4	48.6-63.1	1.0637
19	27	66.6	56.2-79.0	1.0844
29	30	46.7	40.2-54.2	1.0755
28	33	28.0	23.5-33.5	1.0894
		Fed *G. parkeri* reared on *O. fasciatus*		
25	24	147.6	133.5-163.1	1.0498
20	27	162.0	143.4-183.0	1.0600
21	30	137.7	120.3-157.7	1.0671
28	33	73.5	63.9-84.5	1.0708
		Unfed *G. parkeri* reared on *O. fasciatus*		
21	24	58.8	50.3-68.7	1.0775
16	27	82.0	73.1-91.9	1.0551
20	30	53.0	43.0-65.4	1.1051
25	33	33.0	28.4-38.3	1.0755

TABLE 12. Three-way ANOVA for total number of progeny*

	Sum of Squares	DF	Mean Square	FS	Significance of FS
Source of Variation					
Temp	7.885	3	2.628	128.831	0.0**
Feeding	11.796	1	11.796	578.148	0.0
Species	0.381	1	0.381	18.682	0.0
Two-Way Interactions					
Temp x Species	0.073	3	0.024	1.185	0.315 NS
Temp x Feeding	0.189	3	0.063	3.081	0.028 NS
Species x Feeding	0.002	1	0.002	0.074	0.785 NS
Three-Way Interaction					
Temp x Species x Feeding	0.016	3	0.005	0.256	0.857 NS
Explained	20.672	15	1.378	67.548	
Residual	7.080	347	0.020		

*ANOVA tables test data in the logarithmic scale.

**Any significance of FS written as 0.0 means the probability is less than 0.001.

same pattern as noted for the total number of females. In the number of males, fed wasps reared on L. kalmii eggs always produced less males at 24°C than at 27°C. Fed wasps produce between two and two and one-half the total number of progeny in the unfed condition. This was also noted for both males and females. Comparing wasps reared on different species of host reveals O. fasciatus reared G. parkeri always produce greater number of offspring than wasps reared on L. kalmii. These trends closely resemble those seen in males and females, with the magnitude of difference being more like that noted for the total number of females.

A posteriori results in Table 13 reveal overall progeny production for fed wasps reared on either species does not significantly differ between means at 24, 27 and 30°C. The peak number of progeny at 27°C is only significantly separated from means at other temperatures for unfed G. parkeri females reared from O. fasciatus eggs. The large drop in number of progeny at 33°C is significantly lower than the means at all other temperatures for all other test groups. As was indicated for the number of males and females, 33°C appears to be at the upper end of G. parkeri temperature tolerance. The optimal temperatures for total progeny production ranged between 24 and 30°C, similar to that noted for both male and female production.

Feeding has the greatest significant effect on the total number of progeny, just as it did on the number of males and females. Fed wasps reared from either species of host and at all temperatures have more offspring than unfed wasps. Wasps reared on O. fasciatus produced a significantly greater number of progeny than those reared

TABLE 13. *A posteriori* tests for total number of progeny

Fixed Treatment	Test Treatment	Probability
Fed *G. parkeri* reared on *L. kalmii*	Four temperatures (24, 27, 30, and 33°C)	24 27 30 33*
Unfed *G. parkeri* reared on *L. kalmii*	"	24 27 30 33
Fed *G. parkeri* reared on *O. fasciatus*	"	24 27 30 33
Unfed *G. parkeri* reared on *O. fasciatus*	"	24 27 30 33
G. parkeri reared on *L. kalmii* at 24°C	Fed wasps versus unfed wasps	$p < .001$ +
G. parkeri reared on *L. kalmii* at 27°C		$p < .001$ +
G. parkeri reared on *L. kalmii* at 30°C	"	$p < .001$ +
G. parkeri reared on *L. kalmii* at 33°C	"	$p < .001$ +
G. parkeri reared on *O. fasciatus* at 24°C	"	$p < .001$ +
G. parkeri reared on *O. fasciatus* at 27°C	"	$p < .001$ +
G. parkeri reared on *O. fasciatus* at 30°C	"	$p < .001$ +
G. parkeri reared on *O. fasciatus* at 33°C	"	$p < .001$ +
Fed wasps at 24°C	*L. kalmii* reared wasps versus *O. fasciatus* reared wasps	$p = 0.641$ NS
Fed wasps at 27°C		$p = 0.010$ +
Fed wasps at 30°C		$p = 0.106$ NS
Fed wasps at 33°C	"	$p = 0.011$ +
Unfed wasps at 24°C	"	$p = 0.554$ NS
Unfed wasps at 27°C	"	$p = 0.049$ +
Unfed wasps at 30°C	"	$p = 0.298$ NS
Unfed wasps at 33°C	"	$p = 0.157$ NS

*The four temperature means were compared by Student-Newman-Keuls and Duncan's Multiple Ranges Test. Means that are not connected by a line are significantly different at the 5% level.

+ indicates the two means were significantly different at the 5% level.

on L. kalmii in the fed condition at 27 and 30°C and in the unfed condition at 27°C. This tendency was not significantly exhibited in the total number of males. For total number of offspring, the number produced by wasps reared on O. fasciatus exceeds that of those reared on L. kalmii at the temperature where the peak number of offspring was produced, 27°C.

Interactions. The only significant interaction for total number of progeny is between temperature and feeding (Table 12). This indicates that although there was no significant interaction in the majority segment of the population (females), the number of the minority segment (males) shifts the relationships among the means such that there is a significant interaction for the sum of these two groups.

The two-way table for temperature and feeding in Appendix 4 reveals fed values are always greater than unfed values, however, interaction components calculated for these values reveals there is an alternation in sign between values at consecutive temperatures. Values in the fed column exhibit less difference between the peak value at 27°C and adjacent temperatures than those in the unfed column. Feeding, therefore, increases the total number of progeny and buffers the change due to temperature over the 24 to 30°C temperature range. Fed wasps have an external energy and moisture source that allows them to oviposit in greater numbers. The magnitude of change in the data due to temperature and feeding is much greater than that of the interaction.

Discussion of Mean Total Values

Temperature has a significant effect on all the measured variates for longevity and offspring production. Adult longevity reaches a maximum at the lowest test temperature, 24°C. The least amount of difference between means at each temperature occurs between 27 and 30°C for longevity. The optimal temperatures for total offspring production differs from that for optimal longevity. The peak number of total males, females and total number usually occurs at 27°C.

Providing a dilute-honey solution to G. parkeri females appears to have the greatest effect on all variates. Longevity and fecundity are greatly increased under fed conditions. Fed wasps live approximately three to four times longer and produce approximately two times the total number of offspring. Feeding, however, not only increases the length of life and the number of offspring, but also tends to buffer the change due to temperature.

Species of host on which wasps were reared has a significant effect on all the variates except the number of males. It is possible the difference between G. parkeri reared on the two species of host would be significant with a larger sample size. G. parkeri females reared on O. fasciatus generally live longer and produce more offspring than those reared on L. kalmii. Although the difference is smatl, it is consistent.

Overall Rate Data

Although total values elucidate optimal conditions for longevity and fecundity and identify interactions between the main effects,

they reveal nothing about how long the wasps are reproductively active or about the daily change in female production. Table 14 presents intrinsic rates of increase (r_m), net reproductive rates (R_o), mean lengths of generations (T), finite rates of increase (λ), and doubling times. The standardized developmental times for each temperature are included in the table. The major emphasis is placed on the r_m values, since they combine daily survivorship and female production rates into one statistic.

The intrinsic rate of increase of a population is defined as the daily rate of increase a population of a stable-age distribution would have when growing in a constant environment where space is unlimited (Birch, 1948). Several general trends due to the main effects can be discerned for r_m values in Table 14. First, dilute honey-fed G. parkeri females have greater rates of increase than unfed wasps. However, the difference between rates for fed and unfed wasps is amazingly small when compared to the large difference in total fecundity and total longevity under the two treatments. The rapid turnover (reduced longevity) coupled with a relatively high initial rate (see Figures 1-8) in the unfed condition compensates for the lower total fecundity making the intrinsic rates of increase for fed and unfed wasps similar. The largest deviation between r_m values for fed and unfed conditions is a .047 unit difference at 33°C for wasps reared on O. fasciatus. The data suggests that an approximation of r_m values at different temperatures can be made by using wasps in the unfed condition. The close

TABLE 14. Rate data

F E D

Temperature:	24°C		27°C		30°C		33°C	
Host:	O.f.*	L.k.	O.f.	L.k.	O.f.	L.k.	O.f.	L.k.
r_m:	0.2204	0.2170	0.3365	0.3299	0.3606	0.3506	0.3918	0.3716
λ:	1.2455	1.2423	1.4000	1.3918	1.4342	1.4199	1.4796	1.4501
R_o:	123.3	114.7	125.2	110.2	109.3	94.2	65.3	48.7
T:	23.2	23.3	15.5	15.2	13.9	13.8	11.3	10.8
Developmental time:	18	18	12	12	11	11	9	9
Doubling time:	3.1	3.2	2.1	2.1	1.9	2.0	1.8	1.9

U N F E D

Temperature:	24°C		27°C		30°C		33°C	
Host:	O.f.	L.k.	O.f.	L.k.	O.f.	L.k.	O.f.	L.k.
r_m:	0.2028	0.1994	0.3249	0.3107	0.3285	0.3171	0.3448	0.3356
λ:	1.2248	1.2207	1.3839	1.3644	1.3889	1.3731	1.4117	1.3988
R_o:	53.6	49.7	71.3	55.9	48.6	42.6	28.9	26.2
T:	19.8	19.7	13.3	13.1	11.9	11.9	9.8	9.8
Developmental time:	18	18	12	12	11	11	9	9
Doubling time:	3.4	3.5	2.1	2.2	2.1	2.2	2.0	2.1

*O.f. = G. parkeri reared on O. fasciatus; L.k. = G. parkeri reared on L. kalmii.

r_m = ♀/♀/day

λ = ♀/♀/day; $\text{antilog}_e r_m = \lambda$.

R_o = ♀/♀; $\Sigma l_x m_x = R_o$.

T = days; $T = \dfrac{\log_e R_o}{r_m}$.

Doubling time = days; d.t. $= \dfrac{\log_e 2}{r_m}$.

correspondence of the intrinsic rates of increase under all the test conditions indicates an inherent tendency for a rate between 0.2 and 0.4. It also suggests r_m values have a high degree of repeatability for G. parkeri.

Secondly, as temperature increases, the r_m values increase over the 24 to 33°C range. The increase is not in a linear fashion. The largest increase in r_m values between consecutive temperatures occurs between 24 and 27°C. The mean total values for total progeny and number of females at the two temperatures are not significantly different in most cases, however, rate data suggests the rate of progeny production does differ between the two temperatures. The least amount of change occurs between 27 and 30°C and is less in the unfed condition than in the fed. This supports the conclusion that these two temperatures have similar effects on G. parkeri reproduction. The difference between 30 and 33°C is greater than that between 27 and 30°C, but is less than that between 24 and 27°C. The rate data tends to indicate the middle temperatures are separated from the extremes. Since it has been noted that 33°C is probably near the upper end of temperature tolerance for G. parkeri females, it can also be suggested that the rate at 33°C is close to the maximum rate the species will reach. Although the overall progeny production at 24°C is high, the intrinsic rate of progeny production is low. This indicates the daily production is probably lower and the length of time spent ovipositing is longer. The higher intrinsic rates, however, do not indicate optimal conditions. As Birch (1948) pointed out, increasing values of r_m for different test conditions does not mean the species will be

more successful under those conditions. It is assumed evolution has acted on the intrinsic rate of increase such that the values are large enough for the parasites to disperse and have a high probability of finding and successfully parasitizing a segment of the host population, yet small enough that the parasites do not drastically reduce the numbers of host.

The third trend noted for the intrinsic rates of increase is that O. fasciatus reared wasps have consistently higher rates than L. kalmii reared wasps. Although there was not always a significant difference between wasps reared on either species of host for mean total values, Wilcoxon's Signed Ranks Test (Sokal and Rohlf, 1969) reveals that there is a significant difference between r_m values at the 1% level of significance. This might suggest that G. parkeri is better adapted to a host-parasite complex with O. fasciatus. It is also possible the eggs of O. fasciatus produce a "fitter" G. parkeri due to the inherent differences between the eggs of the two bug species.

The finite rates of increase, which in this case measure the number of times the population will increase per day, exhibit the same patterns as noted above for the intrinsic rates.

The net reproductive rates (R_o) in Table 14 approximate the mean total values for female production, therefore, they follow the same patterns as already discussed. Net reproductive rates of fed wasps are more than two times those for unfed wasps and there is a tendency for a peak net reproductive rate at 27°C. G. parkeri reared on O. fasciatus have higher net reproductive rates than

those reared on L. kalmii. Mean generation times (T) in Table 14 decrease with an increase in temperature. The shorter generation times suggest a faster turnover. The generation times in the fed groups are approximately one-half the fed total mean longevities and are 3 to 4 days less than the total longevities in the unfed groups (see Table 3). This suggests that only a portion of the total life of G. parkeri females is spent in active parasitism. The net reproductive rate and mean generation time can be used to compare the different strategies at 24 and 27°C. Although the net reproductive rates are similar at the two temperatures, there is a substantial difference between generation times. G. parkeri females at 27°C are turning over at a faster rate than at 24°C. This is especially evident for fed G. parkeri.

In this study the r_m values as well as the finite rates of increase are very similar and in small units, making assessment of their biological importance difficult. Doubling time, which is the amount of time (in this case, days) it takes a population to double, gives easily understandable units for comparison of intrinsic rates of increase. Rounding doubling times to one-tenth of a day reveals the rates between 27, 30 and 33°C are separated by less than a day. The greatest difference between doubling times of consecutive temperatures occurs between 24 and 27°C. It takes wasps at 24°C one day longer to double their numbers than those at 27°C. Once again, it appears these two temperatures have more different effects on reproduction than total number of progeny would suggest. Rate data

suggests the optimal temperature for reproduction is between 27 and 30°C.

Graphic Analysis of Daily Rate Data

Values for daily mean survivorship (l_x) and daily mean female production (m_x) are plotted against age (x) for each test group in Figures 1-8. Each figure combines the curves for fed and unfed wasps reared on one species of host at one test temperature. They reveal several characteristics not easily deduced from mean total values or overall rate data. The daily rates elucidate patterns of egg laying, as well as, the relationship between survivorship and daily female production.

Wasp survival rates are almost 100% throughout the reproductive period, that is, adult mortality is extremely low during the period of parasitism. The mean total longevity gives no indication that survivorship is so high during active parasitism. The l_x and m_x curves also reveal that total morality of adults and the end of the reproductive period are closer temporally in the unfed condition than in the fed. For both feeding treatments there is a cessation of oviposition prior to death. Mean adult longevity, therefore, approximates the period of active parasitism only of unfed wasps. Hokyo (1966) noted two scelionids, Asolcus mitsukurii Ashmead and Telenomus nakagawai Watanabe, also exhibit a short nonreproductive period prior to death.

Daily female production curves (m_x) for G. parkeri females reveal that for all treatment conditions initial rates (day one through

day three) are the highest the ovipositing females ever reach. They decrease sharply after this period. One reason for the similarity of r_m values between different temperature, feeding and species of host is the similarity of these initial rates. Comparing graphs reveals the early daily female production rates parallel each other the first few days of oviposition for fed and unfed wasps reared on either species of host. This explains the relatively small difference in intrinsic rates for fed and unfed wasps. The graphs also clearly indicate females at 27 and 30°C had the highest initial rates for both feeding conditions and species of host. This supports previous conclusions that these two temperatures have similar effects on G. parkeri females, and they probably represent the optimal temperatures for expression of reproductive capacity. The initial fecundities at 24 and 33°C are similar even though they exhibit the greatest difference in intrinsic rates of increase. This is due to shortened developmental period and reduced adult longevity at the higher temperature, resulting in a faster turnover rate. Telenomus remus (Schwartz and Gerling, 1974), Telenomus nakagawai and Asolcus mitsukurii (Hokyo, et al, 1966) have also been observed to have high initial progeny production with an abrupt decline after several days. This suggests scelionids oviposit the majority of their eggs upon initial contact with suitable hosts.

The Percent Change in Males

The graphs discussed above deal with female survivorship and production rates and reveal nothing about the male segment of the

population. This study was not designed to study Gryon parkeri males, yet data collected on daily production rates suggested sex-ratios change with age of ovipositing females. Since this affects the experimental methods, it was briefly investigated. The pattern for the percentage of males to increase near the end of a parasite's life was especially noted for fed G. parkeri reared on either species of host. It probably was not as evident for unfed wasps since they lived for such a shorter period of time. Although it is normal for wasps to oviposit between one to four males per day, older females occasionally laid only males (as many as 15). Greater than normal all-male ovipositions by older females was most often observed at 27 and 30°C for fed wasps. Presumably, this is due to the higher initial fecundity rates coupled with relatively long life which may deplete the sperm storage and result in all-male ovipositions. Females that lay all-male eggs (unfertilized) due to age still resist mating.

Table 15 lists the percentage of males (males to total number of progeny) for several representative test groups in the fed condition. The table lists the daily change in percentage of males. It indicates that the percentage of males tends to rise with time. The increased percentage is not always due to an increase in absolute number of males. Often it was the result of the number of males remaining relatively constant while the number of females decreased. Schwartz and Gerling (1966) noted Telenomous remus sex-ratios (females to total number of offspring) are initially high

TABLE 15. Percentage of males in four representative test groups*

$$(\% = \frac{\text{daily mean no. males}}{\text{daily no. of males + females}} \times 100)$$

Temp.:	24°C		27°C		30°C		33°C	
Host:	O. fasciatus		L. kalmii		O. fasciatus		L. kalmii	
	(x)**	% males	(x)	% males	(x)	% males	(x)	% males
	18.5	7.4	12.5	9.5	11.5	9.8	9.5	11.4
	19.5	8.8	13.5	15.8	12.5	17.1	10.5	15.8
	20.5	17.8	14.5	18.8	13.5	15.3	11.5	19.5
	21.5	10.4	15.5	13.3	14.5	18.3	12.5	56.7
	22.5	11.7	16.5	22.9	15.5	18.1	13.5	32.1
	23.5	11.7	17.5	22.8	16.5	24.0	14.5	38.9
	24.5	12.9	18.5	30.1	17.5	25.6	15.5	55.2
	25.5	14.3	19.5	37.5	18.5	33.4	16.5	63.6
	26.5	23.4	20.5	47.9	19.5	42.9	17.5	80.0
	27.5	18.8	21.5	39.7	20.5	75.1	18.5	50.0
	28.5	21.0	22.5	90.9	21.5	80.7	19.5	100
	29.5	39.6	23.5	96.6	22.5	82.0	20.5	100
	30.5	42.4	24.5	100	23.5	93.0	21.5	no progeny
	31.5	71.2	25.5	100	24.5	94.3	22.5	no progeny
	32.5	70.5	26.5	100	25.5	94.3	23.5	25.0
	33.5	94.5	27.5	100	26.5	end	24.5	end
	34.5	80.0	28.5	end				
	35.5	33.3						
	36.5	75.0						
	37.5	100						
	38.5	no progeny***						
	39.5	no progeny						
	40.5	8.3						
	41.5	8.3						
	42.5	100						
	43.5	9.1						
	44.5	37.5						
	45.5	40.0						
	46.5	100						
	47.5	end						

*All groups are in the fed condition.

**x is the pivotal age.

***None of the test females laid any eggs on that day.

and decrease near the end of the oviposition period. This indicates shifts in the proportion of the sexes may be common for scelionids. If this is the case, it is probable daily sex-ratios may only rarely correspond to an overall sex-ratio.

FIGURE 1.

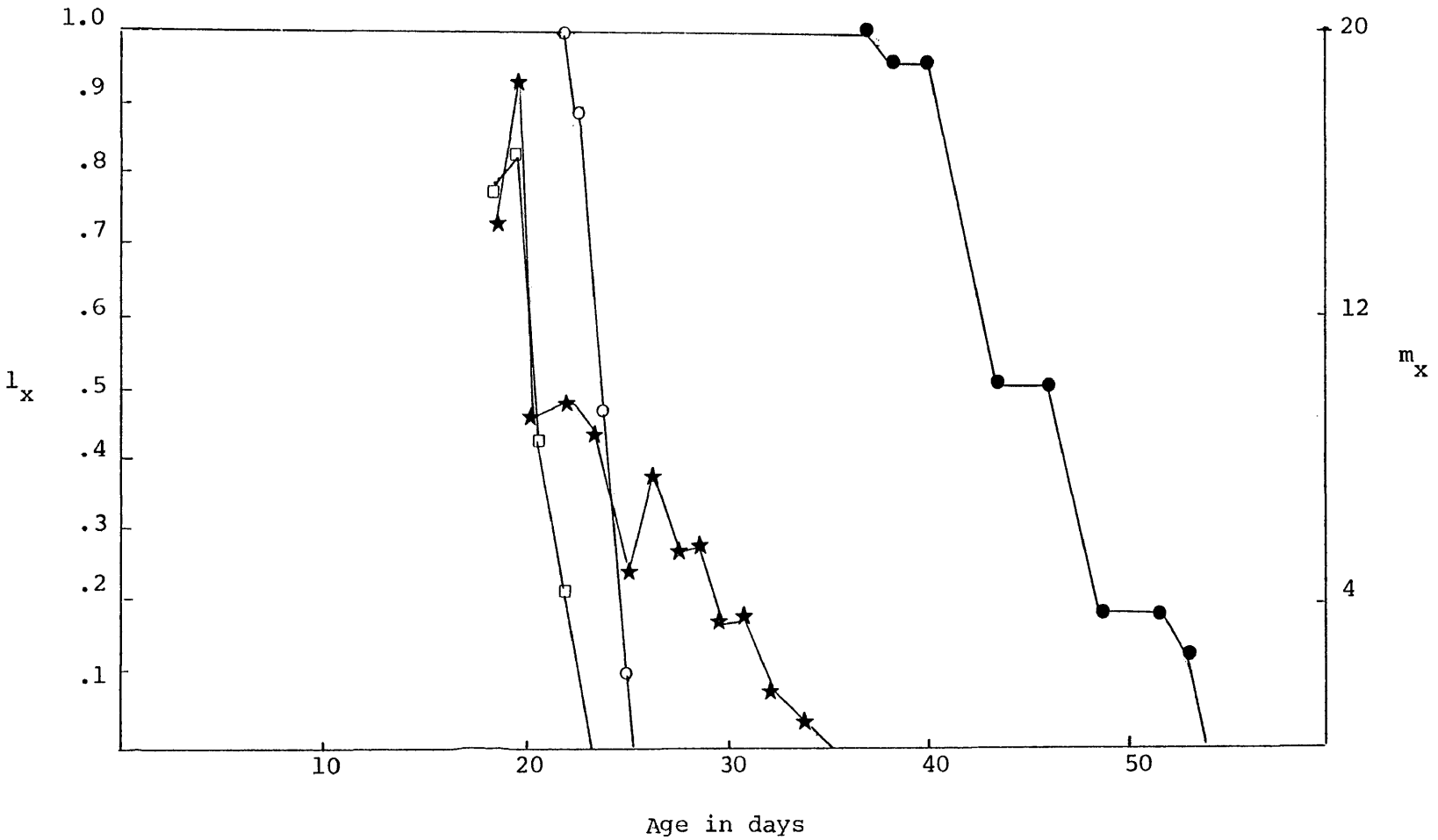


FIGURE 2.

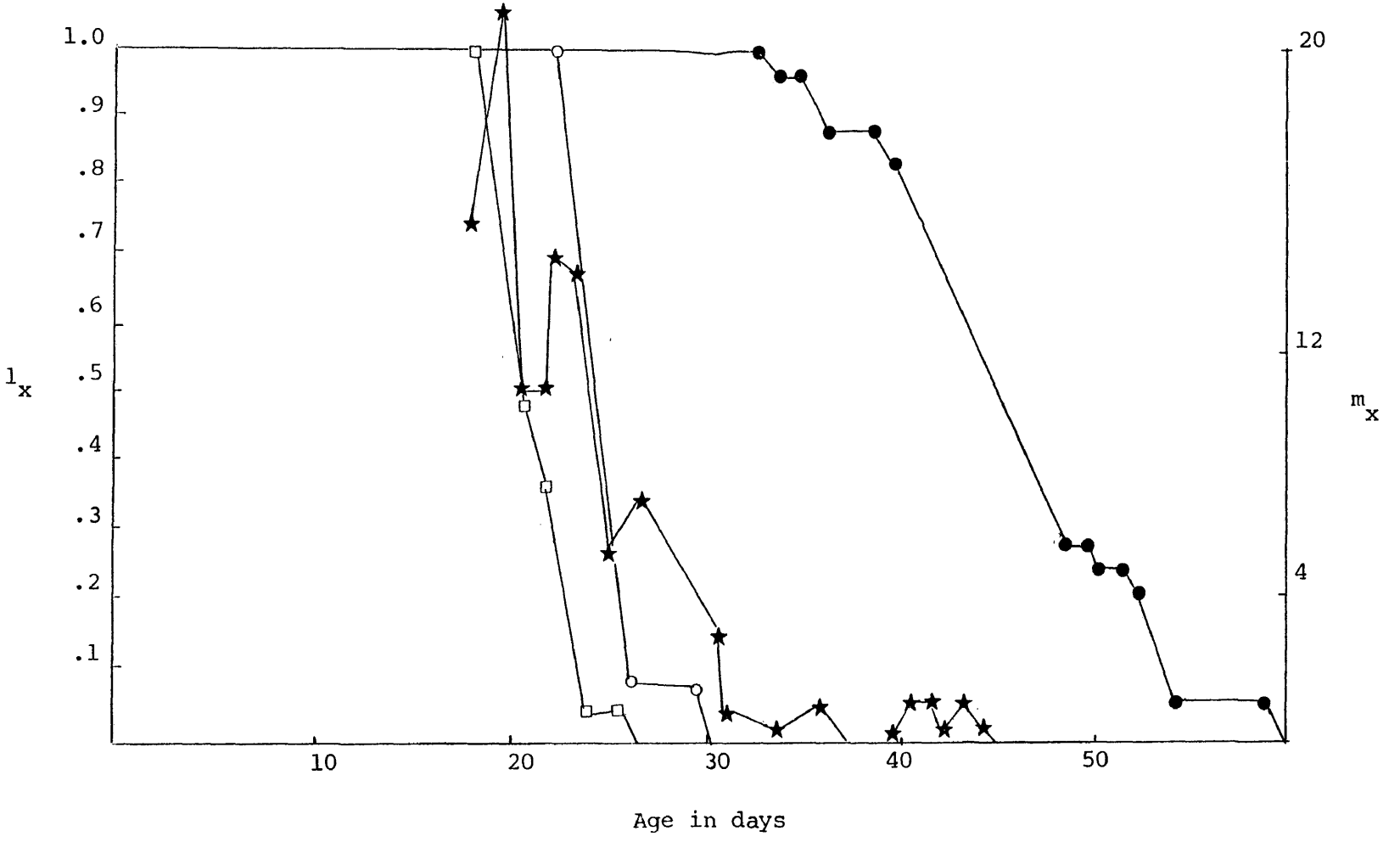


FIGURE 3.

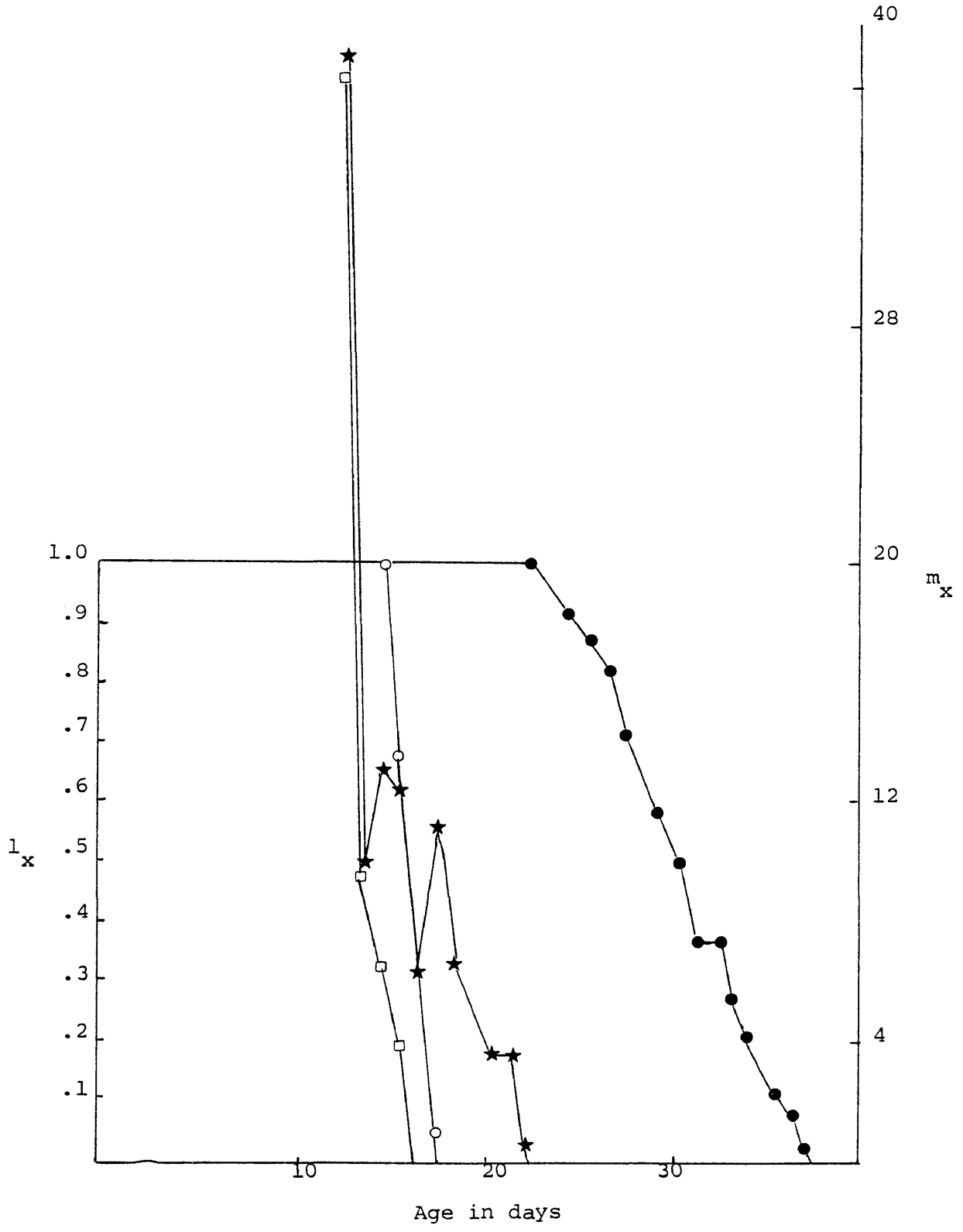


FIGURE 4.

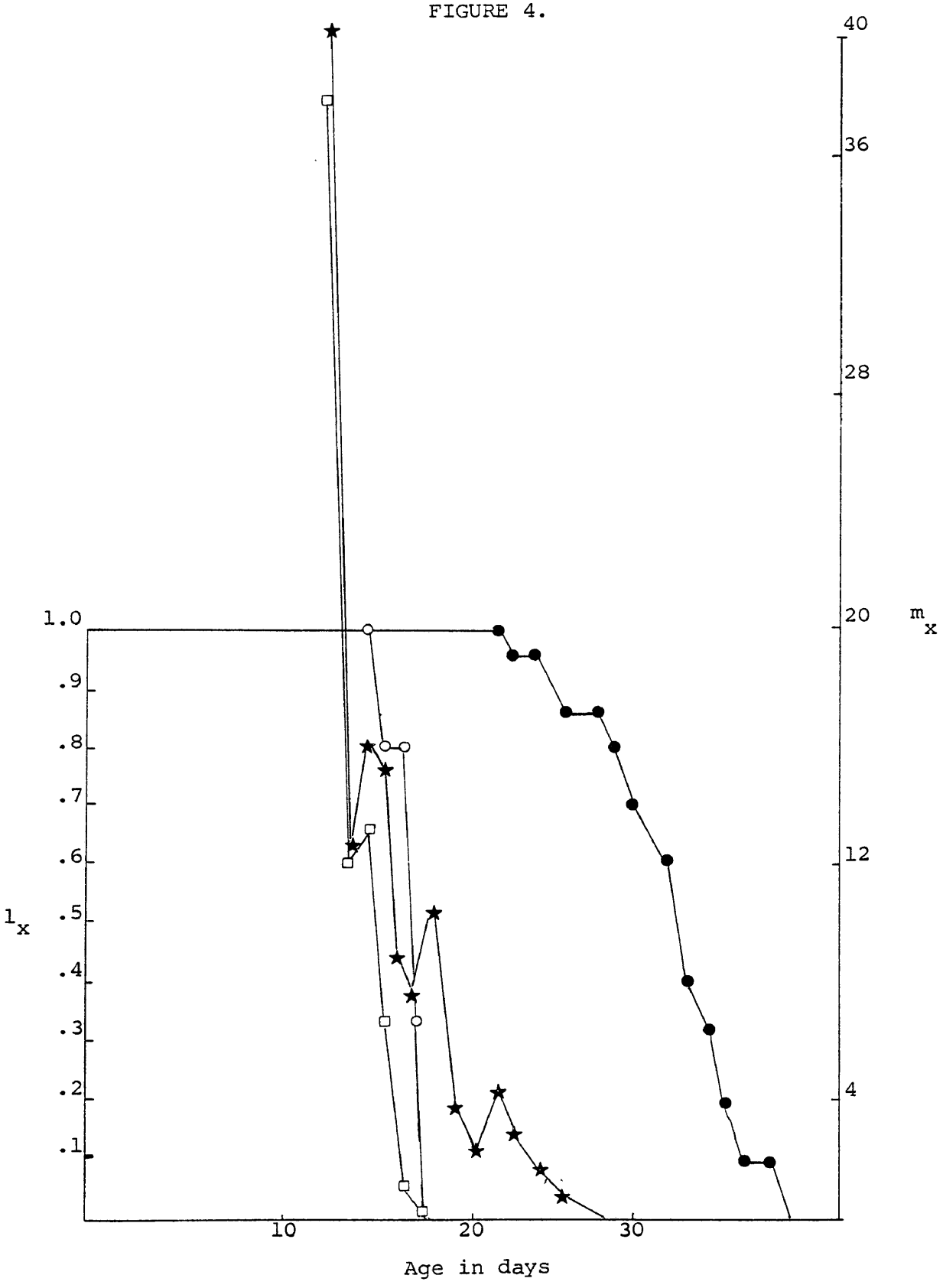


FIGURE 5.

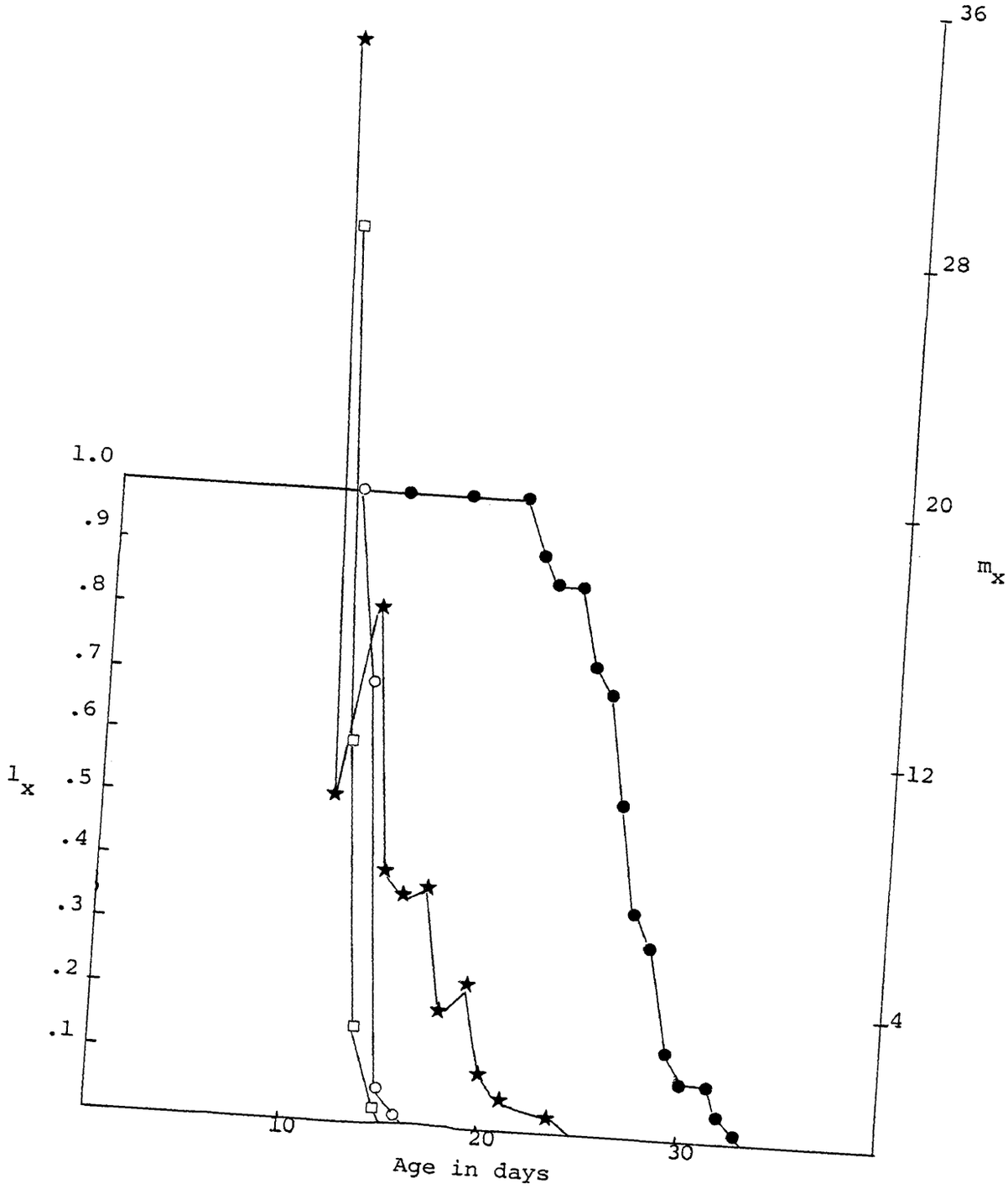


FIGURE 6.

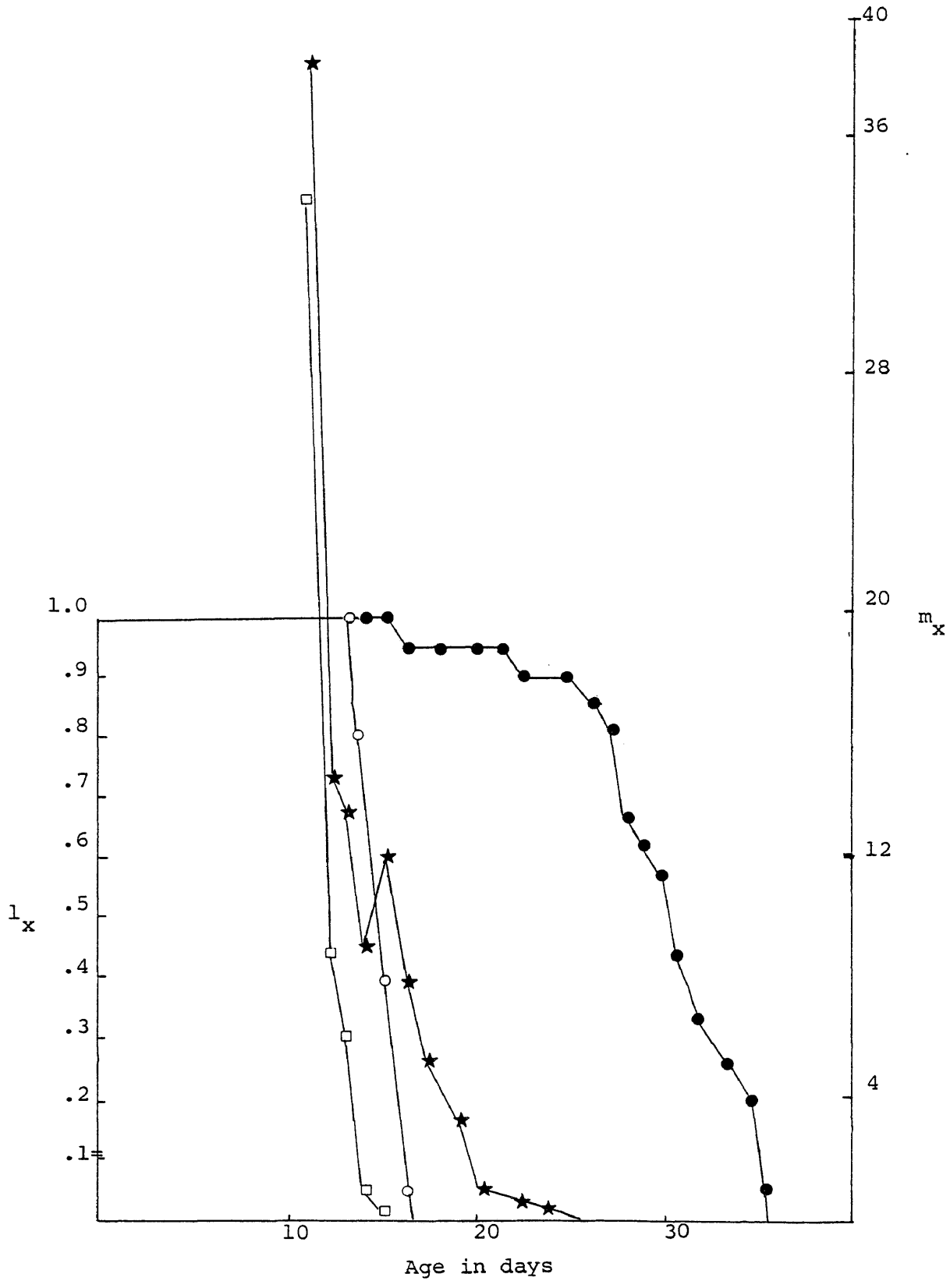


FIGURE 7.

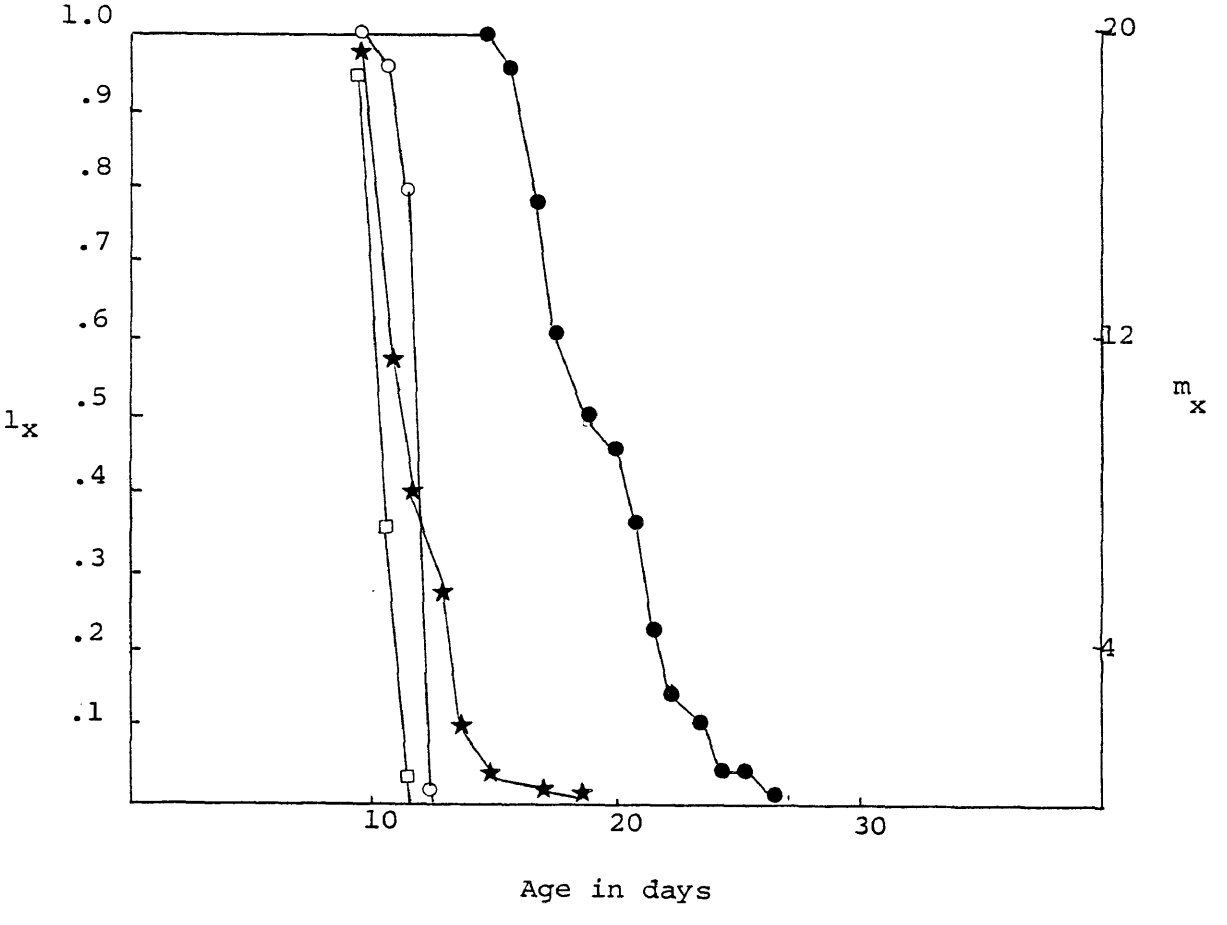
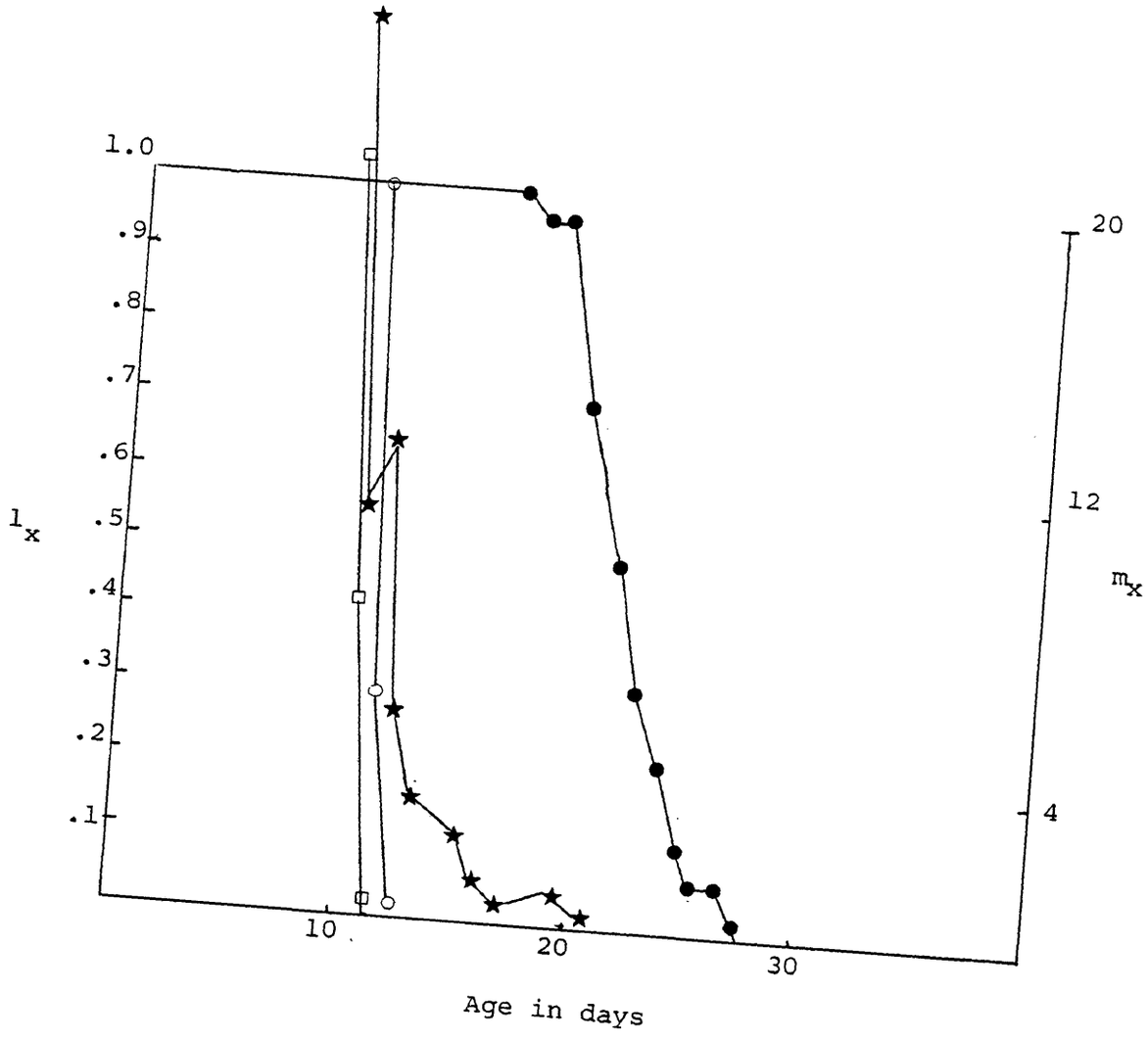


FIGURE 8.



CONCLUSIONS

Variation in temperature and feeding caused greater changes in longevity and fecundity than did species of host. Mean total values suggested there was a tendency for the highest number of offspring to be produced at 27°C, with the second highest number at 24°C. The optimal temperature for longevity was 24°C. Rate data and graphic analysis suggest the optimal temperature actually occurs between 27 and 30°C and that the entire lifespan of the adult female is not spent ovipositing eggs. Feeding had the greatest effect on longevity and fecundity. Surprisingly, the intrinsic rates of increase did not reflect large differences between fed and unfed conditions. Analysis of survival and female production curves revealed that initial mean female production rates of fed and unfed wasps parallel each other. The daily reproductive rates rapidly decline after the first days of oviposition in the fed condition. These high initial rates are probably an adaptation allowing the parasities to gain a rapid foothold in the host population. Feeding also causes a moderation in the change of fecundity and longevity due to temperature. Species of host caused the least amount of change in the variates. Although the difference between wasps reared on different species was usually very small, O. fasciatus reared wasps consistently lived longer, produced more offspring and had faster intrinsic rates of increase than L. kalmii reared wasps. The difference between wasps reared on either species

is probably small because both species of milkweed bug are often found side by side in the field. This study also indicates the fecundity for G. parkeri, provided an unlimited number of hosts, exceeds that recorded for other Gryon species. It may be the estimates in the literature for females is greatly underestimated.

EXPLANATION OF TWO-WAY TABLE IN APPENDICES

The two-way tables combine the means in the logarithmic scale from the three-way tables. The value in each cell is the average of the sum of the means for the particular two-factor combination over all levels of the third factor. The average is in the logarithmic scale since the data was tested for interactions in this scale. The two-way tables can be utilized in several ways. First, the values between columns can be compared. This would indicate whether there is an alternation in magnitude between treatments. Secondly, interaction components (interaction = $\overline{Y}$ - $\overline{Row}$ - $\overline{Column}$ + $\overline{\overline{Y}}$) can be determined for each cell. A change in sign of the interaction components between factors indicates a possible interaction. Thirdly, the difference between consecutive column values and adjacent row values can be calculated from the two-way table. This reveals the pattern of overall change in each two-way table.

It must be emphasized these tables are only helpful in analyzing the two-way interactions and not the main effects. Each table ignores any variation due to the third factor. This is especially evident for the Species x Feeding interaction which averages all the means for each species over the entire 24°C to 33°C temperature range.

APPENDIX 1. Two-way tables for adult longevity

Two-way table for Temp x Species, p = .005

Temp.	Host: *L. kalmii*	*O. fasciatus*
24°C	1.1278	1.1129
27°C	0.9852	1.0032
30°C	0.8896	0.9509
33°C	0.7620	0.8257

Two-way table for Temp x Feeding, p = .001

Temp.	Fed	Unfed
24°C	1.4454	0.7938
27°C	1.2781	0.7086
30°C	1.2434	0.5903
33°C	1.0816	0.5061

Two-way table for Species x Feeding, p = .349

Host	Fed	Unfed
L. kalmii	1.2431	0.6392
O. fasciatus	1.2820	0.6643

APPENDIX 2. Two-way tables for total number of females

Two-way table for Temp x Species, p = .396

Temp.	Host: *L. kalmii*	*O. fasciatus*
24°C	1.8679	1.9015
27°C	1.8841	1.9815
30°C	1.7851	1.8513
33°C	1.5216	1.6158

Two-way table for Temp x Feeding, p = .121

Temp.	Fed	Unfed
24°C	2.0670	1.7053
27°C	2.0642	1.7928
30°C	1.9962	1.6337
33°C	1.7227	1.4146

Two-way table for Species x Feeding, p = .695

Host	Fed	Unfed
L. kalmii	1.9255	1.6039
O. fasciatus	2.0018	1.6732

APPENDIX 3. Two-way tables for total number of males

Two-way table for Temp x Species, p = .096

Temp.	Host: *L. kalmii*	*O. fasciatus*
24°C	1.1280	1.0718
27°C	1.1699	1.2352
30°C	1.0854	1.1199
33°C	0.7681	0.8778

Two-way table for Temp x Feeding, p < .001

Temp.	Fed	Unfed
24°C	1.4345	0.7603
27°C	1.4812	0.9181
30°C	1.4320	0.7696
33°C	1.0348	0.6111

Two-way table for Species x Feeding, p = .288

Host	Fed	Unfed
L. kalmii	1.3395	0.7377
O. fasciatus	1.3531	0.7992

APPENDIX 4. Two-way table for total number of progeny

Two-way table for Temp x Species, p = .315

Temp.	Host: *L. kalmii*	*O. fasciatus*
24°C	1.9490	1.9691
27°C	2.0004	2.0615
30°C	1.8731	1.9318
33°C	1.5987	1.6921

Two-way table for Temp x Feeding, p = .028

Temp.	Fed	Unfed
24°C	2.1622	1.7576
27°C	2.1712	1.8648
30°C	2.1064	1.6920
33°C	1.8079	1.4828

Two-way table for Species x Feeding, p = .785

Host	Fed	Unfed
L. kalmii	2.0301	2.0959
O. fasciatus	1.6710	1.7313

LITERATURE CITED

Andre, F. 1934. Notes on the biology of Oncopeltus fasciatus (Dallas). Iowa State College J. Sci. 9:73-87.

Balduf, W. 1926. Telenomus cosmopeplae Gahan, an egg prasite of Cosmopepla bimaculata Thomas. J. Econ. Ent. 19:829-841.

Birch, L. 1948. The intrinsic rate of natural increase of an insect population. J. Anim. Ecol. 17:15-26.

Blatchley, W. 1926. Heteroptera or true bugs of Eastern North America. Indianapolis: Nature Publishing Co.

Bradoo, B. 1972. Life history and bionomics of Idris sp. (Scelionidae: Hymenoptera) egg parasite of Uloborus, a commensal on the web of social spider Stegodyphus sarasinurum Kargch. Zool. Anz. 188(1/2):43-52.

Buleza, V. 1971. Isbiratel'nost' v poudenii Samok nekotorykh raitseedov [Hym., Scelionidae] pri zarazhenii z hozyaev. Zool. Zh. 50(12):1885-1888.

Caldwell, R. A comparison of the dispersal strategies of two milkweed bugs, Oncopeltus fasciatus and Lygaeus kalmii. Ph.D. dissertation, University of Iowa, 1969.

Chatterji, S. and Rahalkar, G. 1958. Biological notes on Microphanurus sp., a scelionid egg parasite of Eurydema sp. (Pentatomidae: Heteroptera). Ind. J. Ent. 20:162-163.

Clausen, C. 1940. Entomophagous Insects. New York: McGraw-Hill.

Clausen, C. 1976. Phoresy among entomophagous insects. Ann. Rev. Ent. 21:343-368.

Cole, L. 1954. The population consequences of life history phenomena. Quart. Rev. Biol. 29(2):103-137.

Cumber, R. 1951. The introduction into New Zealand of Microphanurus basalis Woll. (Scelionidae: Hymenoptera), egg-parasite of the green vegetable bug, Nezara viridula (L.) (Pentatomidae). N. Z. J. Sci. Tech. B32(5):30-37.

Cumber, R. 1953. The establishment in New Zealand of Microphanurus basalis Woll. (Scelionidae: Hym.), egg-parasite of the green vegetable bug, Nezara viridula L. (Pentatomidae). N. Z. J. Sci. Tech. B34(4):267-269.

Cumber, R. 1964. The egg-parasite complex (Scelionidae: Hymenoptera) of shield bug (Pentatomidae, Acanthosomidae: Heteroptera) in New Zealand. N. Z. J. Sci. 7:536-554.

Dingle, H. 1965. The relation between age and flight activity in the milkweed bug, Oncopeltus. J. Exp. Biol. 42:269-283.

Dingle, H. 1966. Some factors affecting flight activity in individual milkweed bugs (Oncopeltus). J. Exp. Biol. 44:335-343.

Dingle, H. 1967. Regulation of cyclic reproductive and feeding activity in the milkweed bug Oncopeltus by temperature and photoperiod. Biol. Bull. 133:510-525.

Dingle, H. 1968A. The influence of environment and heredity on flight activity in the milkweed bug, Oncopeltus. J. Exp. Biol. 48:175-184.

Dingle, H. 1968B. Life history and population consequences of density, photoperiod, and temperature in a migrant insect, milkweed bug, Oncopeltus. Amer. Nat. 102:149-163.

Dingle, H. and Caldwell, R. 1971. Temperature and reproductive success in Oncopeltus fasciatus, O. unifasciatellus, Lygaeus kalmii, and L. turcicus. Ann. Ent. Soc. Am. 64(5):1171-1172.

Dreyfus and Breur. 1944. No sexo nos hymenopteros arrenotocos. Biologia, determinacao do sexo e cido cromossomico do microhimenoptero parasito Telenomus fariai Lima. Bol. Fac. Filosof. Cienc. Letras. Univ. Sao Paula, Bio. Geral. 5:1-103.

Eberhard, W. 1975. The ecology and behavior of a subsocial pentatomid bug and two scelionid wasps: Strategy and counterstrategy in a host and its parasites. Smith. Contrib. Zool. 205:1-38.

Egwuatu, R. and Taylor, T. 1977. Bionomics of Gryon gindus Nixon (Hymenoptera: Scelionidae), an egg parasite of Acanthomia tomentosicollis Stal (Hemiptera: Coreidae) in Nigeria. Appl. Ent. Zool. 12(1):76-78.

Essig, E. 1926. Insects of Western North America. New York: MacMillan.

Feir, D. 1974. Oncopeltus fasciatus: A research animal. An. Rev. Ent. 19:81-96.

Flanders, F. 1945. The role of the spermatophore in the mass propagation of Macrocentrus ancylivorus. J. Econ. Ent. 38:323-327.

Fouts, R. 1920. Some new parasites with remarks on the genus Platygaster (Hymenoptera). Proc. Ent. Soc. Wash. 22(4):61-72.

Gerling, D. 1972. The developmental biology of Telenomus remus Nixon (Hym., Scelionidae). Bull. Ent. Res. 61:385-388.

Gordh, G. and DeBach, P. 1978. Courtship behavior in the Aphytis linghanensis group, its potential usefulness in taxonomy, and a review of sexual behavior in the parasitic Hymenoptera (Chalcidoidea: Aphelinidae) Hilgardia 46(2):37-75.

Harrell, M. The biology of Gryon parkeri (Fouts). Problems dissertation, Department of Biology, College of William and Mary, 1975.

Hidaka, T. 1958. Biological investigations on Telenomus gifuensis Ashmead (Hym.: Scelionidae) an egg-parasite of Scotinophara lurida Burmeister (Hem: Pentatomidae) in Japan. Acta Hymen. 1:75-93.

Hokyo, N. and Kiritani, K. 1966. Oviposition behavior of two egg parasites, Asolcus mitsukurii Ashmead and Telenomus nakagawai Watanabe (Hym., Proctotrupoidea, Scelionidae). Entomophaga 11(2):191-201.

Hokyo, et al. 1966. Comparative biology of the two scelionid egg parasites of Nezara viridula L. (Hemiptera: Pentatomidae). Appl. Ent. Zool. 1(2):94-102.

Jones, E. 1937. The egg parasites of the cotton bollworm, Heliothis armigera Hubn. (Obsoleta Fabr.) in Southern Rhodesia. Rep. Mazoe Citrus. Exp. Stn. pp. 31-105.

Jubb, G. and Watson, T. 1971. Parasitization capabilities of the penta tomid egg parasite Telenomus utahensis (Hymenoptera: Scelionidae). Ann. Ent. Soc. Am. 64(2):452-456.

Kamal, M. 1938. The cotton green bug, Nezara viridula, L. and its important egg-parasite, Microphanurus megacephalus (Ashmead). Bull. Soc. Ent. Egypte 21:175-207.

Kenaga, E. 1944. Notes on Hadronotus parkeri Fouts (Hymenoptera: Scelionidae). Ent. News 55:173-174.

Kulshreshtha, et al. 1967. Mass multiplication of Telenomus sp. (Hymenoptera: Scelionidae) an egg parasite imported in India for the biological control of the castor semilooper. Achaea junata L. and some observations on its biology. Ind. J. Ent. 29(3):290-299.

Laing, J. 1938. Host-finding by insect parasites. II. The chance of Trichogramma evanescens finding its hosts. J. Exp. Biol. 15:281-358.

Lever, J. 1938. Host-finding by insect parasites. II. The chance of Trichogramma evanescens finding its hosts. J. Exp. Biol. 15:281-358.

Lima, DaCosta. 1928. Notas sobre a biologia do Telenomus fariai Lima, parasito dos ovos de Triatoma. Mem. Inst. Osw. Cruz. 21:201-209.

McColloch, J. and Yuasa, H. 1914. A parasite of the chinch bug. J. Econ. Ent. 7:219-227.

McColloch, J. and Yuasa, H. 1915. Further data on the life economy of the chinch bug egg parasite. J. Econ. Ent. 8:248-261.

Morrill, A. 1907. Description of a new species of Telenomus with observations on its habits and life history. Amer. Nat. 41: 417-430.

Nagel and Pimentel. 1964. The intrinsic rate of natural increase of the pteromalid parasite Nasonia vitripennis (Walk.) on its muscoid host Musca domestica L. Ecol. 45(3):658-660.

Narayanon, E., Subba, and Chacko. 1959. Asolcus euproctiscidis Mani (Scelionidae: Hymenoptera) an egg parasite of Euproctis lunata Walker. Proc. Ind. Acad. Sci. B49:74-81.

Noble, N. 1937. An egg parasite of the green vegetable bug. Agric. Gaz. N. S. W. 48:337-341.

Pemberton, C. 1933A. Notes on the biology of Telenomus nawai Ashm., an important parasite of the armyworm Spodoptera mauritia (Boisd.). Haw. Planters Rec. 37:168-174.

Pemberton, C. 1933B. Introduction to Hawaii of Malayan parasites (Scelionidae) of the Chinese grasshopper Oxya chinensis (Thun.) with life history notes. Proc. Haw. Ent. Soc. 8:253-264.

Pickford, R. 1964. Life history and behaviour of Scelio calopteni Riley (Hymenoptera: Scelionidae), a prasite of grasshopper eggs. Can. Ent. 96:1167-1172.

Rabinovich, J. 1971. Population dynamics of Telenomus fariai (Hymenoptera: Scelionidae), a parasite of Chagas' disease vectors. III. Preferences for and progeny from different age classes of host eggs. Ann. Ent. Soc. Am. 64:29-32.

Rothschild, G. 1970. Gryon flavipes (Ashmead) (Hymenoptera: Scelionidae), an egg-parasite of the rice earbug Leptocorisa oratorius (Fabricius) [Hem. Alydidae]. Entomophaga 15(1): 15-20.

Salt, G. 1935. Experimental studies in insect parasitism. III. Host selection. Proc. Roy. Soc. Ser. B, Biol. Sci. 117:413-435.

Salt, G. 1936. Experimental studies in insect parasitism. IV. The effect of superparasitism on populations of Trichogramma evanescens. J. Exp. Biol. 13(3):363-375.

Salt, G. 1937. Experimental studies in insect parasitism. V. The senses used by Trichogramma to distinguish between parasitized and unparasitized hosts. Proc. R. Soc. Land. 122:57-75.

Safavi, M. 1963. Le comportement sexuel chez les Asolcus nakagawa (Hym., Proctotrupoidea, Scelionidae). Rev. Pathol. Veget. Ent. Agr. France 42:127-134.

Safavi, M. 1968. Etude biologique et ecologique des hymenopteres parasites des oeufs des punaises des cereales. Entomophaga 13(5):381-495.

Sankaran, T. and Nagaraja, H. 1975. Observations on two sibling species of Gryon (Hymenoptera, Scelionidae) parasitic on Triatominae (Hemiptera) in India. Bull. Ent. Res. 65:215-219.

Sauer, D. and Feir, D. 1973. Studies on natural populations of Oncopeltus fasciatus (Dallas), the large milkweed bug. Am. Midland Nat. 90(1):13-37.

Schell, S. 1943. The biology of Hadronotus ajax Girault (Hymenoptera-Scelionidae) a parasite in the eggs of squash-bug (Anusa tristis DeGeer). Ann. Ent. Soc. Am. 36:625-635.

Schneider, F. 1940. Schadinsekten und ihre Bekampfung in ostindischen Gambirkulturen. Mitt. Schweiz. Ent. Ges. 18:77-207.

Schwartz, A. and Gerling, D. 1974. Adult biology of Telenomus remus (Hymenoptera: Scelionidae) under laboratory conditions. Entomophaga 19:482-492.

Simanton, W. and Andre, F. 1936. A biological study of Lygaeus kalmii Stal (Hemiptera: Lygaeidae). Bull. Brooklyn Ent. Soc. 31:99-107.

Slater, J. 1964. A catalogue of the Lygeadae of the world. Vol. 1, Univ. of Conn. Storrs, Conn.

Sokal and Rohlf. 1969. Biometry. W. H. Freeman and Co., San Francisco.

Taylor, T. 1975. Gryon gnidus, a scelionid egg-parasite of Acanthomia tomentosicollis (Hem.: Coreidae) in Nigeria. Entomophaga 20(2):129-134.

Voukassouvitch, P. 1925. Observations biologiques sur Trissolcus simoni parasite de la punaise du chou Eurydema (Pentatoma) ornatum. Feuill. Nat. 46:97-100.

Wilson, F. 1961. Adult reproductive behaviour in Asolcus basalis (Hymenoptera: Scelionidae). Aust. J. Zool. 9(5):737-751.

Wojcik, et al. 1977. Host range testing of Telenomus remus (Hym.: Scelionidae). Fla. Entomol. 59(2):195-198.

Zeledon, R. 1957. Sobre la biologia del Telenomus fariai Lima, 1927 (Hymenoptera: Scelionidae), parasito endofago de huevos de algunos Triatominae. Rev. Biol. Trop. 5(1):1-17.

Zomorrodi, M. 1959. La lutte biologique contre la punaise du ble Eurygaster integriceps Put. par Microphanurus semistriatus Nees., en Iran. Rev. Path. Veg. Ent. Agric. Fr. 38(3):167-174.

VITA

Richard Lee Lampman

Born in Hopewell, Virginia, 28 February, 1953. Graduated from Hopewell High School, 1971. B.S. in Biology with Honors at the College of William and Mary, 1975. Candidate for M.A. in Biology at the College of William and Mary, 1976-1980. Presently, candidate for Ph.D. in Entomology at the University of Illinois, Urbana-Champaign.