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**THE LABORATORY BIOLOGY AND REPRODUCTIVE STRATEGIES OF  
LEPTOPILINA BOULARDI (HYMENOPTERA: CYNIPIDAE)**

*City University of New York*

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THE LABORATORY BIOLOGY AND REPRODUCTIVE  
STRATEGIES OF LEPTOPILINA BOULARDI  
(HYMENOPTERA: CYNIPIDAE)

by

ARTHUR H. KOPELMAN

A dissertation submitted to the Graduate  
Faculty in Biology in partial fulfillment of  
the requirements for the degree of Doctor of  
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1982

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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## CHAPTER 1

### INTRODUCTION TO THE BIOLOGY OF LEPTOPILINA BOULARDI

#### Introduction

Detailed knowledge of the hymenopterous parasitoids of the Drosophilidae is shamefully lacking. Basden (1972) lists 47 species of known drosophilid-parasitoids and states that the list is incomplete. This study details the life-history tactics and certain other aspects of the biology of one such parasitoid species, the eucoilid wasp, Leptopilina bouvardi Barbotin et al (n.comb., Nordlander, 1980). L. bouvardi is an endoparasitoid of first and second instar larvae of Drosophila melanogaster, D. simulans, and D. ananassae in nature (Barbotin et al., 1979). Five other sibling species of the melanogaster sub-group have been successfully parasitized in the laboratory, including : D. mauritania, D. yakuba, D. erecta, D. orena, and D. teissiere (Barbotin et al, 1979; Carton, pers comm). D. arizonensis and D. mojavensis have also been successfully parasitized in the laboratory (Kopelman, unpublished).

## Systematics

The systematics of several genera of the Eucoilidae has recently been clarified by Nordlander (1980). L. boulandi was described by Barbotin et al (1979) as Cothonaspis boulandi but was later placed in the genus Leptopilina Forster, 1869, by Nordlander, and is synonymous with Charips mahensis, Kieffer, 1911 (Nordlander, 1980). The most intensively investigated Drosophila-parasitoid is the closely related species Leptopilina heterotoma Thompson, 1862 (n. comb. Nordlander, 1980), originally described as Pseudeucoila bochei Weld, 1944. Jenni (1951), Nostvik (1954) and a series of papers from the Department of Ecology, University of Leiden (Bakker et al, 1967; Bakker, 1968; Eijsackers and van Lenteren, 1970; Eijsackers and Bakker, 1971; van Lenteren, 1972; Bakker et al, 1972; van Lenteren, 1976; van Lenteren and Bakker, 1978) have described the biology of L. heterotoma.

## Distribution

L. boulandi has been found at host breeding sites in a number of locations in the southeastern U.S., from North Carolina to Maryland (Chabora et al, 1979); Guadeloupe, Brazil, Congo, Tunisia, France (Barbotin et al, 1979), and Italy, Yugoslavia, and South Africa (Nordlander, 1980). L. boulandi and L. heterotoma are sympatric in the Eastern U.S. and Mediterranean, but L. boulandi probably has a more tropical distribution than L. heterotoma (Nordlander, 1980).

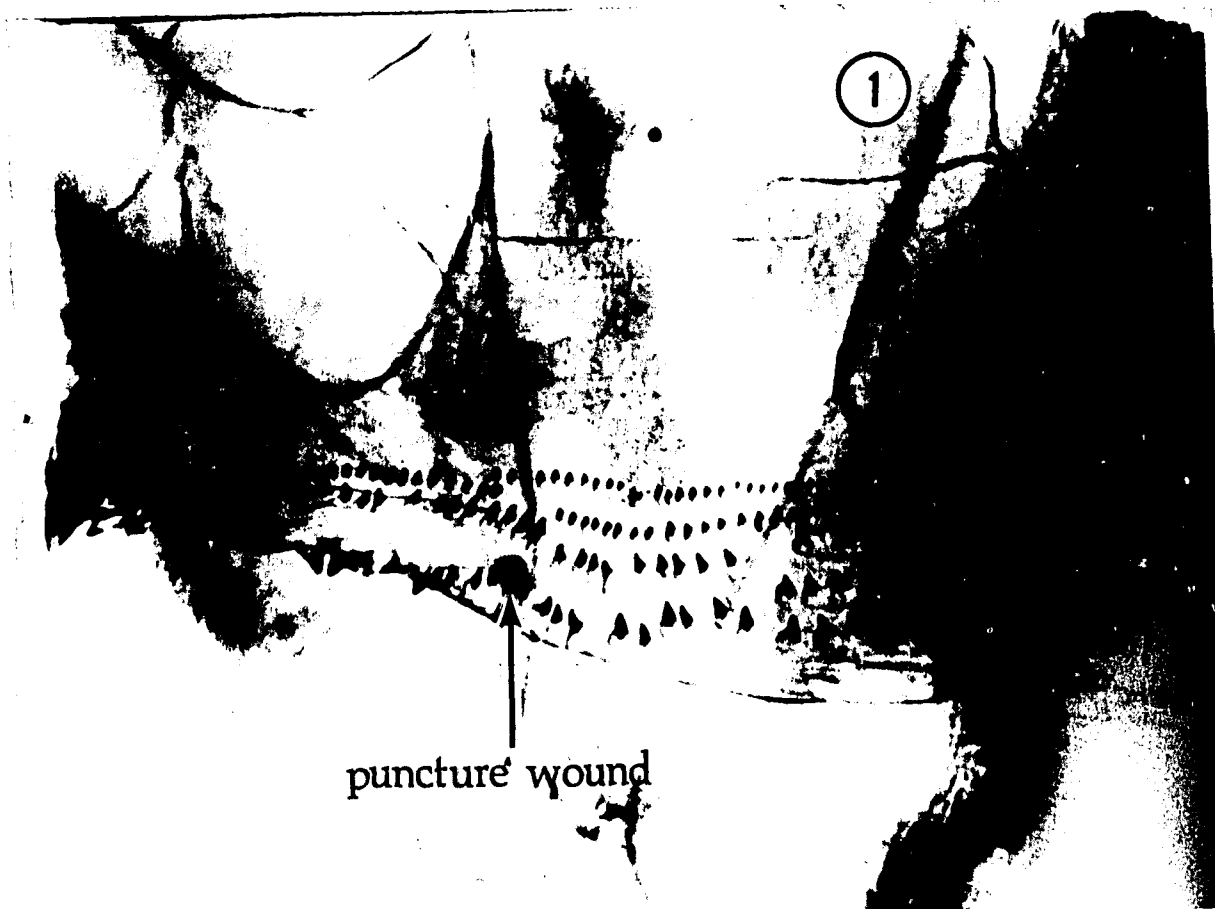
### Oviposition Behavior

Although L. bouhardi females can oviposit in several host species, D. melanogaster and D. simulans are preferred. Host larvae of both species can be successfully parasitized up to 48 hours after eclosion, but not to the same degree. Older hosts (48 hours), because of their thicker cuticle and higher activity, are not as easily parasitized as younger ones. Observation of the puparia of hosts exposed to wasps at 48 hours of age show successful puncture of the larval cuticle had occurred only at intersegmental membranes (see figure 1). Older hosts also have a more competent cellular defense system. Van Lenteren (1976) has described similar host-age discrimination in L. heterotoma.

Females are attracted to potential host patches by olfaction of ethanol produced by fermenting yeast (host food) (Carton, 1978). When a female finds a host patch she elicits certain patch specific behaviors. The female will walk over the patch, antennate, reduce her speed of movement (orthokinesis) and begin rhythmically pricking the host containing patch (the medium) with her ovipositor in a manner similar to that described for L. heterotoma by van Lenteren (1976). Location of the host is accomplished via the ovipositor. If a host is not encountered within 3-5 minutes the female will leave the patch. Following host location the cuticle is pierced and probing (sensu van Lenteren, 1976) occurs in which chemoreceptors on the

Figure 1.

Unstained melanized puncture wound in the intersegmental membrane of a host pupa that had been exposed to wasps at 48 hours after eclosion.



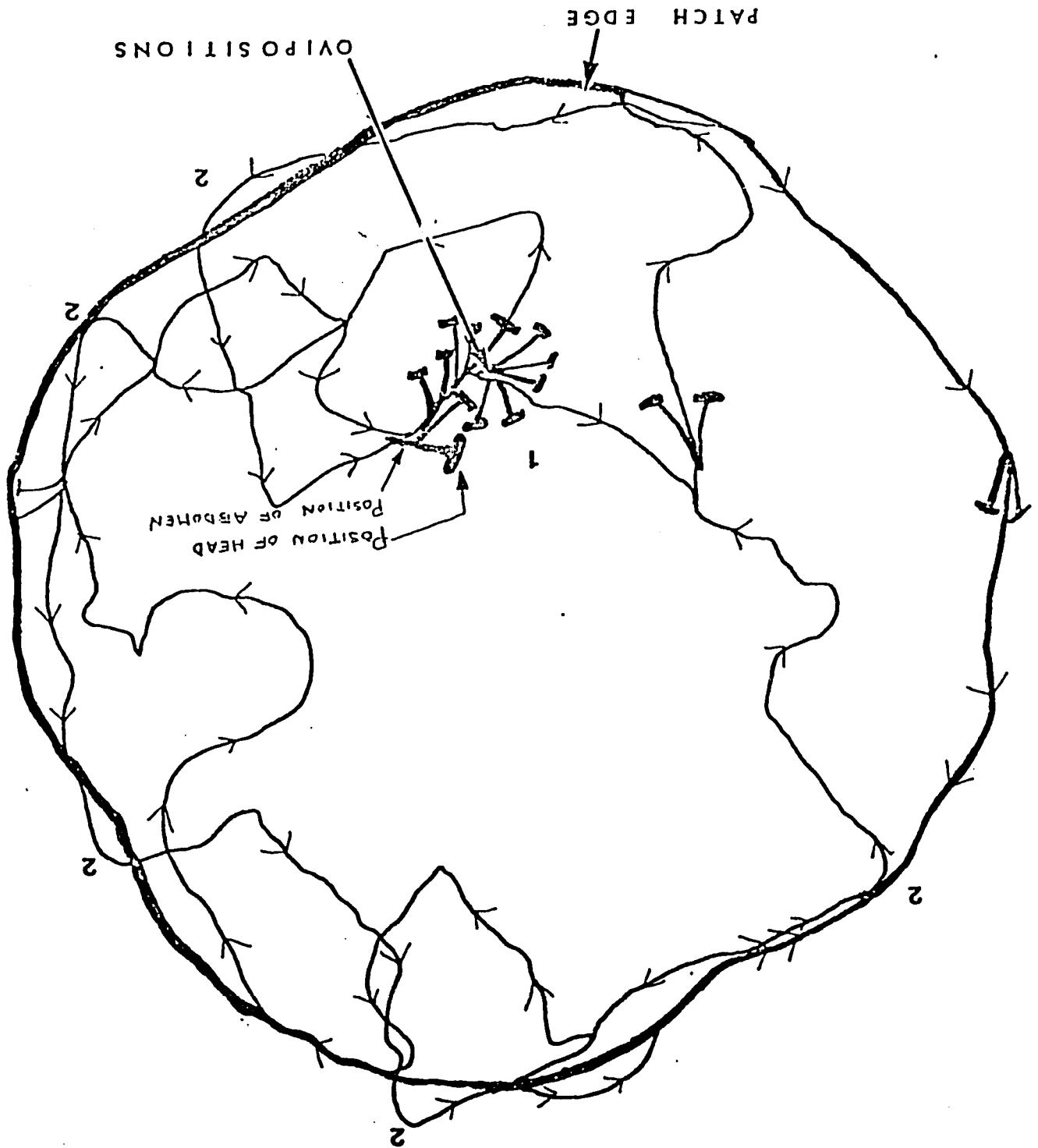


ovipositor tip assess host suitability. If the host is suitable, the ovipositor is extended fully and a single egg is deposited into the host's hemocoel. The entire process of probing and oviposition takes  $13.4 \pm 2.3$  seconds (mean  $\pm$  standard deviation,  $n=153$ ). Parasitoid development proceeds minimally over the ensuing 16-18 days at  $25 \pm 1$  °C, with males beginning to hatch 1-2 days prior to females.

Oviposition in an area of the host patch will cause an increase in turning (klinokinesis) in that area. Females also discriminate between patch and non-patch areas as evidenced by their klinotactic response at the edge of the host patch. Figure 2 is the track of a female while searching a 2.5 cm diameter patch composed of a thick suspension of activated yeast and 16 hosts. Klinokinesis and klinotaxis can be seen at points labelled 1 and 2, respectively.

A parasitized host will only produce one parasitoid. Therefore, selection for the avoidance of superparasitism must be strong. Like L. heterotoma (van Lenteren, 1976), L. boulardi can discriminate against hosts already parasitized by conspecifics. Of the 1000 host larvae dissected within 18 to 30 hours after exposure, only 6 had more than one parasitoid egg. If oviposition was random, with a mean of 1.0 egg per host, one should expect at least 264 multiply-parasitized hosts per 1000 observations. The avoidance of superparasitism can be overcome by placing the

Figure 2. Track of a female wasp searching a 2.5 cm diameter patch of thick yeast suspension containing 16 hosts. (The thick line along the perimeter indicates the patch edge; thick barred line are oviposition attempts. Points labelled 1 and 2 indicate klinokinetic and klinotactic responses, respectively.)



parasitoids under stressed conditions. Carton and Kitano (1979), Rouault (1979) and Carton (pers. comm.) show significant superparasitism in their experiments with L. boulandi but their experimental conditions confined many parasitoids with few hosts for long periods of time.

### Courtship

Mating can occur almost immediately upon hatching. Courtship in L. boulandi involves a specific and stereotyped sequence of reciprocal behavior patterns performed by both sexes prior to copulation. Courtship is easily observed under a low power stereomicroscope with individuals confined in shell vials (95 x 25 mm, or 35 x 10 mm), or plexiglass mating chambers. Behavioral patterns follow a repertoire similar to that described by van den Assem (1969) for L. heterotoma.

The existence of a sex pheromone in young females was tested via the bioassay technique of Weseloh (1976). 1-6 virgin females were placed for 1-3 hours in 35 x 10 mm shell vials previously cleaned with n-hexane, ethanol, and distilled water, inverted on a similarly cleaned glass slide. After removal of the females, conspecific males were placed singly into the vials and their behavior observed. Two sets of controls were also tested: both had been similarly cleaned, one kept empty and the other held 1-6 males with no previous female contact. Males exposed to vials which had contained females responded with

characteristic wing-vibrating behavior. Wing vibrations were not elicited in either sets of controls ( $n = 50$ ). Wing vibrations occur almost universally in courtship (Mathews, 1975) and appear to facilitate male orientation to a female's odor by pulling pheromone laden air over the male.

Upon encountering a female the male touches her with his antennae while continuing to vibrate his wings. A receptive female will usually remain motionless after being touched and allow the male to mount her in a head-tail orientation. Immediately after mounting, the male begins "vibrating and paddling" (sensu van den Assem, 1969). In this behavior, wing vibrations accompany antennal stroking or "paddling". The proximal parts of the male antennae stroke the distal parts of the female antennae with a characteristic (but unquantified) frequency. The female responds to the initiation of vibrating and paddling by changing her antennal posture to an erect parallel position.

After a brief period of vibrating and paddling, the female will signify her receptivity by simultaneously bringing her antennae to a forward position and opening her genital pocket. At this signal the male stops vibrating and paddling, takes a few steps backwards, bends his abdomen and extrudes his genitalia. During copulation, which last approximately 30 seconds, the female is motionless. A brief period of preening follows copulation.

## Female Reproductive Structures

The importance of female reproductive structure with respect to life history strategies is treated by Price (1973a, 1974a,b, 1975) in his discussions of the egg production and energy allocation strategies of parasitoids and ephemeral insects. He notes that unlike the situation in vertebrates where temporal shifts in energy allocation are an important component of the reproductive strategy, "we should expect ephemeral adults to be geared up structurally rather than physiologically for a particular reproductive strategy (Price, 1975a)". L. boulandi has both physiological and structural adaptations for its reproductive strategy. L. boulandi is proovigenic with a strain specific mean number of eggs available to females at hatching (Table 1). Each ovariole contains 5 mature eggs and each of the two ovaries contains 25-35 ovarioles. The reproductive structure in L. heterotoma females is similar where egg production capacity is 500-600 eggs (Chabora and Kopelman, unpublished).

Price (1974a, 1975) correlates adaptations in reproductive structure (number of ovarioles/ovary) with the stage of host attacked, the type of attack, and the probability of parasitoid survival in the Ichneumonidae and Tachinidae attacking various stages of the Swain Jack Sawfly. A negative correlation between the number of ovarioles and the age of host attacked was found for both

TABLE 1. Egg capacity for two strains of L. boulandi (mean  $\pm$  SE).

---

| Strain        | Mean Egg Capacity |
|---------------|-------------------|
| Hampton, 1975 | 349.3 $\pm$ 3.3   |
| Hampton, 1977 | 286.3 $\pm$ 2.0   |

groups. Evidence of different ovariole numbers in Eucoilid parasitoids of Drosophila is now being compiled. Dissections of a species of Gnaspis, also parasitoids of young D. melanogaster larvae, from the El Yunque rain forest in Puerto Rico show only one ovariole per ovary but the females are synovigenic, i.e., they continually produce eggs throughout life. Each of two ovaries are elongated and contain many hundreds of germinal cells at their distal end and only 1 or 2 mature eggs at their proximal end. This species is generally longer lived than L. boulandi or L. heterotoma and can reproduce successfully for more than 25 days at 20 °C (Chabora, unpublished). Their synovigenic nature represents a structural adaptation to an entirely different reproductive strategy than that of L. boulandi, even though both species utilize the same host species and stages. These preliminary observations indicate that the environment and its effect on the availability of hosts may be of prime importance in determining the reproductive strategy of these parasitoid species.



## CHAPTER 2

### REPRODUCTIVE STRATEGIES AND LIFE-HISTORY

#### TACTICS OF LEPTOPILINA BOULARDI

##### Experiment 1. The Effect of Host Species on the Life History Parameters of L. boulandi

#### Introduction

Cole (1954) in the introduction to his seminal paper, "The population consequences of life history phenomena", stated:

"If it is to survive, every species must possess reproductive capacities sufficient to replace the existing population by the time this population has disappeared. It is obvious that the ability of the ancestors of existing species to replace themselves has been sufficient to overcome all environmental exigencies which have been encountered and, therefore, that the physiological, morphological and behavioral adaptations that enable offspring to be produced and survive in sufficient numbers to insure the persistence of a species are of fundamental ecological interest."

Cole's axiomatic assumptions that (1) the reproductive potentials of a species are related to their survival requirements; (2) life history parameters affecting reproductive potential are subject to natural selection; and (3) that these features observed in species should be considered as adaptations, have led the way to an explosion of theoretical activity in the evolution of life-history tactics. However, investigational findings supporting this

theoretical structure have been limited. It is my intention to provide an important and substantial contribution to the data base of life-history theory. These data, based upon the life-history of Leptopilina boulandi in the laboratory, can be used to exemplify an adaptive and plastic life-history strategy in a species that has been exposed to a heterogeneous and unpredictable environment and thereby support Cole's theoretical contentions stated above.

In order to understand the population dynamics of a species, it is necessary to describe the ways in which the probabilities of dying and the rates of reproduction vary within the life span of the individuals of that species. These parameters are conveniently expressed in life tables and life and fertility tables, as age-specific survivorship,  $l(x)$ , defined as the probability of surviving from birth to age  $x$ , and age-specific fertility  $m(x)$ , defined as the mean number of female offspring produced in a unit time by a female of age  $x$  (Birch, 1948), both of which are essential in calculating the net reproductive rate ( $R_0$ ) and intrinsic rate of increase ( $r$ ) of a species under particular environmental conditions.

#### Life tables

Life tables are concise summaries of age-specific population characteristics derived from a cohort of individuals whose members start life together (Deevey, 1947). Southwood (1978) distinguishes two types of life

tables: age-specific (horizontal) life tables, based upon the fate of a real cohort; and time-specific (vertical) life tables based upon the fate of an imaginary cohort found by determining the age structure of sample of individuals at one point in time from a multistage population. This work details the former type.

For every interval of age  $(x)$  in a life table, the following is included: the number of deaths during that interval  $d(x)$ ; the number of survivors remaining  $l(x)$ ; the mortality rate  $q(x)$ ; the expectation of further life  $e(x)$ , and the age structure  $L(x)$ .

Although actuaries and statisticians have used life tables to analyze human populations since the 3rd century A.D. (Deevey, 1947), it was not until the 1920's and 1930's that Pearl and his colleagues began to experimentally analyze the duration of life in other animals (Pearl and Parker, 1921; Pearl, et al., 1927; Pearl and Miner, 1935; Pearl et al., 1941). Pearl and Miner (1935), in their review of the comparative mortality of lower organisms, asked for "more observational data, carefully and critically collected for different species of animals and plants, that will follow through the life-history from birth to death of each individual in a cohort of statistically respectable magnitude." Twelve years later, Deevey (1947) published his paper, "Life tables for natural populations," in which he reviewed, analyzed, and presented "a mass of information

bearing on the survival of animals in nature", based almost entirely on works published since Pearl and Miner's request. Deevey (1947) noted that the information he was to relate "has not heretofore been considered relevant by biometricians working with human populations, nor has it ever been considered in its context by ecologists." He therefore was the first to focus attention on the importance of comparative studies of the age distribution of mortality in natural populations, and the first to critically evaluate the ecological information available on that subject. His goal through that evaluation was to guide ecologists and others in the proper methods of gathering data for life tables. He argued that methods which employed direct observations, at frequent intervals, of the survivorship of a cohort with a definite initial number of members, is the preferred method. Deevey hoped to limit the diverse statistical foundations of life tables so that detailed comparisons between species could be made. In effect, He standardized the ecologists' approach to life tables, and his methodology (or Southwood's (1978) modifications of that methodology) has been employed in all subsequent works.

In one of the earliest studies conducted, I attempted to determine the life table parameters of L. boulandi when cohorts were exposed to two different host species, Drosophila simulans and D. melanogaster. Although this study was initially conducted in order to calculate these

parameters, it became the starting point for a study of the reproductive strategies and life-history tactics of this species.

#### Materials and Methods

Standard life table and age specific reproductive characteristics of female parasitoids were determined by exposure of vials of excess host larvae to individual pairs of parasitoids on a daily basis until the female died.

Cohorts of 50 females per host species were used. For each replicate in the cohort, the following procedures were followed. Six fertile 4-6 day old D. melanogaster or D. simulans females were introduced into 25 x 95 mm shell vials containing 8 ml of yeasted banana medium and allowed to oviposit for 24 hours. The flies were then transferred to a fresh vial, and the vial with the eggs was set aside for an additional 24 hours to allow the larvae to eclose. This procedure ensured that each replicate would be provided with an excess of hosts available for oviposition. On the third day, a droplet of honey and a male and female parasitoid were introduced, and the female was allowed to oviposit for 24 hours. This procedure was repeated daily and exposed vials were set aside for parasitoid development. Ovipositing flies were replaced every 4 to 5 days to assure a constant high density supply of viable eggs. Surviving adult flies emerged after 7-10 days and were cleared daily. Parasitoid progeny began to emerge 16-17 days after initial

exposure and were counted and sexed regularly until no further emergence was found.

The parasitoid stocks used in this experiment (Ha 75) were the descendants of females collected in late August 1975, in Hampton, Virginia. The stock of D. simulans were descendants of flies captured at the same locality and time, while the stock of D. melanogaster was one of the wild type (Oregon R) stocks from the Queens College Genetics Laboratory. All stock maintenance and experiments were conducted in an environmental chamber at  $25 \pm 1$  °C and 60% RH, with a 16L:8D photoperiod and a light intensity of 2000 lux. Life table procedures described by Southwood (1978) were employed.

## Results

### Adult survivorship distribution

Figures 3 and 5 represent the survivorship curves for the D. melanogaster reared and D. simulans reared cohorts, respectively. Both exhibit the "type 1, negatively skew rectangular" curve of Pearl (1928). The mean length of life for females in each cohort are,  $14.4 \pm 0.7$  and  $13.6 \pm 0.4$  days, for the D. melanogaster and D. simulans cohorts, respectively.

### The survivorship-fecundity distribution

The survivorship curves themselves are informative, but when considered in conjunction with daily fertility, a puzzling phenomenon can be observed: i.e., the cohorts

exhibit a markedly long period of post-reproductive survival (see figures 4 and 6 for the D. melanogaster and D. simulans cohorts, respectively, and figure 7 for both).

The fertility values are based upon the total number of female progeny produced during an oviposition period, and are not age-specific natality values (as used by Chabora, et al., 1979). The adult progeny of a single day's ovipositions can hatch from 17.5 to 27.5 days following oviposition. This variation in emergence is a function of the age of host attacked, host density, and genetic variability in developmental rate of the parasitoid and host. The effect of this variation was initially considered to introduce unwanted ambiguity to the analysis. However, since the life-history tactics of a species is truly a birth-death process and the fertility distribution is indeed dependant upon age-specific natality, then age-specific natality should be preferable and is used in later experiments.

Fertility distributions follow similar patterns in both cohorts, an early peak with a rapid subsequent drop leading to an extended post-reproductive period (8 days for the D. simulans cohort; 10 days for the D. melanogaster cohort). Also note the high peak in the D. melanogaster cohort (53.16) in comparison to that in the D. simulans cohort (35.90) (see tables 2 and 3).

The sex ratio of daily successful ovipositions are given in tables 2 and 3 for the D. melanogaster and D. simulans cohorts, respectively. Two facts are evident in these tables. First, that the ovipositions of fertilized and unfertilized eggs decline at differing rates resulting in a shift from female to male bias in the sex ratio. Second, that unfertilized eggs were oviposited for several days after the oviposition of fertilized eggs had ceased.

Tables 2 and 3 also present the life and fertility tables and life table parameters for both cohorts. Although generalized comparisons can be made between the two cohorts regarding these parameters, it is virtually impossible to get a statistical handle on them because of their highly derived nature. It therefore became necessary to reanalyze the data and present them in terms of variables that are direct measurements, statistically treatable and biologically meaningful. Therefore the following data was compiled for each female in a cohort so that mean values and standard errors could be determined and appropriate statistical tests could be applied.

- A) Length of life (LOL);
- B) Days of male production (DOMP);
- C) Days of female production (DOFP);
- D) Total male progeny (TM);
- E) Total female progeny (TF);
- F) Total progeny (TT);



G) Total post-reproductive period (PRP-t) ;

H) Post-reproductive period for female progeny (PRP-f).

Table 4 presents the means and standard errors for these variables in each cohort. Analyses of variance were performed comparing each of the eight reproductive variables and are given in table 52. No significant differences could be found between these cohorts for mean values of LOL, DOMP, DOFP, PRP-t, and PRP-f. Although the production schedules do not differ, the mean number of male, female, and total progeny do differ significantly. The cohort exposed to D. melanogaster larvae produced significantly more progeny than did the D. simulans reared one.

It should be noted that two types of statistical tests can be applied to the data, namely, an Analysis of Variance (ANOVA), or the non-parametric Wilcoxon Rank Sum test. The assumption of normality implicit in using ANOVA's does not hold for these data, and attempts at normalization via logarithmic transformations were not successful. Therefore, non-parametric tests were applied. Outcomes of the non-parametric analyses did not differ from those of the ANOVA's and are therefore not presented.

In later experiments, where either (1) large differences in sample size occurred, or (2) the results of the analyses differed, the Wilcoxon Rank Sum test is the test of choice and is presented, even though its power can not be determined.

TABLE 2. Life, fertility and daily sex ratio table for L. boulandi when presented with D. melanogaster hosts (Q.C. strain).

| x    | l(x) | m(x) | sex ratio | x     | l(x) | m(x) |
|------|------|------|-----------|-------|------|------|
| 17.5 | 1000 | 17.3 | 0.37      | 031.5 | 592  | 0.0  |
| 18.5 | 1000 | 53.1 | 0.33      | 032.5 | 490  | 0.0  |
| 19.5 | 1000 | 26.9 | 0.54      | 033.5 | 408  | 0.0  |
| 20.5 | 939  | 9.6  | 0.68      | 034.5 | 265  | 0.0  |
| 21.5 | 918  | 5.8  | 0.80      | 035.5 | 122  | 0.0  |
| 22.5 | 918  | 4.3  | 0.84      | 036.5 | 61   | 0.0  |
| 23.5 | 918  | 2.2  | 0.90      | 037.5 | 41   | 0.0  |
| 24.5 | 918  | 1.7  | 0.89      |       |      |      |
| 25.5 | 918  | 0.3  | 0.95      |       |      |      |
| 26.5 | 898  | 0.4  | 0.89      |       |      |      |
| 27.5 | 878  | 0.0  | 0.95      |       |      |      |
| 28.5 | 714  | 0.0  | 1.00      |       |      |      |
| 29.5 | 694  | 0.0  |           |       |      |      |
| 30.5 | 633  | 0.0  |           |       |      |      |

R = 120.02  
0

T = 19.20  
c

'r' = 0.249

TABLE 3. Life, fertility and daily sex ratio table for L. boulandi when presented with D. simulans hosts (HA strain).

| x    | l(x) | m(x)   | sex ratio | x    | l(x) | m(x) |
|------|------|--------|-----------|------|------|------|
| 17.5 | 1000 | 27.080 | 0.282     | 31.5 | 400  | 0.00 |
| 18.5 | 980  | 35.898 | 0.287     | 32.5 | 320  | 0.00 |
| 19.5 | 980  | 12.633 | 0.408     | 33.5 | 220  | 0.00 |
| 20.5 | 980  | 7.898  | 0.595     | 34.5 | 80   | 0.00 |
| 21.5 | 980  | 5.204  | 0.711     | 35.5 | 20   | 0.00 |
| 22.5 | 960  | 3.333  | 0.829     |      |      |      |
| 23.5 | 960  | 2.438  | 0.874     |      |      |      |
| 24.5 | 960  | 0.688  | 0.940     |      |      |      |
| 25.5 | 940  | 0.213  | 1.000     |      |      |      |
| 26.5 | 900  | 0.000  | 0.857     |      |      |      |
| 27.5 | 840  | 0.048  | 1.000     |      |      |      |
| 28.5 | 700  | 0.000  | 1.000     |      |      |      |
| 29.5 | 620  | 0.000  |           |      |      |      |
| 30.5 | 520  | 0.000  |           |      |      |      |

R = 95.06  
0.

T = 18.99  
c

'r' = 0.239

TABLE 4. Reproductive variables for simultaneous cohorts of L.\_\_\_\_boulardi continuously exposed to D.\_\_\_\_melanogaster (n=45) and D.\_\_\_\_simulans (n=49) (mean  $\pm$  SE) .

| Variable                                        | <u>D.____melanogaster</u><br>reared cohort | <u>D.____simulans</u><br>reared cohort |
|-------------------------------------------------|--------------------------------------------|----------------------------------------|
| Length of life                                  | 14.4 $\pm$ 0.7                             | 13.6 $\pm$ 0.4                         |
| Days of male production                         | 9.9 $\pm$ 0.4                              | 9.7 $\pm$ 0.2                          |
| Days of female production                       | 4.8 $\pm$ 0.3                              | 5.2 $\pm$ 0.3                          |
| Total male progeny                              | 163.8 $\pm$ 10.2                           | 90.9 $\pm$ 5.0 *                       |
| Total female progeny                            | 129.6 $\pm$ 9.8                            | 93.5 $\pm$ 5.0 *                       |
| Total progeny                                   | 293.4 $\pm$ 10.1                           | 184.4 $\pm$ 5.2 *                      |
| Post reproductive period<br>for fertilized eggs | 9.8 $\pm$ 0.7                              | 8.4 $\pm$ 0.6                          |
| Total post reproductive<br>period               | 4.6 $\pm$ 0.4                              | 4.0 $\pm$ 0.4                          |

Symbols: \*=  $p < .05$ , \*\*=  $p < .01$ , @= not comparable

Figure 3. Survivorship curve for the Ha75 strain of L. bouhardi exposed to D. melanogaster (Q.C. strain) hosts.

Survivorship curve for  
the CONTINUOUS cohort, 24 hour exposure  
host, *Drosophila melanogaster*  
HA/OC

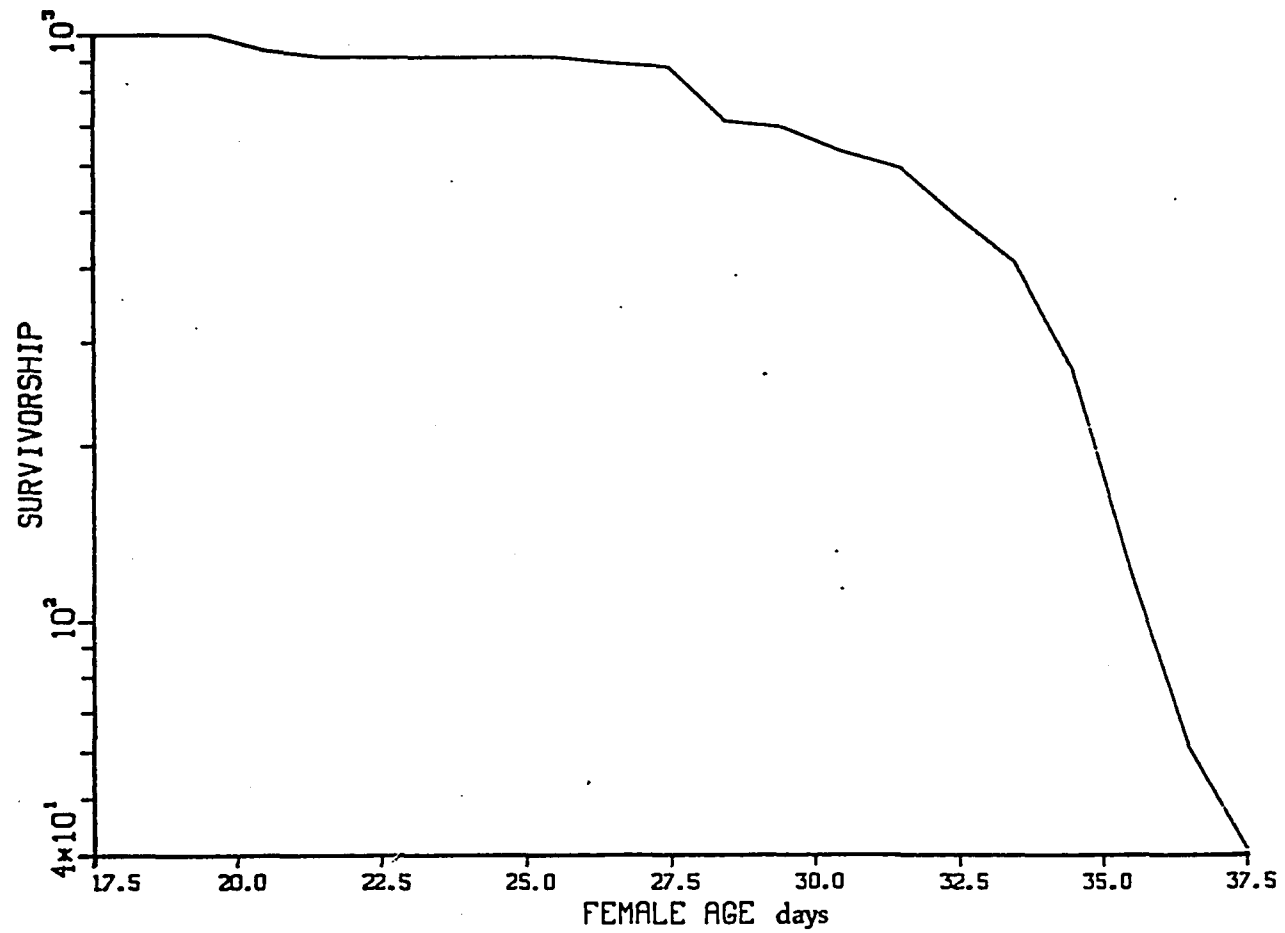


Figure 4. Fertility curve for the Ha75 strain of L. bouhardi exposed to D. melanogaster (Q.C. strain) hosts.

Fertility curve for  
the CONTINUOUS cohort, 24 hour exposure  
host, *Drosophila melanogaster*  
HA/QC

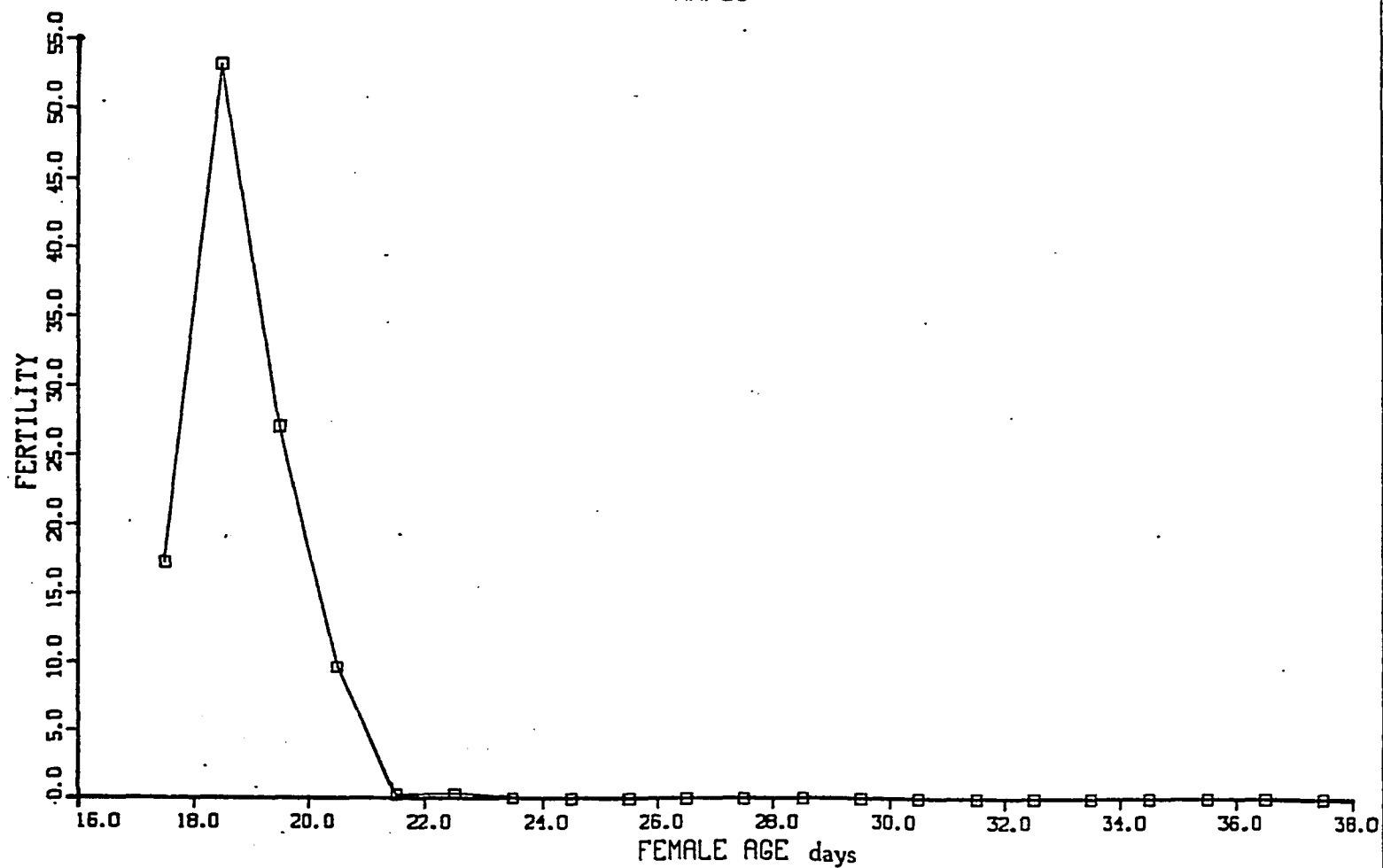




Figure 5. Survivorship curve for the Ha75 strain of L. bouhardi exposed to D. simulans (Ha strain) hosts.

Survivorship curve for  
the CONTINUOUS cohort, 24 hour exposure  
host, Drosophila simulans  
HA/HA

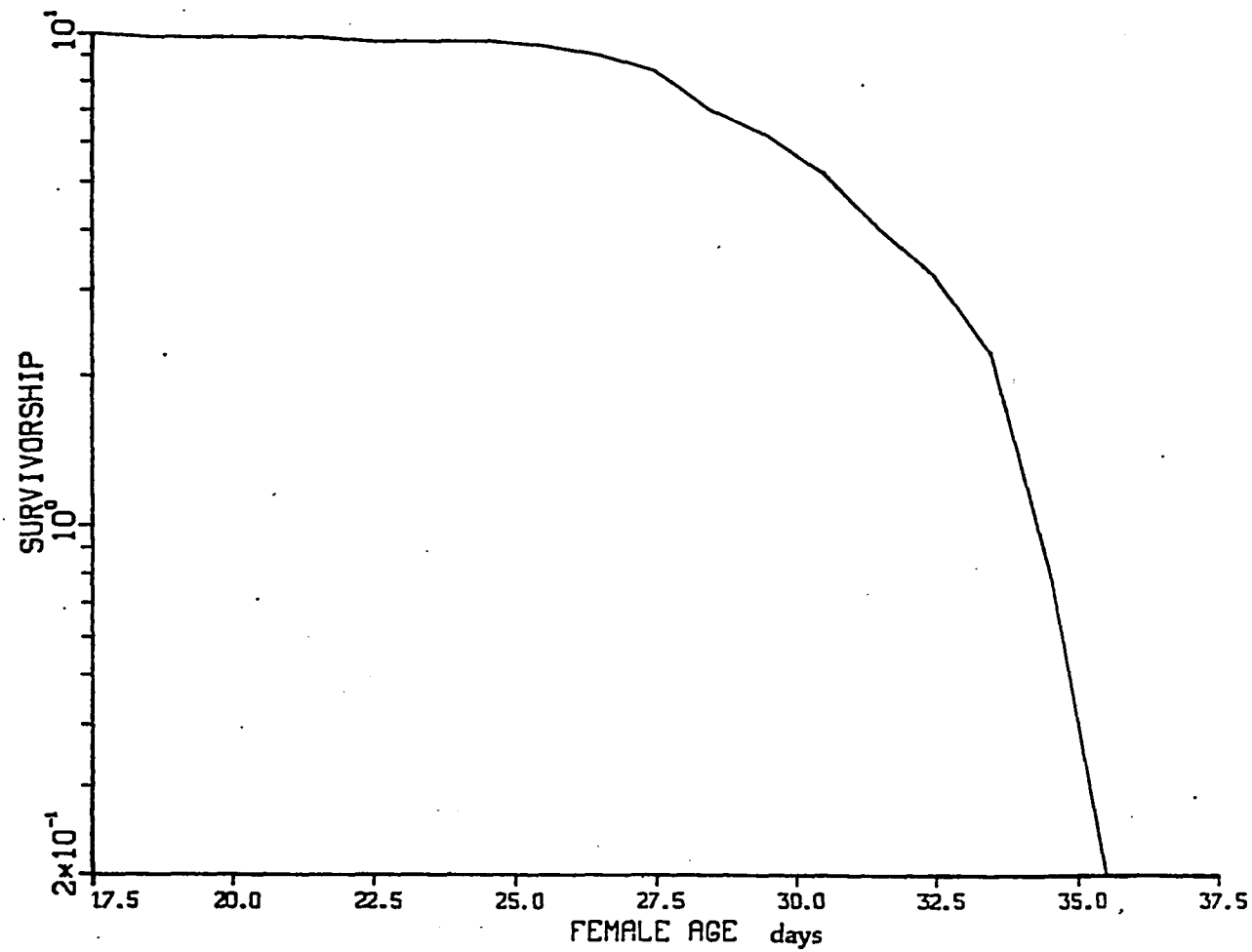


Figure 6. Fertility curve for the Ha75 strain of L. bouhardi exposed to D. simulans (Ha strain) hosts.

Fertility curve for  
the CONTINUOUS cohort, 24 hour exposure  
host, *Drosophila simulans*  
HA/HA

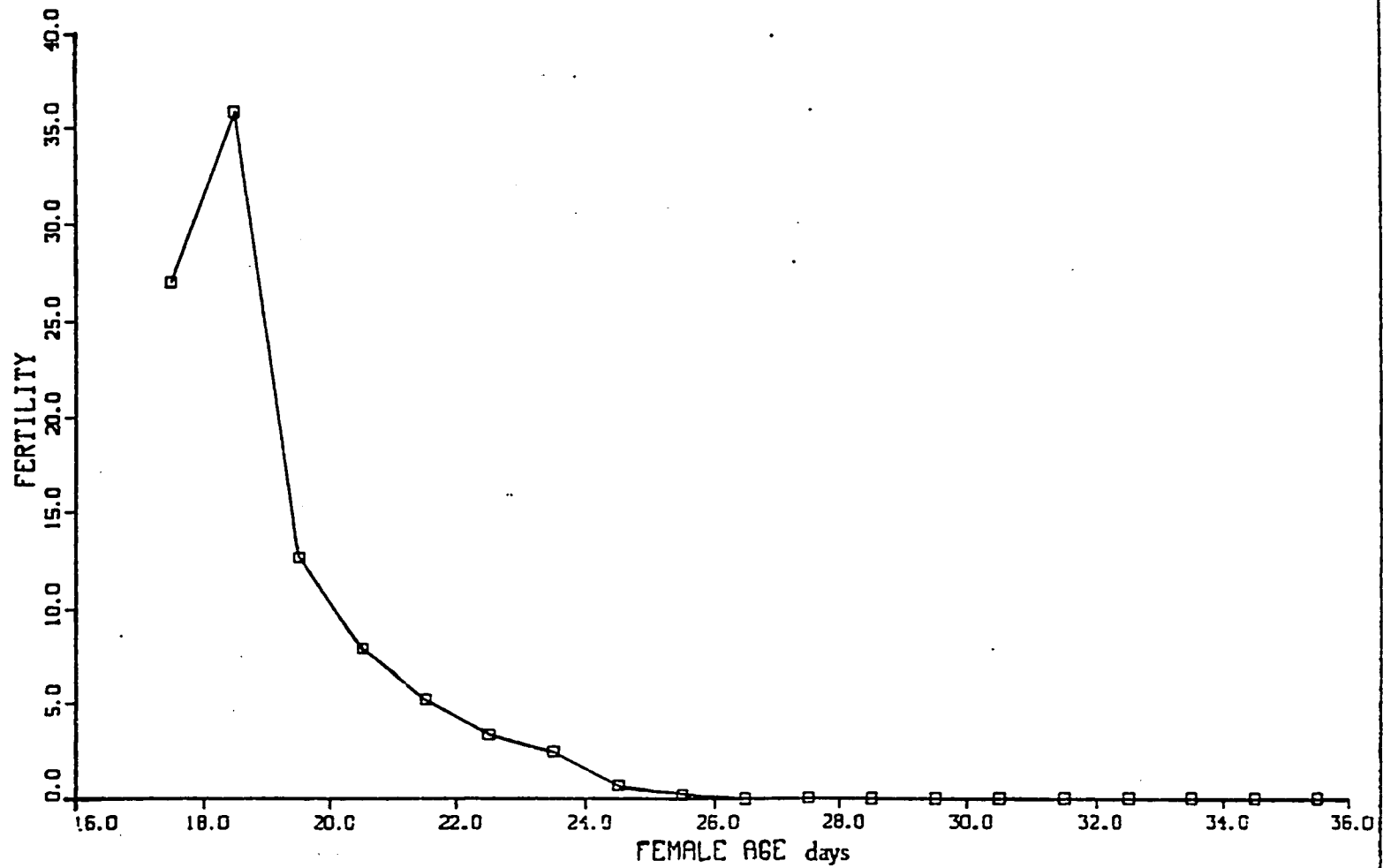
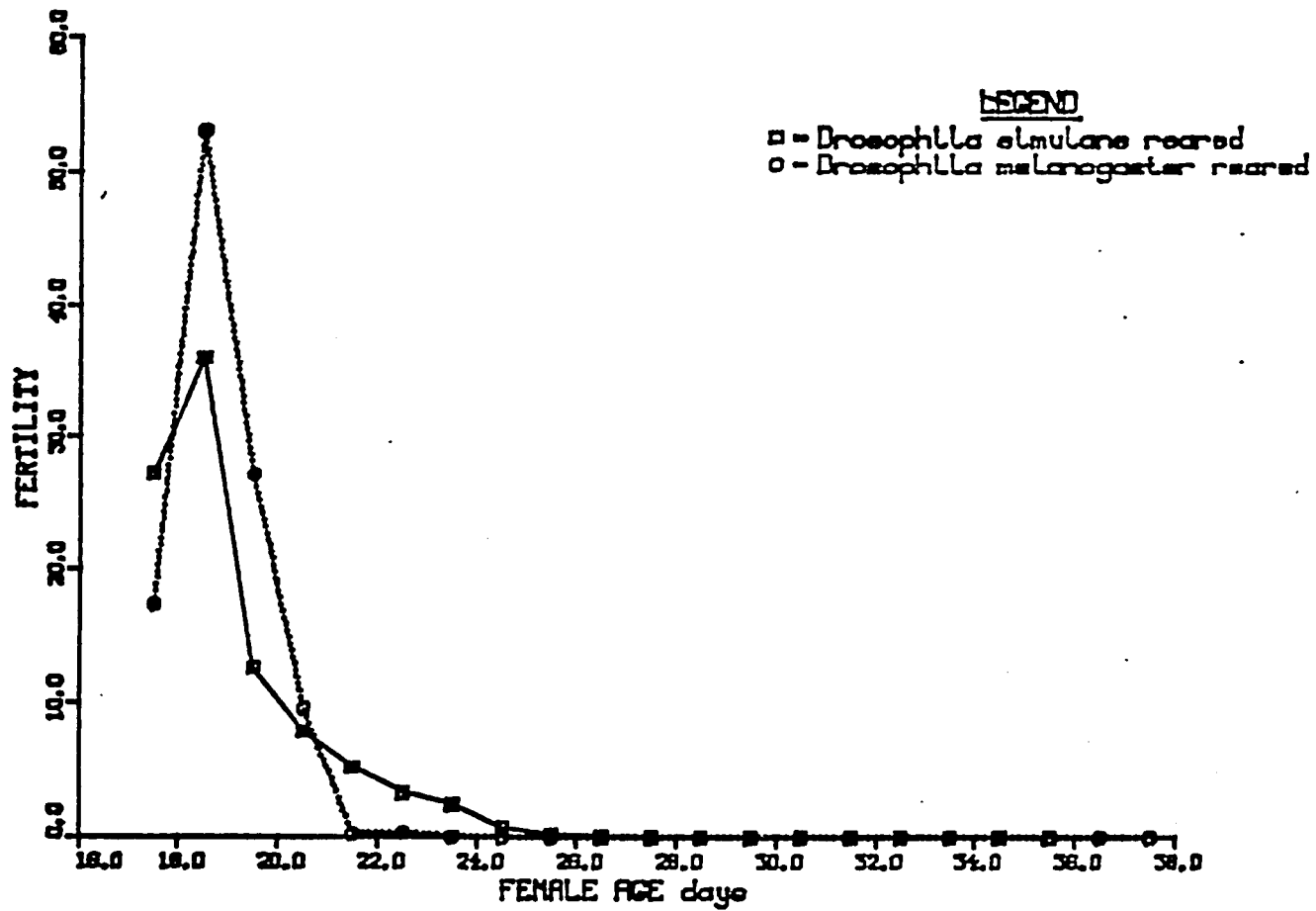


Figure 7. Composite of the fertility curves for both cohorts

Fertility curves for  
cohorts exposed to  
Drosophila simulans  
and Drosophila melanogaster



Females in both cohorts spent approximately 70% of their average life span producing male progeny (ovipositing unfertilized eggs), while only 30-40% of their average life span was spent producing female progeny (ovipositing fertilized eggs). Since the fertility distribution for a sexual species is, in the strict sense, limited to the number of female progeny produced per female per unit time; then both cohorts must exhibit long periods of post-reproductive survival in their life and fertility tables. In actuality most females continued to oviposit successful male producing eggs for some time after the cessation of ovipositing fertilized eggs.

#### Discussion

The adult survivorship distribution shows the typical insect pattern of high survivorship early in adult life followed later by a sharp increase in mortality. The differential total fertility of L. boulandi utilizing D. melanogaster compared to those utilizing D. simulans is significant, but also not unexpected. Barbotin et al (1979), as well as Rouault (1979) have shown similar data and attribute the differences in host suitability to differential defense reactions of the host species to the developing parasitoid larvae. D. simulans tends to produce stronger melanic capsule responses to L. boulandi larvae than does D. melanogaster (Rouault, 1979; Kopelman, unpublished data). This differential reproductive success

on different host species will be evident throughout the experiments to be described later.

Data from this experiment can be used to calculate parasitoid larval mortality in both host species. Assume that L. bouhardi females of any strain will, on the average, produce a characteristic number of total offspring given a particular host species under particular experimental conditions. Further, assume that females in any parasitoid strain have a characteristic maximum number of eggs available to them after emergence, and these females exhaust their entire egg complement during life. We can use these values to estimate the average developmental mortality of any specific parasitoid strain, given a known host species and known environmental conditions.

Parasitoid females of the Ha 75 strain have an average egg complement of  $349.3 \pm 3.3$  eggs per female after emergence. When exposed to D. simulans larvae, above, they produced an average of  $183.5 \pm 10.5$  total offspring, yielding an estimated average developmental mortality of 47%. The same parasitoid strain, when exposed to D. melanogaster produced an average of  $293.4 \pm 16.4$  total offspring, yielding an estimated average developmental mortality of 16%.

Using data combined from comparable subsequent experiments utilizing D. simulans it was found that the Ha 75 strain produced an average of  $189.5 \pm 10.5$  total



offspring, which equates to 45% mortality. The Ha 77 strain, which has an average egg compliment of  $286.3 \pm 2.0$  eggs at hatching, produced an average of  $261.1 \pm 16.4$  total offspring when exposed to D. melanogaster, again equivalent to a 16% developmental mortality rate.

Perhaps the most interesting conclusion of this experiment is the similarity and uniqueness of the fertility distributions of these two cohorts. The early peaks and subsequent decline in the fertility distribution is similar to that of many other species including Drosophila, Daphnia, and the Herring gull, and is proposed to be the general case for organisms living in temporally heterogeneous environments (Giesel, 1976). What is unusual, however, is the markedly protracted post-reproductive survival of the females in both cohorts. By the fifth day of oviposition 95% of all female eggs were laid and within a few days the production of female eggs ceased. This was followed by four days of male egg oviposition prior to a 7-10 day period of survival without producing any progeny at all.

The changes in the sex ratio of successful ovipositions with age of the cohort at oviposition show a marked change from females ovipositing a high percentage of fertilized eggs during early exposure periods to females ovipositing fewer and eventually no fertilized eggs during later oviposition periods. This shift in sex ratio is in accordance with the views of Flanders (1939) who aptly notes

that although innumerable variables contribute to the determination of sex ratios in parasitoids exposed to high densities of hosts for long periods of time, sperm depletion and/or exhaustion of the spermathecal gland secretions are the probable internal causes of shifts towards male biased sex ratios. Differential mortality and developmental duration are probable external causes (Rotary and Gerling, 1973; Doutt, 1959).

Of course this explanation is only valid when females are monandrous. The selection pressures for monandrous and polygynous mating systems in parasitic wasps are very powerful and have been reviewed extensively by Mathews (1975). Mathews contends that monandry is the general rule in parasitic wasps and this seems to be borne out by the elaborate studies of Van den Assem and Povel (1973) with the pteromalid Muscidifurax; Van den Assem (1970) with the pteromalid Lacrochagus distinguendis, and Van den Assem (1969) with the cynipid Pseudeucoila bochei (L. heterotoma), a congener of L. boulardi.

Van den Assem (1969) described the elaborate courtship behavior of L. heterotoma and a phenomenon he called "pseudovirginity". Pseudovirginity, or pseudoinsemination as it is termed by Mathews (1975) occurs when females reach a critical point in the courtship sequence (in this case, the adoption of a copulatory posture with open genital pockets) and whether inseminated or not, are subsequently

not receptive to courting males. Whether monandry occurs in L. boulandi as it does in L. heterotoma is still not known. As part of an experiment to be discussed next, I conducted an indirect test for monandry by exposing females in a cohort to new males every fourth day and analyzing the production schedules and sex ratios of their progeny. However, since direct observation of matings or attempted mating were not made, the results obtained are not conclusive.

One further question must be asked at this point concerning the life-history and fertility data described above : Why does this species exhibit protracted post-reproductive survival under these experimental conditions? The apparent strategy of explosive reproduction with long periods of post-reproductive survival makes little sense. A number of different plausible hypotheses may be suggested. Perhaps this early short burst of intense parasitization was due to the long confined exposure to high host density patches. Although this may lead to a high percentage of parasitism during early exposure periods, the females may be exhausting their egg complement early in life under these unnatural laboratory conditions. Or, perhaps as suggested by Streams (1968) for L. heterotoma, after 5 days of intense parasitization the adult female can no longer provide her eggs with adequate protection against encapsulation by its host and any eggs laid would not survive.

These hypotheses and others were tested in the following series of experiments which involved analyzing the responses of females to (1) various schedules of host availability that approached more natural conditions, (2) a new protein enriched food source, and (3) the availability of new males.

#### Summary

The life-history parameters and reproductive variables of two cohorts of Leptopilina boucardi were compared when presented hosts on a 24 hour per day continuous schedule. One cohort was presented with D. melanogaster larvae, the other with D. simulans larvae.

The survivorship distributions did not differ between the cohorts, both exhibited the "type 1", negative skew rectangular curve of Pearl (1928). Both fertility distributions followed similar unusual patterns marked by an early peak and rapid subsequent drop leading to an extended period of post-reproductive survival. A shift in the sex ratio from female to male biased was coincidental with the drop in progeny production. Prior to the complete cessation of oviposition, females spent several days ovipositing only male eggs.

The reproductive variables describing the progeny production schedule did not differ significantly between the cohorts. The mean number of male, female, and total progeny per female, on the other hand, were significantly higher in the cohort utilizing D. melanogaster. The differential

reproductive success may be attributable to differential defense responses (Carton, 1979; Rauoult, 1979) in the host species and differential developmental mortality. The mortality in D. simulans larvae is estimated at 47%, while in D. melanogaster larvae it is estimated at 16%, regardless of the parasitoid strain. Finally, certain hypothesis are presented to explain the unusually long post-reproductive periods. These hypotheses are the focal points of the experiments described next.

Experiment 2. The Effect of Host Availability and Other Factors on the Life History Parameters and Reproductive Variables in *L. boulandi* When Utilizing *D. simulans* as Hosts

Materials and Methods

In an attempt to test the various hypotheses mentioned above a series of simultaneous experiments were conducted using sympatric strains of *D. simulans* and *L. boulandi* captured originally in Hampton, Virginia during late August, 1975. Cohorts of 25 females each were presented with vials of excess hosts under the following conditions:

Series I. Continuous hosts - in which hosts were presented for 24 hours daily.

Series II. Intermittent hosts - in which hosts were presented for 24 hour periods every third day.

Series III. Delayed hosts - in which hosts were withheld for the first four days of the cohorts existence.

Series IV. New males - in which hosts were presented on a continuous basis and the females were presented with new males every fourth day.

Series V. Honey-Yeast food source - in which hosts were presented on a continuous basis and the parasitoids were provided with a new food source of honey mixed with activated yeast.

When parasitoids were not given hosts they were kept in shell vials (95 x 25 mm) with 8 ml of standard *Drosophila* medium and a droplet of honey. In order to prevent wasps

from drowning in the bacterial slime growing across the surface of unused medium, the hostless vials were changed every two to three days. Unfortunately, this did not eliminate mortality due to drowning prior to host exposure in Series III.

The same procedures used for procuring hosts in the previous experiments were followed here. Survivorship data, as well as age-specific reproductive characteristics were collected as described earlier.

## Results

### Survivorship

Here, as in the previous experiments, we find the typical "type 1" survivorship curves of Pearl (1928) (see figures 8-12). Comparisons of the survivorship distribution and mean length of life of an average female in each respective cohort yield two interesting phenomena. First, when hosts were presented on a discontinuous basis (Series II and III) we find that survivorship decreased in comparison to the control (Series I), but this difference is not significant (see tables 10 and 11). Secondly, we see that in Series V, in which yeast was added to the honey solution, survivorship increased, but not significantly, to a mean length of life of  $11.7 \pm 0.9$  days (table 13).

### Survivorship-fecundity distribution

Series I. The pattern of early explosive reproduction is seen clearly in this cohort. The  $116.1 \pm 7.5$  males produced

by an average female were deposited in hosts during 84.4 % of the average female's life span. On the other hand, the  $66.0 \pm 7.2$  female progeny produced per female were deposited in hosts during only 33.8% of the average life span. We find that Series I females had produced 94% of their female progeny in three days, and 100% of their female progeny in six days (see tables 5, 10, and figure 13).

The peak in female progeny production for this cohort occurred during the first exposure period (table 5, figure 13); the peak in total progeny production occurred during the second exposure period, while the peak in male progeny production occurred during the third exposure period. By the second exposure period the sex ratio of ovipositions shifted from female to male biased. This preceded a 66% drop in total daily progeny production (see table 5).

The life and fertility table (table 5) clearly shows the extent of post reproductive survival of this cohort. Net reproductive rate, generation time, and 'r', the approximate intrinsic rate of increase are also presented in table 6.

Series II. The oviposition of successful female eggs was extended to later oviposition periods than Series I (see figures 14 and 18). The average female produced  $48.4 \pm 8.1$  male progeny and  $60.9 \pm 6.2$  female progeny. The cohort, exposed to hosts for  $3.5 \pm 0.2$  days, produced male progeny during 98.8%, and female progeny during 83.1% of its exposure time. We find that by the fourth oviposition



period, 99% of all female progeny had been produced. The average post-reproductive periods of this cohort are correspondingly low,  $0.0 \pm 0.0$  days for PRP-t and  $0.5 \pm 0.2$  days for PRP-f (see tables 6 and 10, and figures 9 and 14).

The age distribution of total and female progeny production reached its peak during the first exposure period, while the second exposure period exhibits the peak in total successful male progeny production. Table 6 presents the life and fertility tables, the sex ratio of daily progeny production, and the population growth parameters of this cohort.

Series III. In this cohort females were able to extend the successful oviposition of fertilized eggs to later ages and thereby reduce their post-reproductive periods. Unfortunately, due to high mortality prior to exposure and the presence of unfertilized females, only nine replicates can be included here. The cohort was exposed to hosts for an average of  $4.4 \pm 0.4$  days and produced male progeny during 92.3% of its exposure time. Female progeny were produced during 65% of its exposure time. The post-reproductive period for total offspring was  $0.2 \pm 0.15$  days, while the post-reproductive period for female progeny was  $1.6 \pm 0.4$  days. By the fifth day of exposure 89% of all female progeny had been produced (tables 7 and 11).

The first day of exposure produced the peak in female and total progeny production (figure 15), while the following

day produced the peak in male progeny production. These data, as well as the daily changes in progeny sex ratio are given in table 7. The sex ratio is male biased during the first three oviposition periods, but becomes female biased during the next two when only 39 and 15 progeny are produced. The last successful oviposition period produced only 1 male offspring from the last surviving female.

The life and fertility table for this cohort is given in table 7.  $R_0$ , calculated as 23.08, and ' $r$ ', calculated as 0.1403, are both comparatively low. The effects of the low  $m_x$  values on ' $r$ ' are compounded by the delay in host availability, which shifts the age of first reproduction to the right. The calculated generation time is the highest of all cohorts, again a consequence of the delay in oviposition.

Series IV. This cohort produced  $65.4 \pm 6.5$  males during 87.1%, and  $124.2 \pm 7.0$  females during 73.2% of the average female life span. Hence, the post-reproductive period for total and female progeny were both low. After 6 days of exposure 93% of all female progeny had been produced, and by day 10, 100% of all female progeny had been produced (see tables 8 and 12, and figure 16).

The second day of exposure produced the peaks in male and female progeny production, as well as the lowest daily sex ratio (see table 8). During the fourth exposure period total progeny production decreased by 55% from the previous

day, and during the following exposure period the sex ratio of progeny produced became male biased, where it remained until the 11th day when an equal number of males and females were produced. During the last successful exposure period only one offspring was produced, that being a female.

The life and fertility table, the daily progeny sex ratios and the population growth parameters for this cohort are presented in table 8. This cohort produced the highest  $R_0$  of any cohort, 114.96.  $T_c$  was calculated as 19.27; and ' $r$ ', as 0.246. The high productivity of this cohort as indicated by  $R_0$  is also evident in the mean number of female progeny produced per female (TF), which is significantly higher than that of any other cohort ( $p < .05$ ; see tables 12, 15, 17, 19).

Series V. This cohort produced an average of  $71.6 \pm 8.0$  males during  $7.64 \pm 0.465$  days (65% of life span) and produced an average of  $92.9 \pm 8.7$  females in  $4.9 \pm 0.56$  days (43.2% of life span). 93% of all female offspring were produced within 5 days and 99% were produced within 8 days (see figure 16 and table 13). The life and fertility table, daily progeny sex ratio and population growth parameters for this cohort are given in table 9.

The second exposure period produced the peak value in the progeny production distributions (figure 17). The first three exposure periods, as expected, exhibited a female biased sex ratio. During the fourth exposure period (day

20.5) the total number of successful offspring produced decreased by 70% in comparison with previous day's total, and the sex ratio of became decidedly male biased where it remained for the subsequent reproductive life of the cohort.

### Discussion

Analyses of variance and nonparametric tests were performed comparing each of the 8 reproductive variables in every possible combination of cohorts. One can not, however, directly compare the absolute values for days of progeny (male or female) production between cohorts that were presented hosts on discontinuous schedules, or between these cohorts and "continuous" ones. In these cases the progeny production schedules are considered in terms of the ratio of exposure time spent in producing successful progeny over total exposure time. Tables 10-19 present the data and tables 53-62 (in the appendix) present the analyses.

### Length of life

The mean length of life of the fertilized females in each cohort did not differ significantly, regardless of the treatment.

### Days of male production and total post-reproductive period

For these variables, only cohorts with continuous exposure schedules (i.e., Series I, IV, and V) can be meaningfully compared. No significant differences exist between these three cohorts for days of male progeny production.

Figure 8. Survivorship curve for the Series I cohort.

Survivorship curve for  
the CONTINUOUS cohort, 24 hour exposure  
host, *Drosophila simulans*  
SERIES I

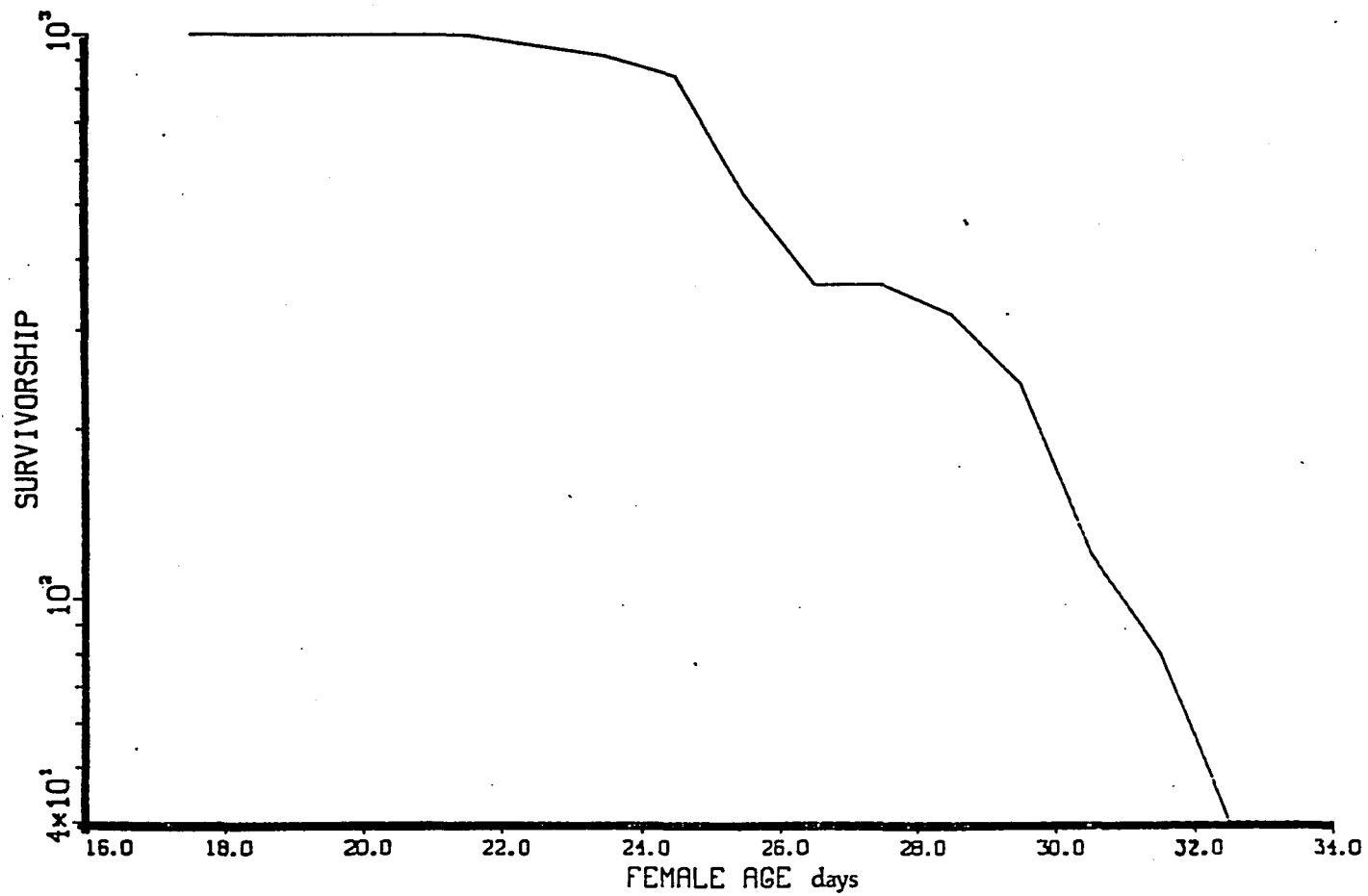


Figure 9. Survivorship curve for the Series II cohort.

Survivorship curve for  
the INTERMITTENT cohort, 24 hour exposure  
host, *Drasophila simulans*  
SERIES II

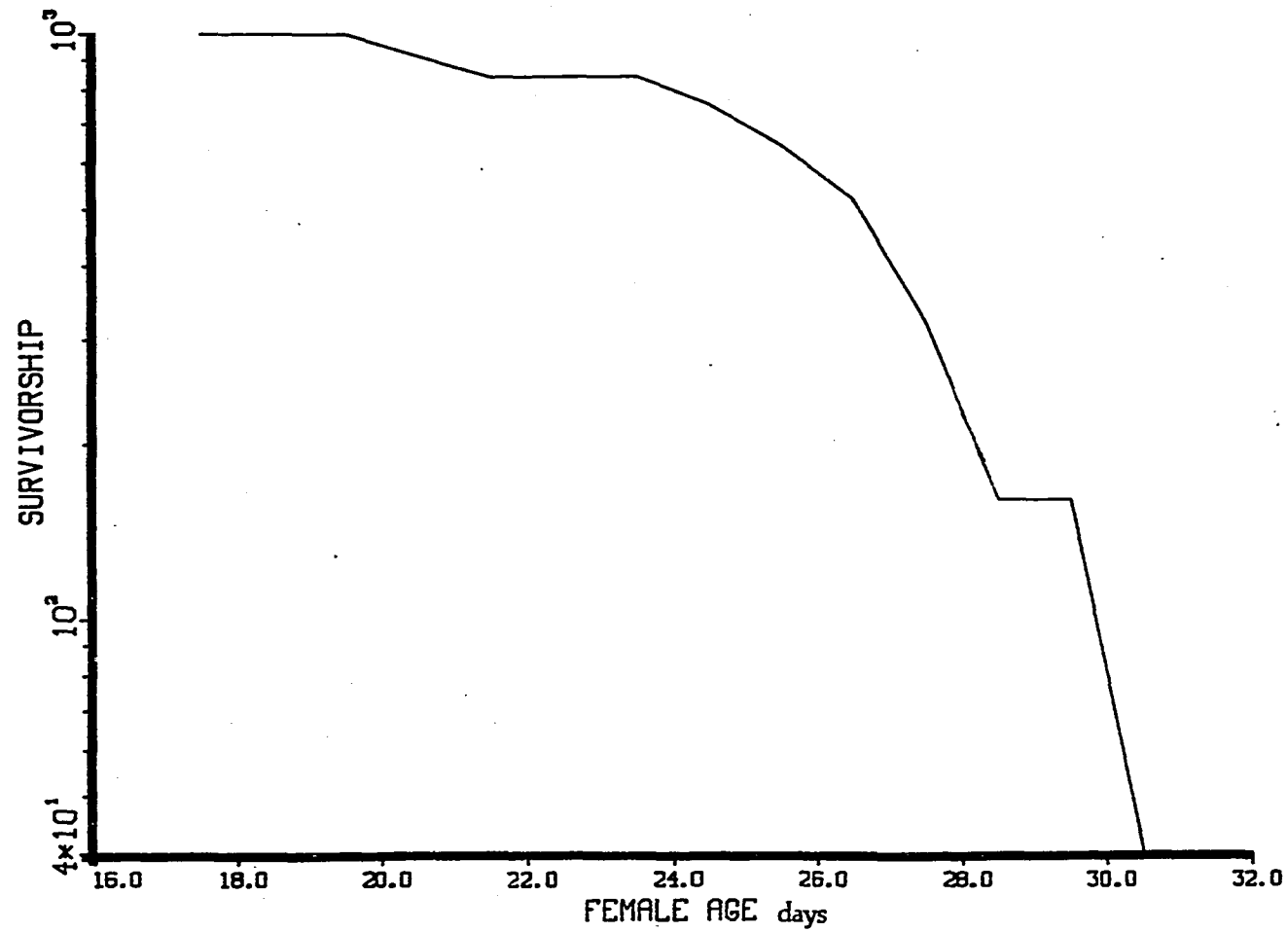




Figure 10. Survivorship curve for the Series III cohort.

Survivorship curve for  
the DELAYED cohort, 24 hour exposure  
host, *Drosophila simulans*  
SERIES III

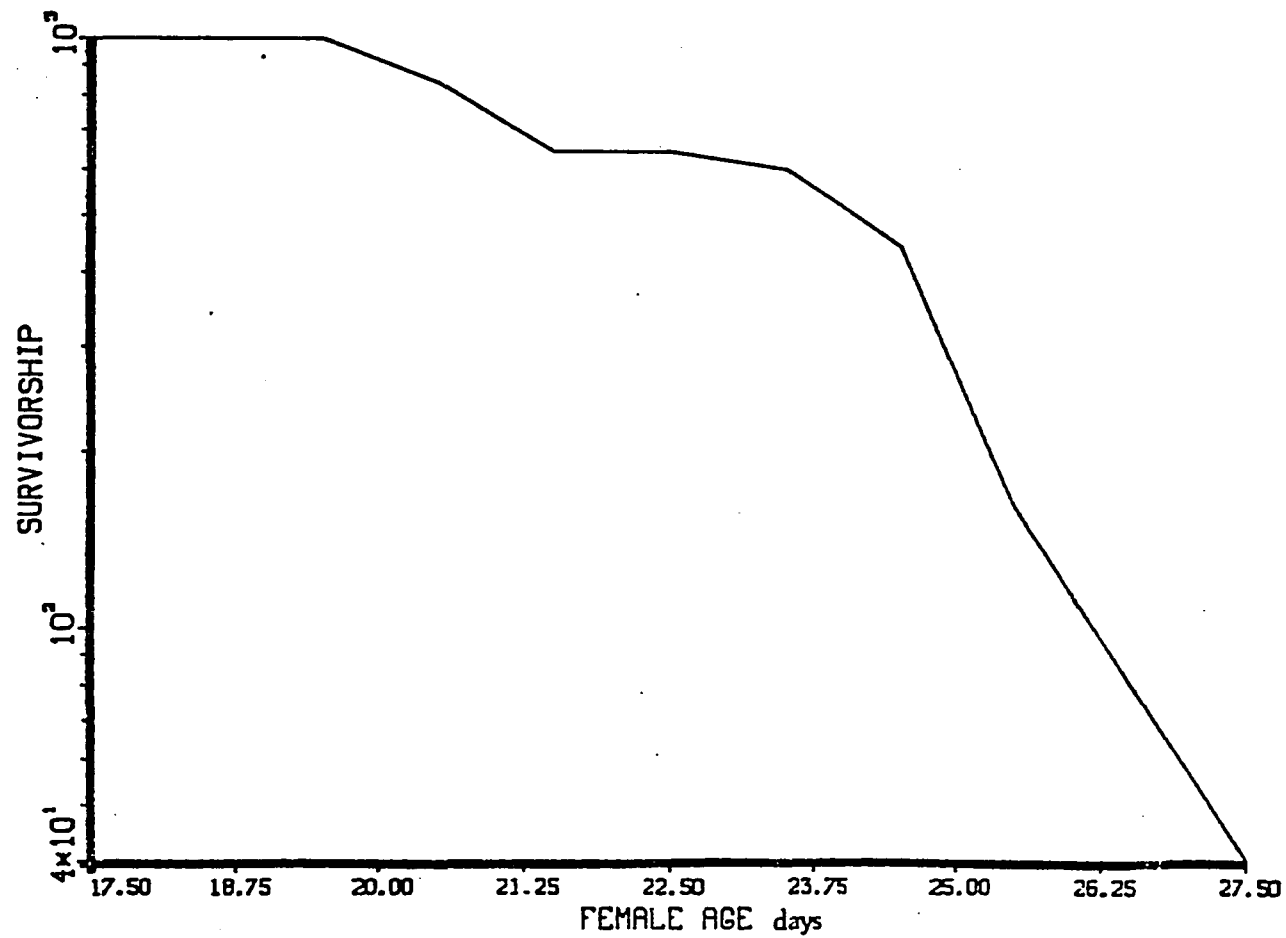


Figure 11. Survivorship curve for the Series IV cohort.

Survivorship curve for  
the NEW MALES cohort, 24 hour exposure  
host, *Drosophila simulans*  
SERIES IV

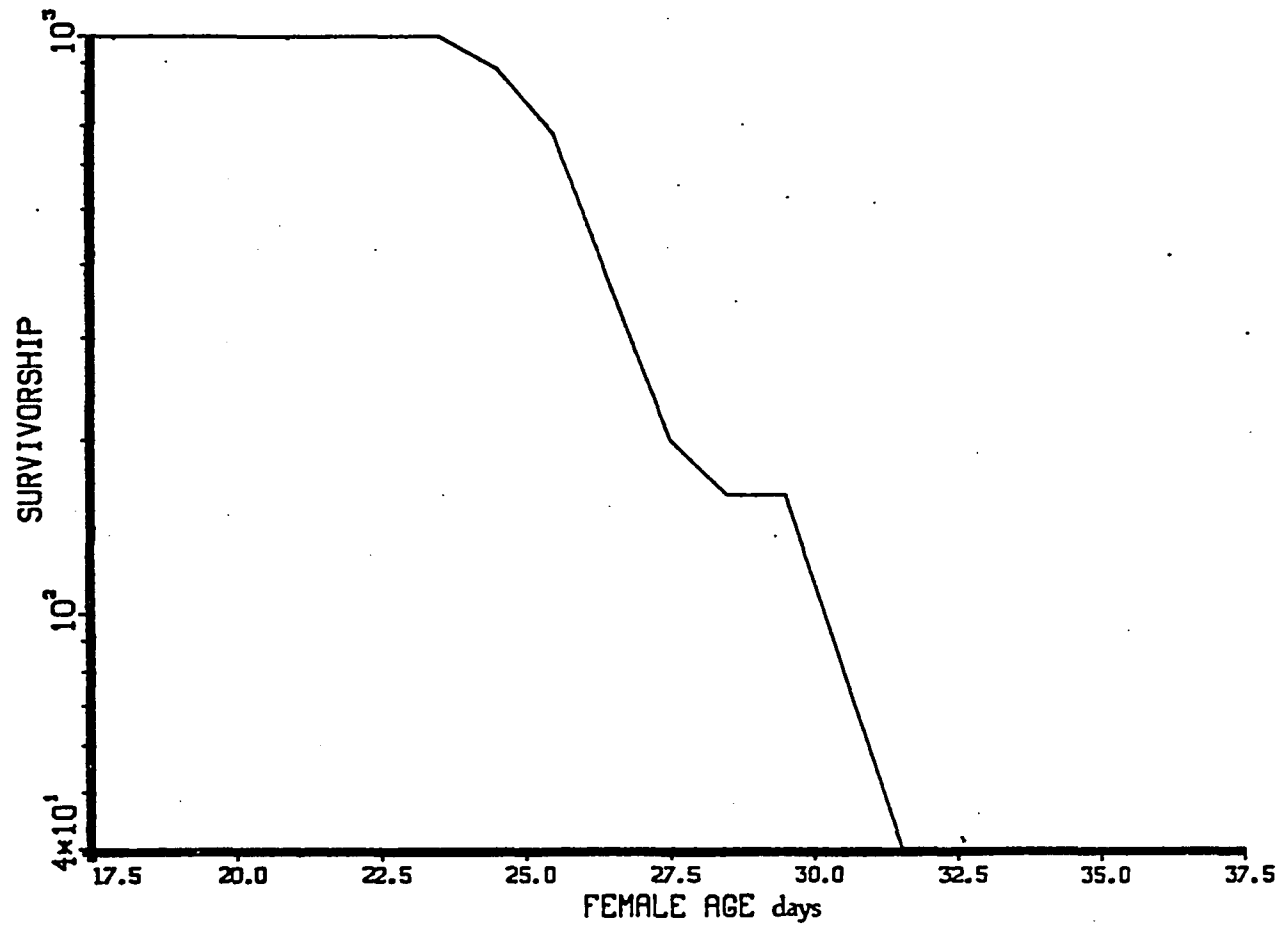


Figure 12. Survivorship curve for the Series V cohort.

Survivorship curve for  
the HONEY YEAST cohort, 24 hour exposure  
host, *Drosophila simulans*  
SERIES V

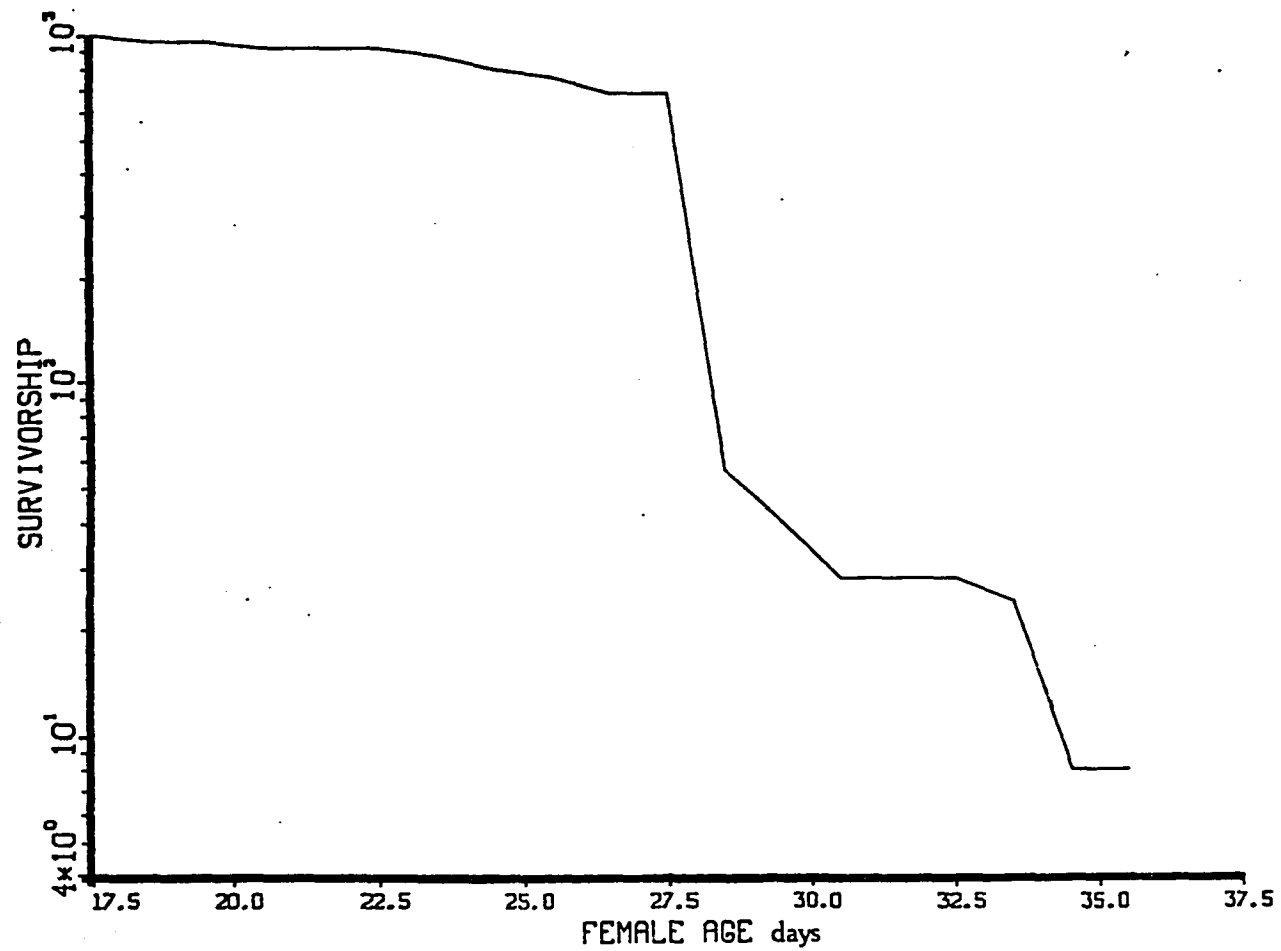


Figure 13. Fertility curve for the Series I cohort.

Fertility curve for  
the CONTINUOUS cohort, 24 hour exposure  
host, *Drosophila simulans*  
SERIES I

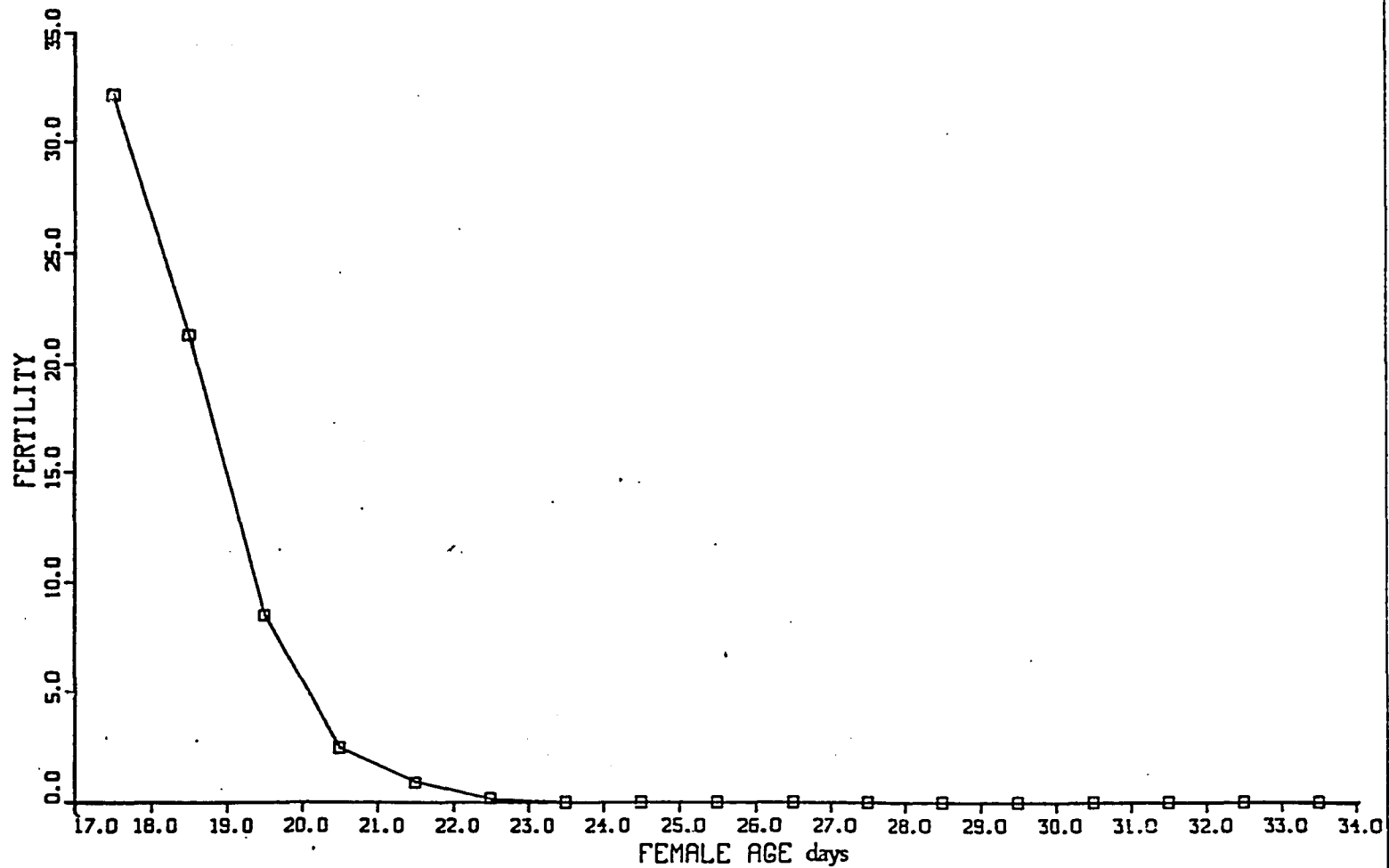




Figure 14. Fertility curve for the Series II cohort.

Fertility curve for  
the INTERMITTENT cohort, 24 hour exposure  
host, *Drosophila simulans*  
SERIES II

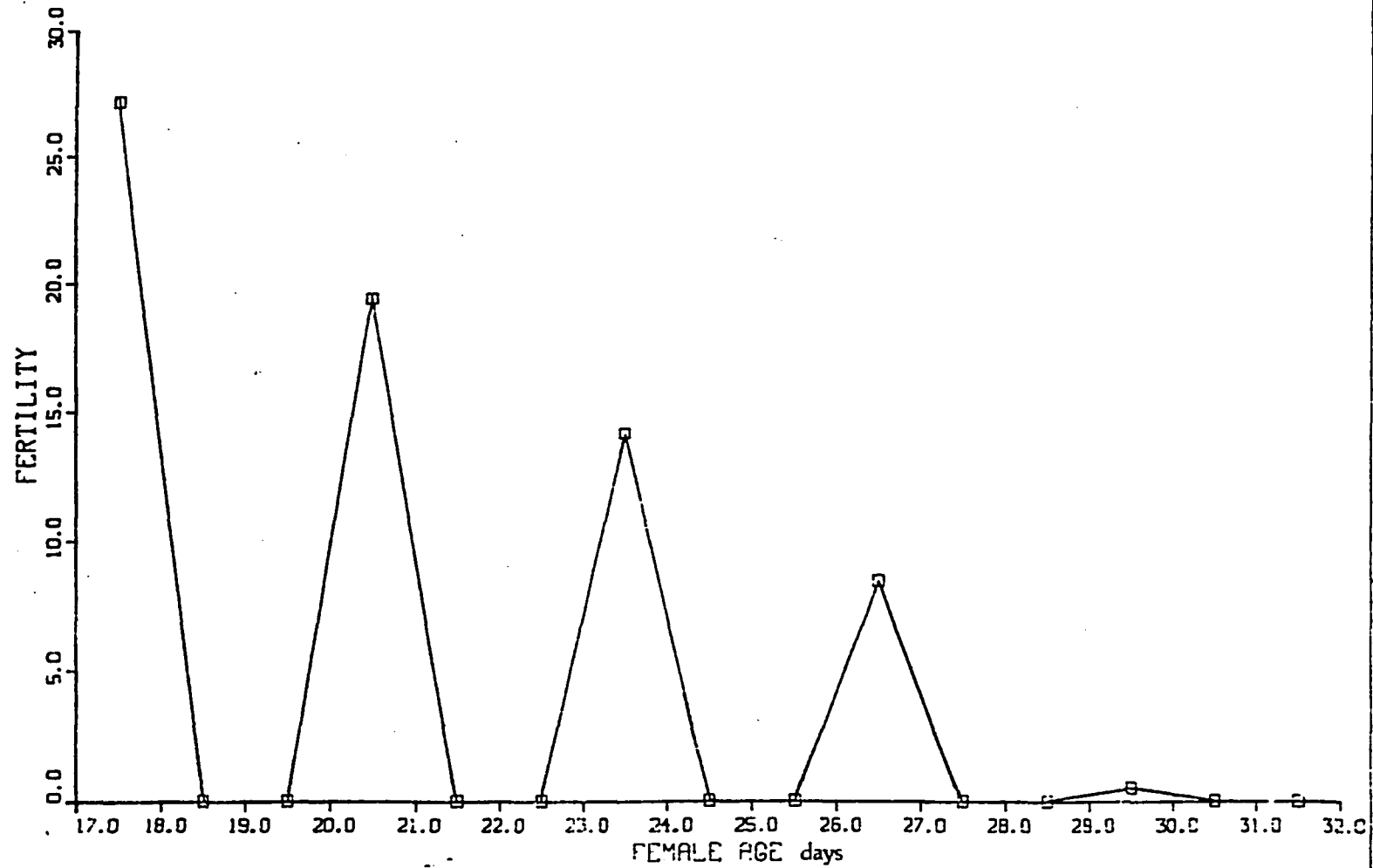


Figure 15. Fertility curve for the Series III cohort.

Fertility curve for  
the DELAYED cohort, 24 hour exposure  
host, *Drosophila simulans*  
SERIES III

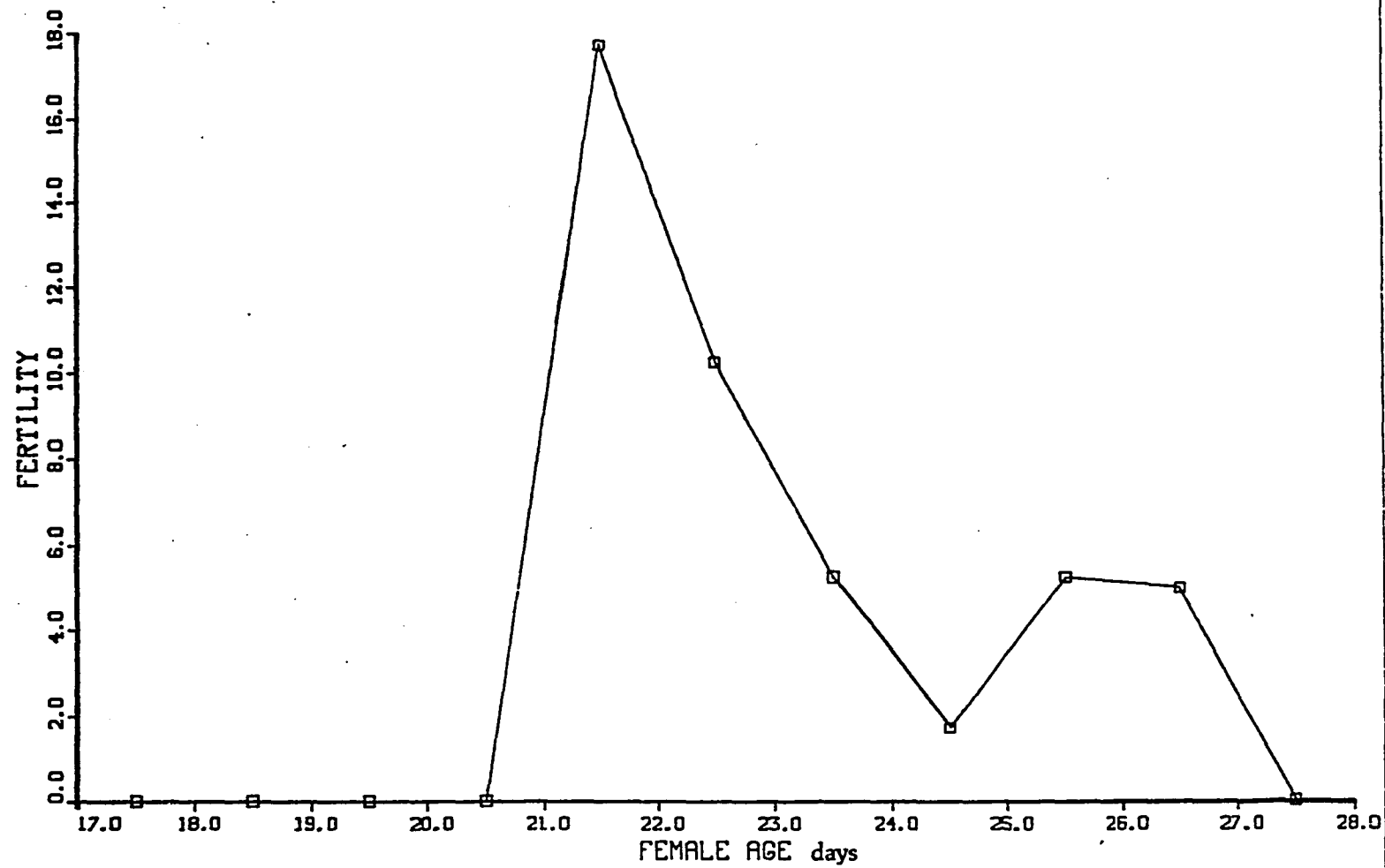


Figure 16. Fertility curve for the Series IV cohort.

Fertility curve for  
the NEW MALES cohort, 24 hour exposure  
host, *Drosophila simulans*  
SERIES IV

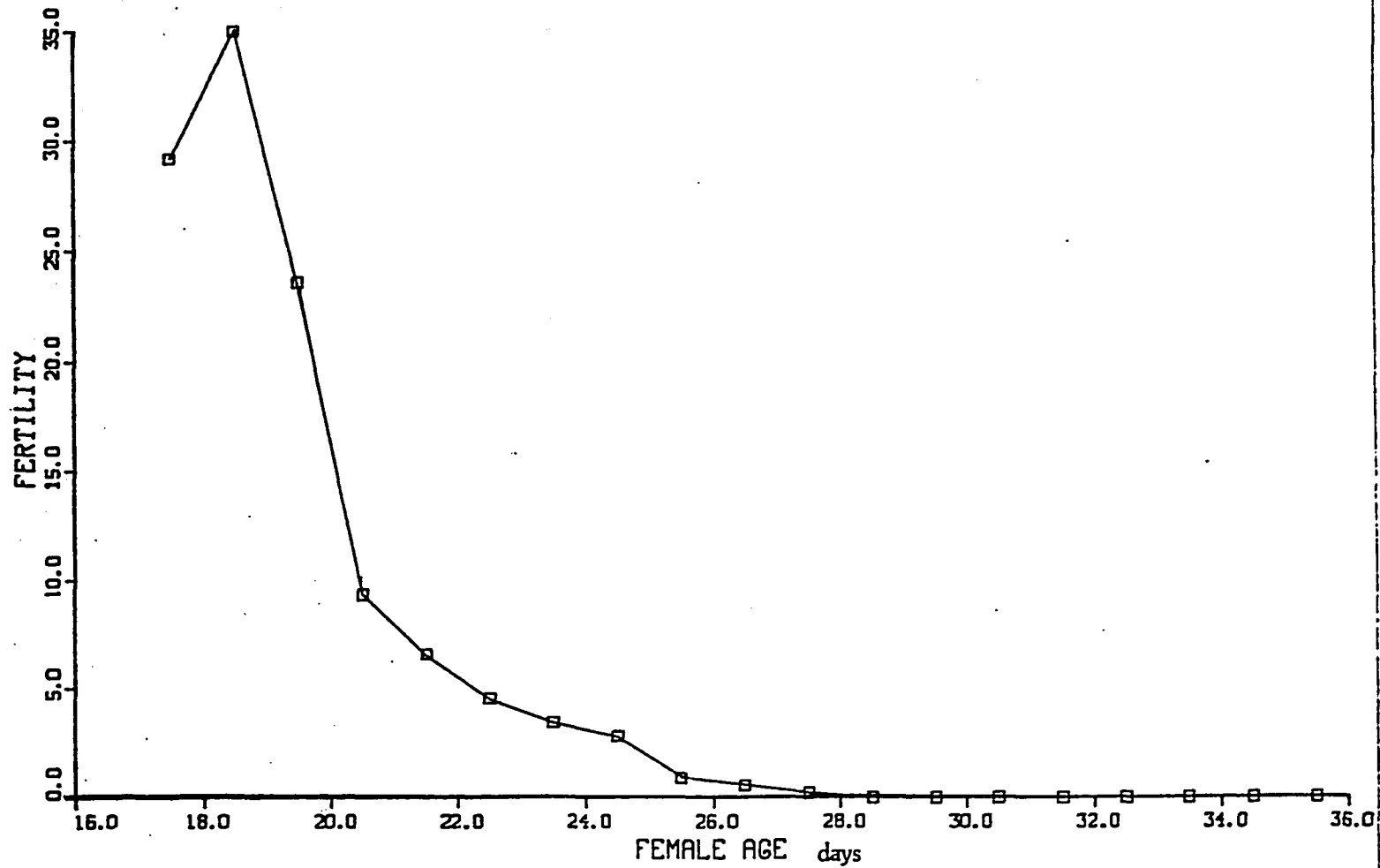


Figure 17. Fertility curve for the Series V cohort.

Fertility curve for  
the HONEY YEAST cohort, 24 hour exposure  
host, *Drosophila simulans*  
SERIES V

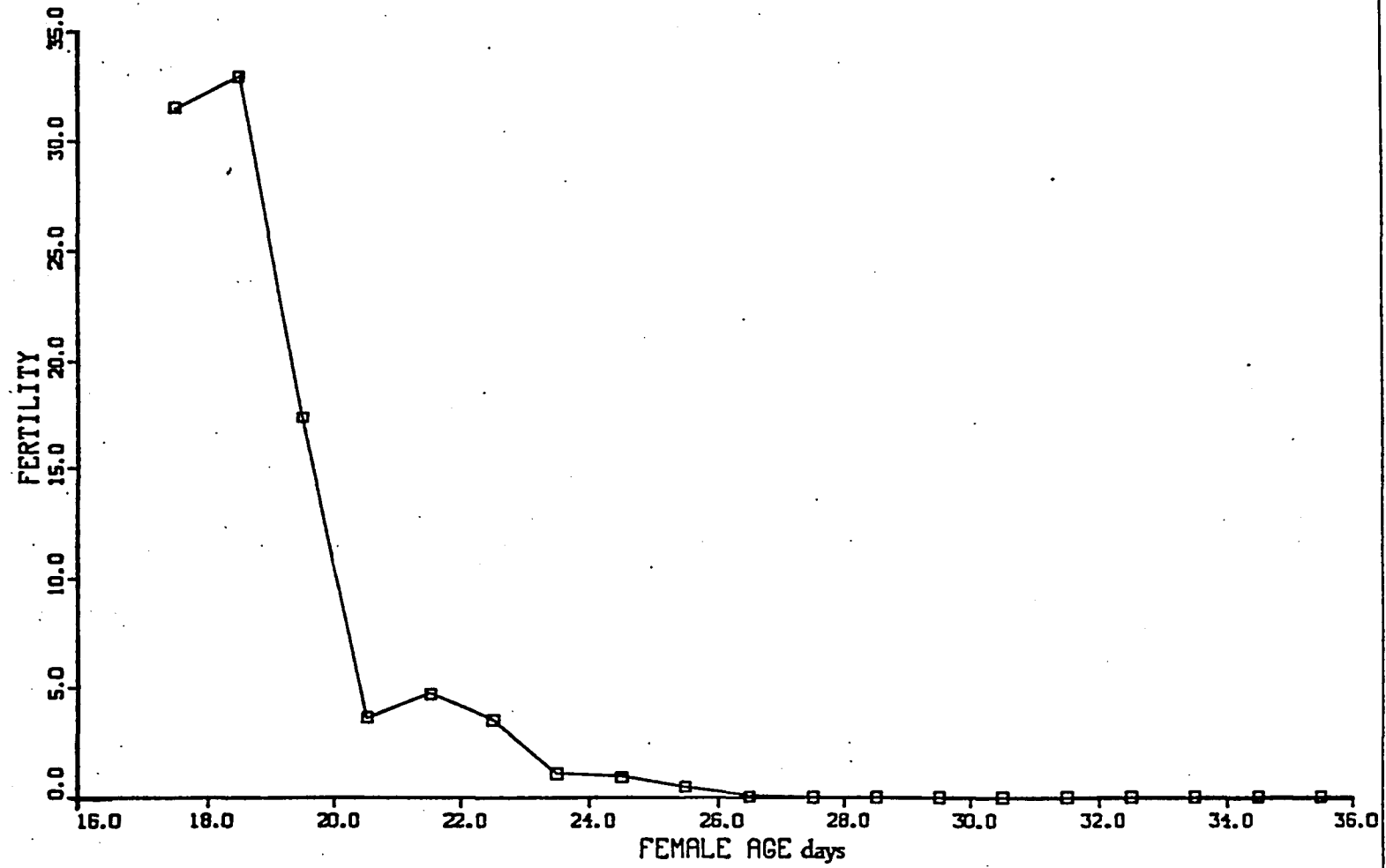




Figure 18. Composite of the fertility curves for all five cohorts.

Fertility curves for  
cohorts exposed to  
Drosophila simulans

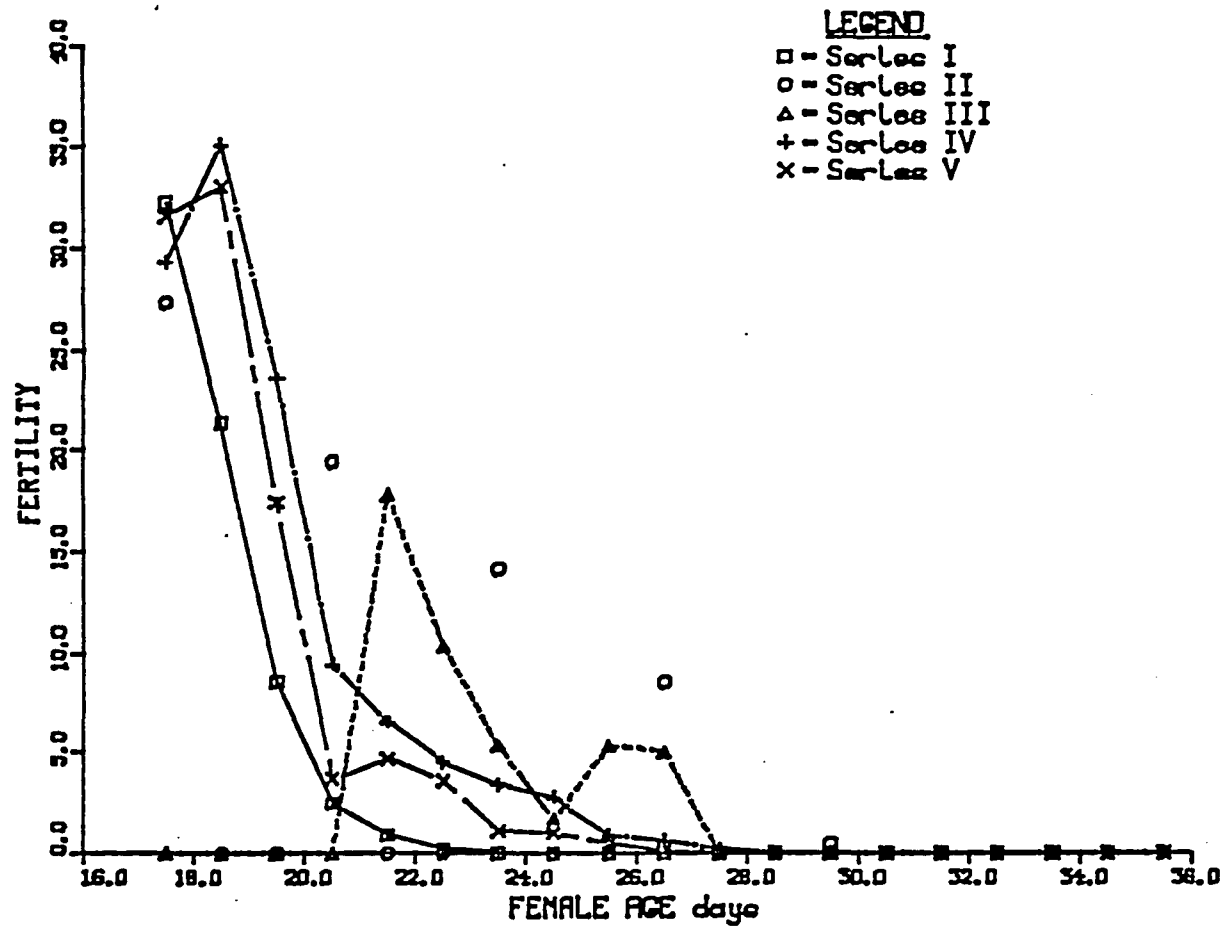


TABLE 5. Life and fertility table and daily sex ratio  
for the 24h continuous contact cohort (Series I),  
exposed to Drosophila simulans.

| x    | l(x) | m(x)  | sex ratio |
|------|------|-------|-----------|
| 17.5 | 1000 | 32.16 | 0.274     |
| 18.5 | 1000 | 21.28 | 0.548     |
| 19.5 | 1000 | 8.50  | 0.793     |
| 20.5 | 1000 | 2.48  | 0.895     |
| 21.5 | 1000 | 0.88  | 0.933     |
| 22.5 | 960  | 0.17  | 0.985     |
| 23.5 | 920  | 0.00  | 1.000     |
| 24.5 | 840  | 0.00  | 1.000     |
| 25.5 | 520  | 0.00  | 1.000     |
| 26.5 | 360  | 0.00  | 1.000     |
| 27.5 | 360  | 0.00  |           |
| 28.5 | 320  | 0.00  |           |
| 29.5 | 240  | 0.00  |           |
| 30.5 | 120  | 0.00  |           |
| 31.5 | 80   | 0.00  |           |
| 32.5 | 40   | 0.00  |           |
| 33.5 | 40   | 0.00  |           |

$R_0 = 65.46$

$T_c = 18.26$

$'r' = 0.229$

TABLE 6. Life and fertility table and daily sex ratio  
for the intermittent contact cohort (Series II),  
exposed to Drosophila simulans.

| x    | l (x) | m (x) | sex ratio |
|------|-------|-------|-----------|
| 17.5 | 1000  | 27.20 | 0.291     |
| 18.5 | 1000  | ----- | -----     |
| 19.5 | 1000  | ----- | -----     |
| 20.5 | 920   | 19.44 | 0.425     |
| 21.5 | 840   | ----- | -----     |
| 22.5 | 840   | ----- | -----     |
| 23.5 | 840   | 14.14 | 0.486     |
| 24.5 | 760   | ----- | -----     |
| 25.5 | 640   | ----- | -----     |
| 26.5 | 520   | 8.46  | 0.715     |
| 27.5 | 320   | ----- | -----     |
| 28.5 | 160   | ----- | -----     |
| 29.5 | 160   | 0.50  | 0.923     |
| 30.5 | 40    | ----- | -----     |
| 31.5 | 40    | ----- | -----     |

$R_0 = 61.44$

$T_c = 20.58$

'r' = 0.200

TABLE 7. Life and fertility table and daily sex ratio  
for the delayed contact cohort (Series III),  
exposed to Drosophila simulans.

---

| x    | l (x) | m (x) | sex ratio |
|------|-------|-------|-----------|
| 17.5 | 1000  | ----- | -----     |
| 18.5 | 1000  | ----- | -----     |
| 19.5 | 1000  | ----- | -----     |
| 20.5 | 840   | ----- | -----     |
| 21.5 | 640   | 17.75 | 0.503     |
| 22.5 | 640   | 10.25 | 0.660     |
| 23.5 | 600   | 5.27  | 0.688     |
| 24.5 | 440   | 1.73  | 0.924     |
| 25.5 | 160   | 5.25  | 0.462     |
| 26.5 | 80    | 5.00  | 0.333     |
| 27.5 | 40    | 0.00  | 1.000     |

R = 23.08  
.0

T = 22.37  
c

'r' = 0.140

TABLE 8. Life and fertility table and daily sex ratio for the 'new male' cohort (Series IV), exposed to Drosophila simulans.

| x    | l(x) | m(x)  | sex ratio |
|------|------|-------|-----------|
| 17.5 | 1000 | 29.24 | 0.321     |
| 18.5 | 1000 | 35.08 | 0.298     |
| 19.5 | 1000 | 23.60 | 0.373     |
| 20.5 | 1000 | 9.36  | 0.443     |
| 21.5 | 1000 | 6.52  | 0.508     |
| 22.5 | 1000 | 4.48  | 0.627     |
| 23.5 | 1000 | 3.40  | 0.593     |
| 24.5 | 880  | 2.77  | 0.667     |
| 25.5 | 680  | 0.88  | 0.595     |
| 26.5 | 360  | 0.56  | 0.333     |
| 27.5 | 200  | 0.20  | 0.500     |
| 28.5 | 160  | 0.00  |           |
| 29.5 | 160  | 0.00  |           |
| 30.5 | 80   | 0.00  |           |
| 31.5 | 40   | 0.00  |           |
| 32.5 | 40   | 0.00  |           |
| 33.5 | 40   | 0.00  |           |
| 34.5 | 40   | 0.00  |           |
| 35.5 | 40   | 0.00  |           |

R = 114.96  
0

T = 19.27  
c

'r' = 0.246

TABLE 9. Life and fertility table and daily sex ratio  
for the 'honey yeast' cohort (Series V),  
exposed to Drosophila simulans.

| x    | l(x) | m(x)  | sex ratio |
|------|------|-------|-----------|
| 17.5 | 1000 | 31.56 | 0.299     |
| 18.5 | 960  | 33.04 | 0.348     |
| 19.5 | 960  | 17.42 | 0.477     |
| 20.5 | 920  | 3.65  | 0.607     |
| 21.5 | 920  | 4.70  | 0.639     |
| 22.5 | 920  | 3.55  | 0.689     |
| 23.5 | 880  | 1.09  | 0.822     |
| 24.5 | 800  | 0.95  | 0.824     |
| 25.5 | 760  | 0.47  | 0.727     |
| 26.5 | 680  | 0.06  | 0.800     |
| 27.5 | 680  | 0.00  | 1.000     |
| 28.5 | 560  | 0.00  |           |
| 29.5 | 400  | 0.00  |           |
| 30.5 | 280  | 0.00  |           |
| 31.5 | 280  | 0.00  |           |
| 32.5 | 280  | 0.00  |           |
| 33.5 | 240  | 0.00  |           |
| 34.5 | 80   | 0.00  |           |
| 35.5 | 80   | 0.00  |           |

R = 93.06  
0

T = 18.82  
c

'r' = 0.241

Evaluating the days of male production as a percentage of the total exposure period allows all cohorts to be compared. Continuously exposed cohorts produced male progeny during 65%, 87.1%, and 84.4% of their average life span (Series V, IV, and I respectively), while Series II produced male progeny during 98.8% of its total exposure time and Series III, during 92.3% of its exposure time.

This difference in effective use of time in producing male progeny is reflected in the variable PRP-t, the post-reproductive period for total offspring. In general, females tended to produce male progeny for a longer period of time than they produced female progeny. However, in certain instances the opposite was true, or both sexes were produced over an equal time period. Therefore the mean total post-reproductive period, or the mean number of days that females survived and produced no offspring at all is essentially equivalent to the mean post-reproductive period for male progeny production.

Series V, the longest lived cohort, spent 35% of its life span not producing male progeny and its corresponding PRP-t is significantly longer than any other comparable cohort. Series I and IV show no difference in PRP-t. Series II produced progeny throughout its exposure periods and hence had PRP-t=0.0. Series III had a PRP-t of  $0.2 \pm 0.1$  (mean  $\pm$  standard error) and hence although also quite low, did



differ significantly from that of Series II. The total post reproductive period for Series III did not differ significantly from that of Series I or IV (see tables 10-19).

Generally, we find that cohorts discontinuously presented with hosts are able to extend their male production schedules and utilize available exposure periods more effectively than their continuously exposed counterparts.

Days of female production and the  
post-reproductive period for  
female progeny production

Series I produced female progeny for only  $3.3 \pm 0.3$  days. This value is significantly lower than that of the two other comparable cohorts. Series IV, the cohort with a periodic influx of males, produced female progeny for  $7.1 \pm 0.5$  days (73.2%). This value is significantly higher than those of Series I, or V, and is comparable to the corresponding percentages of time spent in female production in Series II (83.1%) and Series III (65%) (see tables 10-19).

Correspondingly, the mean number of days spent living past the last day of female progeny production (i.e., PRP-f) is significantly lower in Series IV than in Series I or V. Although Series V females spent significantly more absolute time in female progeny production than Series I, both cohorts spent relatively equivalent percentages of their life spans in producing females (33.8% and 43.2% for Series

I and V, respectively). Indeed, no significant difference could be found between their PRP-f's.

Series II, the intermittent exposure cohort, which spent 83.1% of its exposure time in female production, exhibited the lowest PRP-f; significantly lower than that of any other cohort. Series III, the delayed cohort, which spent 65% of its life span in female production had a significantly lower PRP-f than Series I or V, but did not differ significantly from Series IV (see tables 10-19).

From the daily changes in sex ratio it seems that females in cohorts that were presented with single males and hosts on a continuous basis exhausted their sperm supply within the first 2-4 days of oviposition and thereafter produced a preponderance of male progeny. However, in later experiments, dissections of spermathecae from comparably treated "older females" did show the presence of sperm in some instances. Therefore, we must look for some other phenomena, such as exhaustion of spermathecal gland secretions, with results that are essentially equivalent to sperm depletion.

Although Series IV did produce female progeny for a significantly longer period of time than any other cohort and did show a decrease in sex ratio later in its existence, this data can not resolve the question of monandry. Somehow the presence of new males affected the distribution of female progeny in this cohort, and although the data here

may be suggestive of multiple matings, there is no hard evidence to support that contention.

#### Numbers of progeny

Series I produced a significantly higher mean number of male progeny per fertilized female than any other cohort. This same cohort produced significantly fewer female offspring, on the average, than all comparable cohorts (i.e., Series IV and V). Series IV produced a significantly higher mean number of female progeny than any other cohort (see tables 10-19). The mean number of total progeny produced per female does not differ significantly between the three continuously exposed cohorts, nor between them and the continuous cohort described earlier. The assumption made earlier that females of the same strain, given similar exposure schedules and the same host species, have an equal capacity to produce successful adult progeny is validated. The availability, viability, and distribution of sperm is the variable that will determine the shape of the fertility (s.s) distribution and the net reproductive rate. Furthermore, the distribution of successful fertilizations is a function of host availability and the intensity of oviposition. The mean number of female progeny produced per female does not differ significantly between Series I, II, or III. The mean number of total offspring does not differ significantly between Series II and III, but both cohorts produce significantly fewer total offspring than their continuously exposed counterparts.

## Survivorship

The marked, but not significant, decrease in survivorship in series II and III can be attributed to two major causes. In both cohorts, when females were not exposed to hosts they were kept in standard vials with medium and honey. The lack of host larvae in these vials led to the development of a bacterial slime on the surface of the medium and many females died after being caught in this slime. Other females died while attempting to escape from the hostless vials. In these escape attempts, the females would become embedded in the foam stoppers and die there. Joop C. van Lenteren (pers. comm.) has found the same problem to occur with L. heterotoma and James (1928) encountered a similar problem with Kleidotoma.

The increased longevity in Series V, although not significant, may be attributable to the addition of activated yeast to the honey droplet fed to the parasitoids.

## Fecundity

The fecundity distribution of Series I follows the typical pattern, i.e. early explosive reproduction followed by a rapid and significant decline leading to an extended post-reproductive period.

Series II and III show trends that might be expected when host availability was intermittent or delayed. In both cases the females were able to successfully reproduce at

later ages than their Series I counterparts. In addition, females were able to reproduce through a greater percentage of their oviposition periods. It should be noted that the longevities are shorter and fecundities lower in these cohorts when compared to those from Series I, IV, and V but this is due, as will become evident in later experiments, to handling problems more than anything else. The fecundity distribution for Series V is essentially the same as that for any 'continuous exposure' cohort, while the fecundity distribution for Series IV is an interesting variation on that theme, with its significantly high number of female offspring coupled with increased time spent in female production.

The questions posed after the first set of experiments concerning post-reproductive survival now have been partly answered. By altering the schedules of host availability we can significantly increase the efficient utilization of host patches in producing female progeny. Although the absolute number of progeny may be decreased, the time spent in female progeny production, relative to lifespan and overall exposure time increases, and the post reproductive survival period decreases, significantly.

Interpretation. Two factors are evidently involved in the overall progeny production schedules. The first is the age of the female. A comparison of the progeny production schedules in Series I and Series III indicates that older

TABLE 10. Reproductive variables for the Series I and Series II cohorts exposed to D. simulans (mean  $\pm$  SE).

| Variable                                        | Series I<br>(24) | Series II<br>(24)  |
|-------------------------------------------------|------------------|--------------------|
| Length of life                                  | 9.9 $\pm$ 0.6    | 9.2 $\pm$ 0.7      |
| Days of male production                         | 8.3 $\pm$ 0.4    | 3.4 $\pm$ 0.2 @    |
| Days of female production                       | 3.3 $\pm$ 0.3    | 2.9 $\pm$ 0.2 @    |
| Total male progeny                              | 116.1 $\pm$ 7.5  | 48.4 $\pm$ 8.1 **  |
| Total female progeny                            | 66.0 $\pm$ 7.2   | 60.9 $\pm$ 6.2     |
| Total progeny                                   | 182.1 $\pm$ 6.4  | 109.3 $\pm$ 9.2 ** |
| Post reproductive period<br>for fertilized eggs | 6.4 $\pm$ 0.7    | 0.5 $\pm$ 0.2 **   |
| Total post reproductive<br>period               | 1.6 $\pm$ 0.4    | 0.0 $\pm$ 0.0 **   |

Symbols: \* =  $p < .05$ , \*\* =  $p < .01$ , @ = not comparable

TABLE 11. Reproductive variables for the Series I and Series III cohorts exposed to D. simulans (mean  $\pm$  SE).

| Variable                                        | Series I<br>(24) | Series III<br>(9)   |
|-------------------------------------------------|------------------|---------------------|
| Length of life                                  | 9.9 $\pm$ 0.6    | 8.4 $\pm$ 0.4       |
| Days of male production                         | 8.3 $\pm$ 0.4    | 4.2 $\pm$ 0.4 @     |
| Days of female production                       | 3.3 $\pm$ 0.3    | 2.9 $\pm$ 0.5 @     |
| Total male progeny                              | 116.1 $\pm$ 7.5  | 56.8 $\pm$ 11.5 **  |
| Total female progeny                            | 66.0 $\pm$ 7.2   | 46.2 $\pm$ 9.7      |
| Total progeny                                   | 182.1 $\pm$ 6.4  | 103.0 $\pm$ 10.4 ** |
| Post reproductive period<br>for fertilized eggs | 6.4 $\pm$ 0.7    | 1.6 $\pm$ 0.4 **    |
| Total post reproductive<br>period               | 1.6 $\pm$ 0.4    | 0.2 $\pm$ 0.1 *     |

Symbols: \* =  $p < .05$ , \*\* =  $p < .01$ , @ = not comparable

TABLE 12. Reproductive variables for the Series I and Series IV cohorts exposed to D. simulans (mean  $\pm$  SE).

| Variable                                        | Series I<br>(24) | Series IV<br>(23)  |
|-------------------------------------------------|------------------|--------------------|
| Length of life                                  | 9.9 $\pm$ 0.6    | 9.7 $\pm$ 0.5      |
| Days of male production                         | 8.3 $\pm$ 0.4    | 8.1 $\pm$ 0.2      |
| Days of female production                       | 3.3 $\pm$ 0.3    | 7.1 $\pm$ 0.5 **   |
| Total male progeny                              | 116.1 $\pm$ 7.5  | 65.4 $\pm$ 6.5 **  |
| Total female progeny                            | 66.0 $\pm$ 7.2   | 124.2 $\pm$ 7.0 ** |
| Total progeny                                   | 182.1 $\pm$ 6.4  | 189.7 $\pm$ 6.6    |
| Post reproductive period<br>for fertilized eggs | 6.4 $\pm$ 0.7    | 2.7 $\pm$ 0.6      |
| Total post reproductive<br>period               | 1.6 $\pm$ 0.4    | 1.2 $\pm$ 0.4 **   |

Symbols: \* =  $p < .05$ , \*\* =  $p < .01$ , @ = not comparable



TABLE 13. Reproductive variables for the Series I and Series V cohorts exposed to D. simulans (mean  $\pm$  SE).

| Variable                                        | Series I<br>(24) | Series V<br>(25)  |
|-------------------------------------------------|------------------|-------------------|
| Length of life                                  | 9.9 $\pm$ 0.6    | 11.7 $\pm$ 0.9    |
| Days of male production                         | 8.3 $\pm$ 0.4    | 7.6 $\pm$ 0.5     |
| Days of female production                       | 3.3 $\pm$ 0.3    | 4.9 $\pm$ 0.6 *   |
| Total male progeny                              | 116.1 $\pm$ 7.5  | 71.6 $\pm$ 8.0 ** |
| Total female progeny                            | 66.0 $\pm$ 7.2   | 92.9 $\pm$ 8.7 *  |
| Total progeny                                   | 182.1 $\pm$ 6.4  | 164.5 $\pm$ 9.3   |
| Post reproductive period<br>for fertilized eggs | 6.4 $\pm$ 0.7    | 6.8 $\pm$ 1.0     |
| Total post reproductive<br>period               | 1.6 $\pm$ 0.4    | 3.8 $\pm$ 0.6 **  |

Symbols: \* =  $p < .05$ , \*\* =  $p < .01$ , @ = not comparable

TABLE 14. Reproductive variables for the Series II and Series III cohorts exposed to D. simulans (mean  $\pm$  SE).

| Variable                  | Series II<br>(24) | Series III<br>(9) |
|---------------------------|-------------------|-------------------|
| Length of life            | 9.2 $\pm$ 0.7     | 8.4 $\pm$ 0.4     |
| Days of male production   | 3.4 $\pm$ 0.2     | 4.2 $\pm$ 0.4     |
| Days of female production | 2.9 $\pm$ 0.2     | 2.9 $\pm$ 0.5     |
| Total male progeny        | 48.4 $\pm$ 8.1    | 56.8 $\pm$ 11.5   |
| Total female progeny      | 60.9 $\pm$ 6.2    | 46.2 $\pm$ 9.7    |
| Total progeny             | 109.3 $\pm$ 9.2   | 103.0 $\pm$ 10.4  |
| Post reproductive period  |                   |                   |
| for fertilized eggs       | 0.5 $\pm$ 0.2     | 1.6 $\pm$ 0.4 *   |
| Total post reproductive   |                   |                   |
| period                    | 0.0 $\pm$ 0.0     | 0.2 $\pm$ 0.1     |

Symbols: \* =  $p < .05$ , \*\* =  $p < .01$ , @ = not comparable

TABLE 15. Reproductive variables for the Series II and Series IV cohorts exposed to D. simulans (mean  $\pm$  SE).

| Variable                                        | Series II<br>(24) | Series IV<br>(23)  |
|-------------------------------------------------|-------------------|--------------------|
| Length of life                                  | 9.2 $\pm$ 0.7     | 9.7 $\pm$ 0.5      |
| Days of male production                         | 3.4 $\pm$ 0.2     | 8.1 $\pm$ 0.2 @    |
| Days of female production                       | 2.9 $\pm$ 0.2     | 7.1 $\pm$ 0.5 @    |
| Total male progeny                              | 48.4 $\pm$ 8.1    | 65.4 $\pm$ 6.5 *   |
| Total female progeny                            | 60.9 $\pm$ 6.2    | 124.2 $\pm$ 7.0 ** |
| Total progeny                                   | 109.3 $\pm$ 9.2   | 189.7 $\pm$ 6.6 ** |
| Post reproductive period<br>for fertilized eggs | 0.5 $\pm$ 0.2     | 2.7 $\pm$ 0.6 **   |
| Total post reproductive<br>period               | 0.0 $\pm$ 0.0     | 1.2 $\pm$ 0.4 **   |

Symbols: \*=  $p < .05$ , \*\*=  $p < .01$ , @= not comparable

TABLE 16. Reproductive variables for the Series II and Series V cohorts exposed to D. simulans (mean  $\pm$  SE).

| Variable                                        | Series II<br>(24) | Series V<br>(25)   |
|-------------------------------------------------|-------------------|--------------------|
| Length of life                                  | 9.2 $\pm$ 0.7     | 11.7 $\pm$ 0.9 *   |
| Days of male production                         | 3.4 $\pm$ 0.2     | 7.6 $\pm$ 0.5 @    |
| Days of female production                       | 2.9 $\pm$ 0.2     | 4.9 $\pm$ 0.6 @    |
| Total male progeny                              | 48.4 $\pm$ 8.1    | 71.6 $\pm$ 8.0 **  |
| Total female progeny                            | 60.9 $\pm$ 6.2    | 92.9 $\pm$ 8.7     |
| Total progeny                                   | 109.3 $\pm$ 9.2   | 164.5 $\pm$ 9.3 ** |
| Post reproductive period<br>for fertilized eggs | 0.5 $\pm$ 0.2     | 6.8 $\pm$ 1.0 **   |
| Total post reproductive<br>period               | 0.0 $\pm$ 0.0     | 3.8 $\pm$ 0.6 **   |

Symbols: \* =  $p < .05$ , \*\* =  $p < .01$ , @ = not comparable

TABLE 17. Reproductive variables for the Series III and Series IV cohorts exposed to D. simulans (mean  $\pm$  SE).

| Variable                                        | Series III<br>(9) | Series IV<br>(23)  |
|-------------------------------------------------|-------------------|--------------------|
| Length of life                                  | 8.4 $\pm$ 0.4     | 9.7 $\pm$ 0.5      |
| Days of male production                         | 4.2 $\pm$ 0.4     | 8.1 $\pm$ 0.2 @    |
| Days of female production                       | 2.9 $\pm$ 0.5     | 7.1 $\pm$ 0.5 @    |
| Total male progeny                              | 56.8 $\pm$ 11.5   | 65.4 $\pm$ 6.5     |
| Total female progeny                            | 46.2 $\pm$ 9.7    | 124.2 $\pm$ 7.0 ** |
| Total progeny                                   | 103.0 $\pm$ 10.4  | 189.7 $\pm$ 6.6 ** |
| Post reproductive period<br>for fertilized eggs | 1.6 $\pm$ 0.4     | 2.7 $\pm$ 0.6      |
| Total post reproductive<br>period               | 0.2 $\pm$ 0.1     | 1.2 $\pm$ 0.4 *    |

Symbols: \* =  $p < .05$ , \*\* =  $p < .01$ , @ = not comparable

TABLE 18. Reproductive variables for the Series III and Series V cohorts exposed to D. simulans (mean  $\pm$  SE).

| Variable                                        | Series III<br>(9) | Series V<br>(25)   |
|-------------------------------------------------|-------------------|--------------------|
| Length of life                                  | 8.4 $\pm$ 0.4     | 11.7 $\pm$ 0.9 *   |
| Days of male production                         | 4.2 $\pm$ 0.4     | 7.6 $\pm$ 0.5 @    |
| Days of female production                       | 2.9 $\pm$ 0.5     | 4.9 $\pm$ 0.6 @    |
| Total male progeny                              | 56.8 $\pm$ 11.5   | 71.6 $\pm$ 8.0     |
| Total female progeny                            | 46.2 $\pm$ 9.7    | 92.9 $\pm$ 8.7 **  |
| Total progeny                                   | 103.0 $\pm$ 10.4  | 164.5 $\pm$ 9.3 ** |
| Post reproductive period<br>for fertilized eggs | 1.6 $\pm$ 0.4     | 6.8 $\pm$ 1.0 **   |
| Total post reproductive<br>period               | 0.2 $\pm$ 0.1     | 3.8 $\pm$ 0.6 **   |

Symbols: \* =  $p < .05$ , \*\* =  $p < .01$ , @ = not comparable

TABLE 19. Reproductive variables for the Series IV and Series V cohorts exposed to D. simulans (mean  $\pm$  SE).

| Variable                                        | Series IV<br>(23) | Series V<br>(25)  |
|-------------------------------------------------|-------------------|-------------------|
| Length of life                                  | 9.7 $\pm$ 0.5     | 11.7 $\pm$ 0.9    |
| Days of male production                         | 8.1 $\pm$ 0.2     | 7.6 $\pm$ 0.5     |
| Days of female production                       | 7.1 $\pm$ 0.5     | 4.9 $\pm$ 0.6 **  |
| Total male progeny                              | 65.4 $\pm$ 6.5    | 71.6 $\pm$ 8.0    |
| Total female progeny                            | 124.2 $\pm$ 7.0   | 92.9 $\pm$ 8.7 ** |
| Total progeny                                   | 189.7 $\pm$ 6.6   | 164.5 $\pm$ 9.3 * |
| Post reproductive period<br>for fertilized eggs | 2.7 $\pm$ 0.6     | 6.8 $\pm$ 1.0 **  |
| Total post reproductive<br>period               | 1.2 $\pm$ 0.4     | 3.8 $\pm$ 0.6 **  |

Symbols: \* =  $p < .05$ , \*\* =  $p < .01$ , @ = not comparable

females, when presented with hosts for the first time, are not as productive as younger females. This conclusion, although intuitively pleasing can not be accepted without differentiating between the effects of stress and the effects of age on the reproductive physiology of Series III females. The extremely low survivorship of the cohort, the loss of females prior to host exposure and their suicidal attempts at dispersal from the hostless vials can not be overlooked. It is commonly accepted that selection in predators and parasitoids should act to maximize the rate of host utilization or energy intake (Cook & Hubbard, 1977; Hassel, 1978; Waage, 1978, 1979), and therefore that a host patch should be left when it no longer becomes profitable to search. This has been shown by van Lenteren (1976) to occur in L. heterotoma. Moreover, as Doutt (1959), Vinson (1976) and Waage (1978, 1979) have pointed out, the initiation of searching by a parasitoid is not random, but is in response to stimuli associated with the presence of hosts within a particular patch. Although fermenting activated yeast is a long range host habitat cue and an arrestment and searching stimulus for L. bouhardi (Carton, 1978), yeasted banana medium is not (Kopelman, unpublished data). As Waage (1979) points out, there are at least two levels of stimuli that elicit arrestment (orthokinesis) and searching behavior in a parasitoid : (1) stimuli such as host-produced contact chemicals that induce arrestment in a particular patch, and



(2) stimuli associated with direct prey contact that maintain the level of foraging within the patch. Neither stimuli are present in hostless vials. It is not surprising therefore that females engage in energy consuming and often suicidal attempts at dispersal. Indeed, dispersal from a useless host patch must be a part of any adaptive searching strategy. Therefore, the "drive" to disperse and the energy utilized to do so may significantly affect the subsequent physiology and reproductive capacity of a female.

A decrease in progeny production with time is, on the other hand, a natural consequence of organisms that reproduce repeatedly (Giesel, 1976). What is the second factor in this species that determines the reproductive schedule of a female? The data indicates quite clearly that the amount of previous ovipositional experience is a factor, which in addition to age, determines the reproductive schedule of a female. In this species it is the interaction between age and previous host exposure that determines the "time-specific" reproductive characteristics.

These proovigenic females emerge as adults with their entire egg complement, and can be inseminated and begin ovipositing successfully within 24 hours. If high density host patches are available for oviposition, the female will utilize them to produce a maximum yield of progeny. In continuously exposed cohorts this maximal effort will continue at a high rate for the first three to four days of

exposure. In all above cases the total number of progeny produced on the fourth day of exposure decreased 55-70% from the previous days total and became successively lower with time. After three days of oviposition, Series I, IV and V had produced 72, 69 and 75% of their total successful ovipositions. This point in time also corresponded to the point at which the sex ratio changed from female to male biased. We can infer from these points that the explosive rates of oviposition early in life led to (a) rapid exhaustion of sperm or spermathecal gland secretions, and either (b) exhaustion of ovipositor musculature, or (c) a significant loss in the "drive" to oviposit by virtue of a significant decrease in the number of eggs in the female's ovaries. These effects, coupled with the effect of age, must determine the reproductive schedules of females. Thus the term "age-specific reproductive characteristics" must be used carefully with the knowledge that much more than "age" is involved.

These first sets of experiments involved in altering the patterns of host availability did seem to corroborate the hypothesis stated earlier that the reproductive tactics of *L. boulandi* are determined by host availability and not necessarily by the age of the female. However, further experiments were conducted and are discussed next.

## Summary

A simultaneous series of life-history experiments were conducted using sympatric strains of D. simulans and L. bouhardi. Five cohorts were presented with hosts under continuous (Series I, IV, V), intermittent (Series II), and delayed (Series III) schedules. In the three continuously exposed cohorts females were periodically presented with new males in one, yeast was added to the parasitoids' food as a source of protein in another, and the third acted as a control.

Although females were shorter lived in the discontinuously exposed cohorts and longer lived in the honey-yeast fed cohort, the differences were not significant in comparison to the control. All cohorts exhibited the type 1 survivorship curve of Pearl (1928). The continuously exposed cohorts exhibited the early peaked, "explosive" progeny production schedules with extensive post-reproductive periods. Females in the delayed and intermittent cohorts produced fewer progeny per female, but maintained progeny production through later ages and all but eliminated their post-reproductive periods. While the number of total progeny per female did not differ between the continuously exposed cohorts, the cohort presented periodically with new males did produce significantly more females per female than any other. The assumption that females of the same strain, given similar exposure schedules

and the same host species have an equal capacity to produce successful progeny, is validated. Further, it is suggested that the availability, viability, and the distribution of sperm that will determine the shape of the fertility (s.s.) distribution. The distribution of successful fertilization is shown to be a function of host availability, the intensity of oviposition, as well as age.

### Experiment 3. Host-Parasitoid Contact Limited to Daily One Hour Periods

#### Introduction

In an attempt to further extend the reproductive life span of L. boulardi another life table experiment was conducted in which female wasps were exposed to D. simulans larvae for a 1 hour period daily throughout their lives.

The previous experiments involving varied host availability schedules were an attempt to exposed wasps to a more natural situation in which hosts were patchily distributed in time. This led to an extension of oviposition distributions to later parasitoid ages. Following in this trend, it was my intention in this experiment to extend the distribution of successful ovipositions to its physiological limit by allowing host-parasitoid contact for only extremely short daily period.

#### Materials and Methods

L. boulardi from the Ha 75 stock and a sympatric population of D. simulans were used in this experiment. Conditions described earlier for the maintenance and production of host vials were followed. A cohort of 50 individual pairs of wasps were simultaneously presented vials of hosts for 1 hour per day until all females died. As before, daily survivorship was recorded and parasite emergence data was taken on a regular basis begining 17.5 days after the first oviposition period. Mean female

progeny production per female per day of exposure are used as the fertility value. When females were not presented with hosts, they were kept in standard vials with medium and honey. To insure against females dying in the bacterial overgrowth in hostless vials, the vials were changed every other day. As before, all experiments and stock maintenance was conducted at  $25 \pm 1$  °C, 70% RH and 16L:8D photoperiod.

### Results

Of the fifty females, one was lost during the experiment and two were not fertilized. The survivorship data is based upon a cohort of 49, while all other data is based upon a cohort of 47.

The survivorship and fecundity distributions

This cohort, as all others, displayed the typical "type 1" survivorship distribution (Pearl, 1928), with a mean length of life of  $11.5 \pm 0.3$  days. The survivorship and fecundity distributions (figures 19 and 20) show that this cohort was able to extend its production of female progeny throughout all but its last day of existence. Both male and female progeny were produced throughout 88% of the cohort's average life span ( $10.1 \pm 0.3$ , and  $10.1 \pm 0.3$  for males and females, respectively) (see tables 20-21), with a post-reproductive period of  $1.4 \pm 0.3$  for female progeny production and  $0.1 \pm 0.2$  for total progeny production. 95% of all female progeny were not produced until the 10th oviposition period. The sex ratio of the progeny produced

Figure 19. Survivorship curve for the Ha75 strain of L. bouhardi exposed to D. simulans (Ha strain) hosts for 1 limited periods daily.

Survivorship curve for  
the LIMITED cohort, one hour exposure  
host, *Drosophila simulans*  
LTD

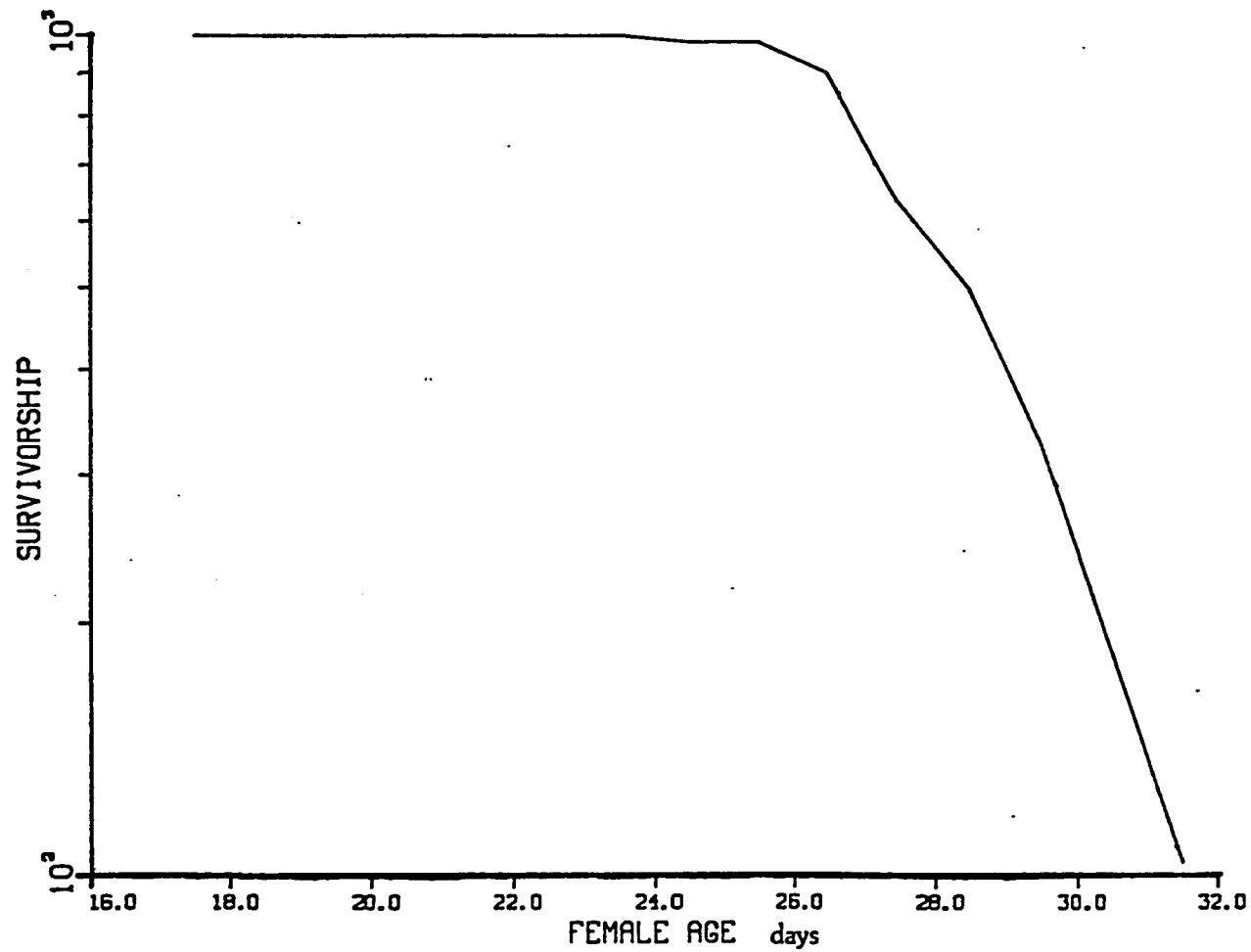
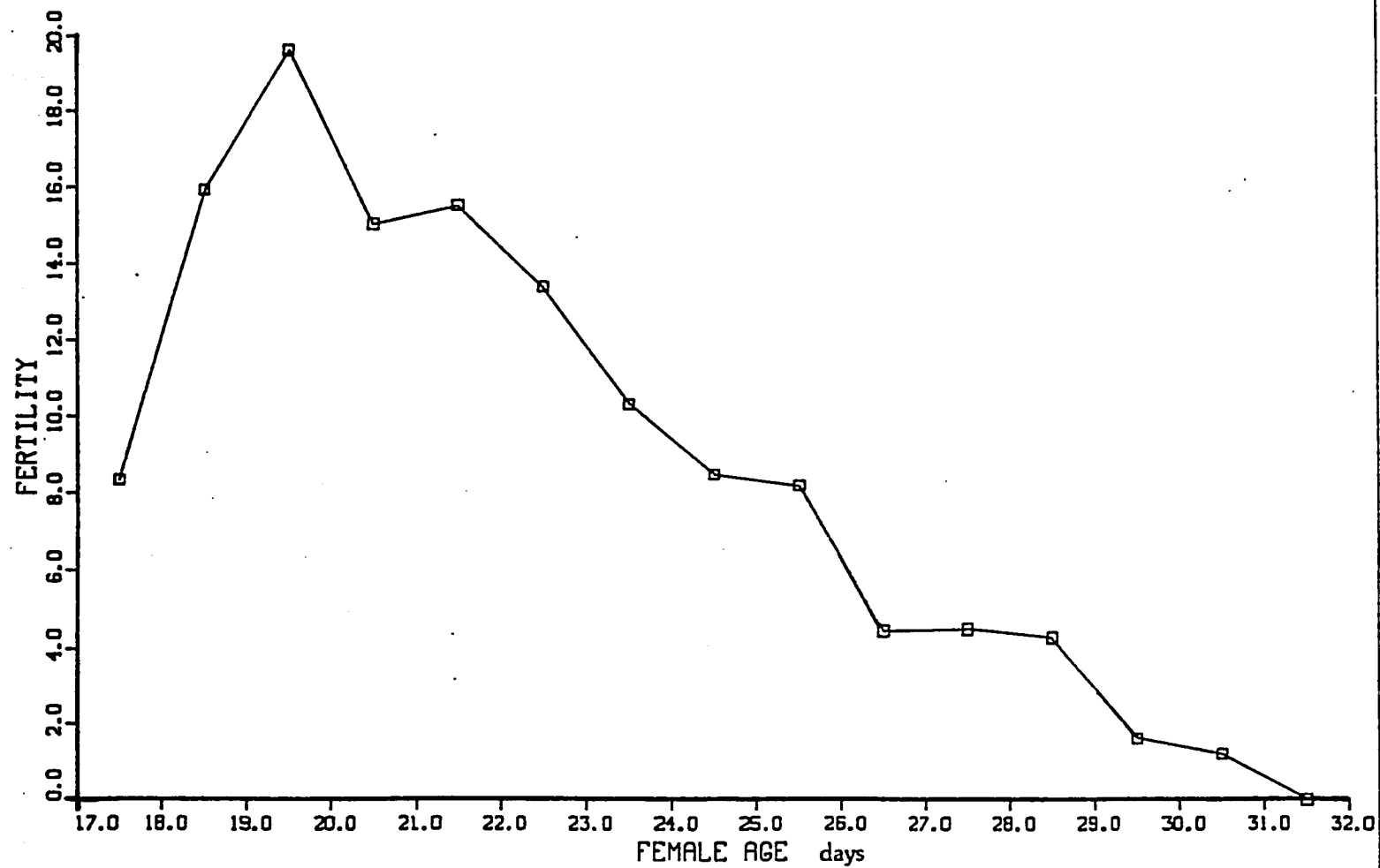




Figure 20. Fertility curve for the Ha75 strain of L. bouhardi exposed to D. simulans (Ha strain) hosts for 1 limited periods daily.

Fertility curve for  
the LIMITED cohort, one hour exposure  
host, *Drosophila simulans*  
LTD



per day of exposure (see table 20 ) was highly female biased for much of the reproductive span of this cohort and unlike the other experiments, the daily sex ratio never rose above 0.593.

To better appreciate the data presented here one must compare it to that of a representative continuously exposed cohort. Lacking a simultaneously conducted continuous exposure cohort, I have chosen to use the data from the D. simulans reared cohort in the first experiment. Both cohorts have a similar number of replicates (49 and 47) and the same host species, and were conducted under the same conditions differing only in the daily period of host-parasite contact. However, these cohorts were conducted at two different times, and comparisons must be considered in that light. Even though the absolute values of the variables are not directly comparable, the trends that they express are nonetheless realistic and meaningful. Table 21 presents the variables, and table 63 (appendix), the analyses.

Length\_\_of\_\_life. The limited exposure cohort was significantly shorter lived than the earlier continuous cohort. Of all the variables, length of life is the least comparable between experiments run at different times. However, in light of the trends exhibited in other experiments in which the discontinuously exposed cohorts are

TABLE 20. Life and fertility table and daily sex ratio  
for the limited contact cohort exposed to  
Drosophila simulans for 1 hr periods daily.

---

| x    | l(x)  | m(x)   | sex ratio |
|------|-------|--------|-----------|
| 17.5 | 1000  | 8.340  | 0.232     |
| 18.5 | 1000  | 15.940 | 0.215     |
| 19.5 | 1000  | 19.620 | 0.251     |
| 20.5 | 1000  | 15.041 | 0.264     |
| 21.5 | 1000  | 15.531 | 0.247     |
| 22.5 | 1000  | 13.388 | 0.281     |
| 23.5 | 1000  | 10.306 | 0.311     |
| 24.5 | 979.6 | 8.479  | 0.364     |
| 25.5 | 979.6 | 8.188  | 0.377     |
| 26.5 | 898   | 4.477  | 0.396     |
| 27.5 | 632.7 | 4.516  | 0.453     |
| 28.5 | 498.9 | 4.292  | 0.411     |
| 29.5 | 326.6 | 1.625  | 0.552     |
| 30.5 | 183.7 | 1.222  | 0.593     |
| 31.5 | 104.1 | 0.000  |           |

$$R_0 = 124.267$$

$$T_c = 21.61$$

$$'r' = 0.223$$

TABLE 21. Reproductive variables for the limited (1 hour) exposure cohort (n=47) and the continuous exposure cohort (n=49) exposed to D. simulans (mean  $\pm$  SE).

| Variable                                        | Limited cohort  | Continuous cohort |
|-------------------------------------------------|-----------------|-------------------|
| Length of life                                  | 11.5 $\pm$ 0.3  | 13.6 $\pm$ 0.4 ** |
| Days of male production                         | 10.1 $\pm$ 0.3  | 9.7 $\pm$ 0.2     |
| Days of female production                       | 10.1 $\pm$ 0.3  | 5.2 $\pm$ 0.3 **  |
| Total male progeny                              | 45.4 $\pm$ 2.7  | 90.9 $\pm$ 5.0 ** |
| Total female progeny                            | 129.3 $\pm$ 4.7 | 93.5 $\pm$ 5.0 ** |
| Total progeny                                   | 174.7 $\pm$ 5.7 | 184.4 $\pm$ 5.2   |
| Post reproductive period<br>for fertilized eggs | 1.4 $\pm$ 0.3   | 8.4 $\pm$ 0.6 *   |
| Total post reproductive<br>period               | 1.0 $\pm$ 0.2   | 4.0 $\pm$ 0.4 *   |

Symbols: \* =  $p < .05$ , \*\* =  $p < .01$ , @ = not comparable

generally shorter lived than their continuously exposed counterparts, this result is not surprising.

Days of male production. The mean number of days spent by females in ovipositing successful male progeny does not differ significantly. Male progeny production encompassed 71% of the mean female life span in the continuous cohort, and 88% in the limited cohort.

Days of female production and post-reproductive survival. The limited cohort spent significantly more exposure periods ovipositing female eggs than did the continuous cohort. The average female in the continuous cohort spent 38.2% of her life span producing female eggs, while her counterpart in the limited cohort produced female progeny for 88% of her mean life span. This highly significant difference is not an artifact of the longer life span of the earlier cohort, but represents a biologically meaningful fact exhibited clearly in the previous experiment. That is, that limiting daily host exposure can increase the length of time during which a female can successfully oviposit fertilized eggs. Moreover, the most important comparisons are those comparing both PRP-t and PRP-f between these cohorts. Both variables were significantly lower in the limited cohort. In fact, in this cohort, only two females survived for just one day past the last period of producing successful female progeny (see tables 20-21).

Male, female, and total progeny production. The average female in the limited cohort produced significantly fewer

total male progeny than her continuously exposed counterpart, but also produced significantly more female progeny. The mean total number of progeny produced, although lower in the limited cohort, was not significantly lower.

#### Discussion

These data indicate that my previous contentions concerning the effects of host availability on the reproductive schedule of L. boulandi were correct. Here we find that not only can one spread successful reproduction throughout 88% of the cohorts' life span, but that one can also significantly affect the sex ratio of daily ovipositions. In this case of extremely limited host-parasite contact it has been possible to manipulate encounters so that female parasites could produce viable female progeny throughout all but the last day of their cohort's existence. Although the daily totals for female production are low in comparison to the continuous schedules described earlier, the  $R_0$  and the mean number of female progeny per female is significantly higher than in comparable cohorts. These data indicate that females are highly efficient in their utilization of hosts that are patchily distributed through time. It is also evident that the rapid change to a male biased sex ratio indicative of continuous host availability can be altered dramatically.

The life-history scenario developed after the first set of experiments must now be qualified. Limiting or delaying the period of host parasite contact led to significantly altered female progeny production schedules, without (except for 1 case) significantly changing mean life expectancy. Successively limiting the periods of host contact led to successive increases in the time spent in successful female progeny production ranging from 30 to 88% of the average life span. Indeed, in the most limited case of 1 hour exposure, the mean number of total females produced was significantly higher than that of many other cohorts. The average efficiency of females in terms of the number of progeny produced per hour of exposure was increased by two orders of magnitude when hosts schedules were changed from 24 hours to 1 hour exposure periods.

L. boulardi exhibits a reproductive strategy that can vary anywhere between two extremes. When hosts are available at high densities for long periods of time, progeny production is explosive early in life and tails off rapidly thereafter with long post-reproductive survival and rapid shifts in the sex ratio of the progeny from female to male biased. However, when host contacts are limited in duration (this is equivalent to limiting host density (Cook and Hubbard, 1976)), reproduction peaks later in life, is extended further, and the sex ratio becomes less male biased.



## Summary

In an effort to test the effects of extremely limited daily host-parasitoid contact on the survivorship and reproductive variables of L. boulandi, fifty pairs of parasitoids were exposed to excess D. simulans larvae for daily 1 hour periods throughout their lives. Survivorship and progeny production schedules were analyzed and compared to an appropriate continuous exposure cohort.

Survivorship followed the type 1 distribution of Pearl (1928). Females in the limited contact cohort produced successful male and female progeny for 88% of their average life span. The daily oviposition sex ratio was female biased through much of the cohort's existence and never rose above 0.59. Females in the limited contact cohort spent significantly more exposure periods ovipositing female eggs than did those of the comparable continuous contact cohort. More importantly, the limited contact cohort females produced significantly more female progeny per female and an equivalent number of total progeny per female in comparison to the continuous contact females.

The data from the first three sets of life-history experiments are used to describe the reproductive strategy of L. boulandi. The strategy is that of an ultimate opportunist adapted to utilizing hosts in fluctuating environments that we speculate are patchily distributed in time and space. It is adapted to maximizing 'r', and

bet-hedging and can exploit host patches efficiently under a continuous range of host distribution patterns.

## Experiment 4. Oviposition Rate vs. Oviposition Success

### Introduction

Streams (1968) noted that after five days of extensive oviposition L. heterotoma did not produce many viable offspring. He hypothesized that this resulted from the adult female's loss of ability to chemically protect her eggs from encapsulation. Oviposition success, rather than oviposition rate was the factor that he considered responsible for the drop in reproduction. Since progeny production in L. boularoi also decreases after 3-5 days of extensive ovipositions, an experiment was conducted testing whether oviposition rate or success, or both, were responsible for the decrease.

### Materials and Methods

A life table experiment was conducted using a cohort of 30 females exposed to D. simulans larvae on a "continuous" schedule. The progeny of 29 females were allowed to develop normally, while the daily oviposition rate was determined for the remaining female by dissecting host larvae 24 hours after exposure. The daily oviposition rate was calculated as the number of parasitized hosts per total number of hosts per day. In addition, the remaining egg complement of each female was determined after death by dissection of the ovaries.

## Results

The data presented for this cohort is based (unless otherwise specified) on 27 fertilized females out of the 29 in which progeny was allowed to hatch. The average female lived  $13.8 \pm 0.9$  days. An average of  $95.2 \pm 6.3$  male progeny was produced during  $9.6 \pm 0.3$  days (69.9% of life span), while  $136.7 \pm 6.5$  females were produced on the average during  $7.1 \pm 0.5$  days (51.9% of life span).

The daily oviposition rate and changes in the percent of available hosts parasitized per day are given in table 23. Table 22 presents the life and fertility table, sex ratio, and population growth parameters, and figures 21 and 22, the survivorship and fertility curves, respectively. Figure 23 shows the relationship between the number of eggs left in the ovaries and the age of death.

## Discussion

The life table data presented here is typical for *L. boulandi* when presented an excess of hosts for 24 hours daily. The rapid decline in reproductive capability could have been attributed to either a decrease in the rate of oviposition, or to a decrease in the successful development of parasitoid larvae. The data presented here indicates that the former possibility is the correct one. We find that after 5 days the percentage of available hosts parasitized per day dropped from an average of 91.04% to 30.9%, a two thirds decrease.

Figure 21. Survivorship curve for the oviposition rate experiment.

Survivorship curve for  
the CONTINUOUS cohort, 24 hour exposure  
host, *Drosophila simulans*  
OVIPOSITION RATE vs OVIPOSITION SUCCESS

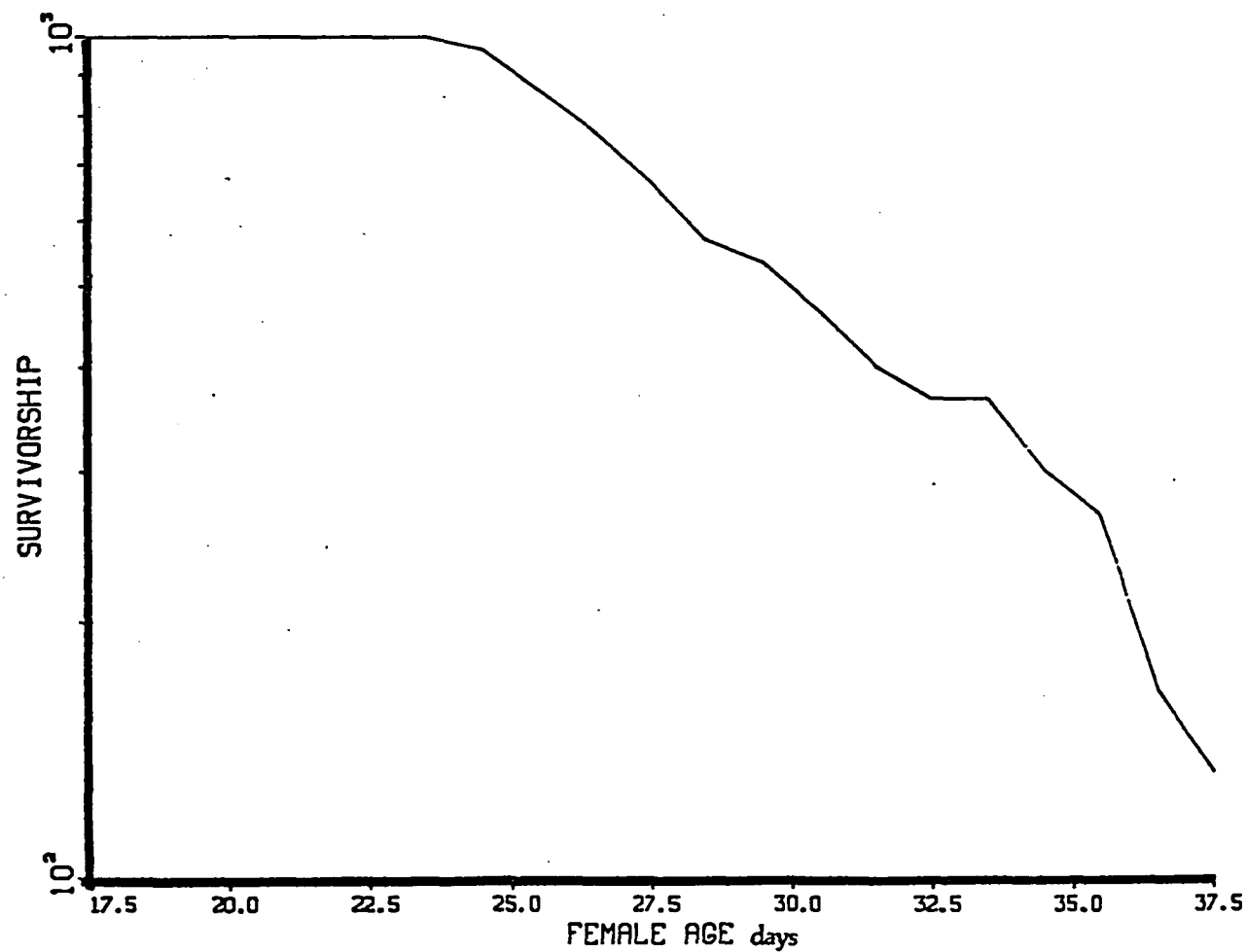


Figure 22. Fertility curve for the oviposition rate experiment.

Fertility curve for  
the CONTINUOUS cohort, 24 hour exposure  
host, Drasophila simulans  
OVIPOSITION RATE vs OVIPOSITION SUCCESS

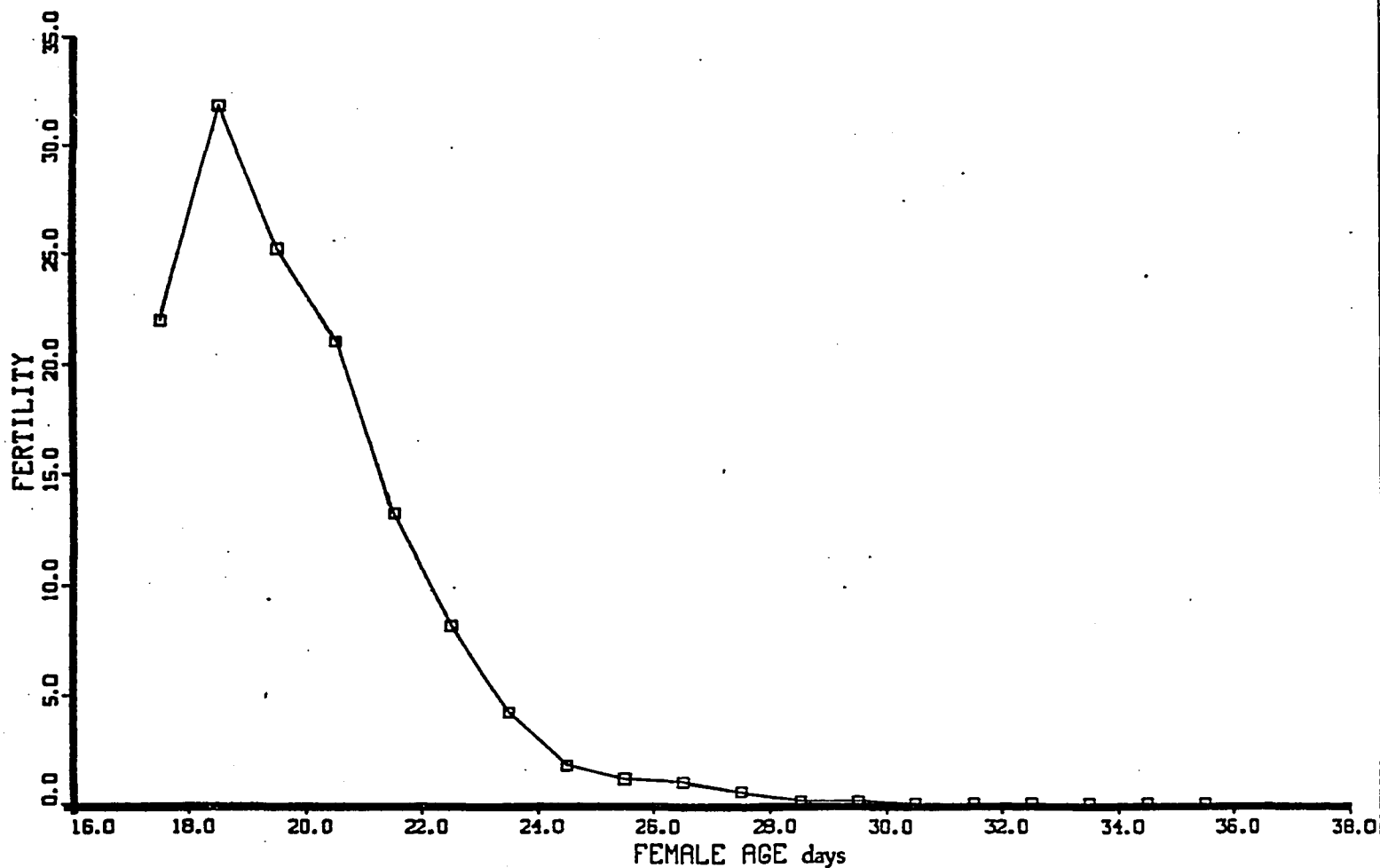




Figure 23. Relationship between the age of female wasps at death and the number of eggs left in the ovaries ( $r = -0.78$ ).

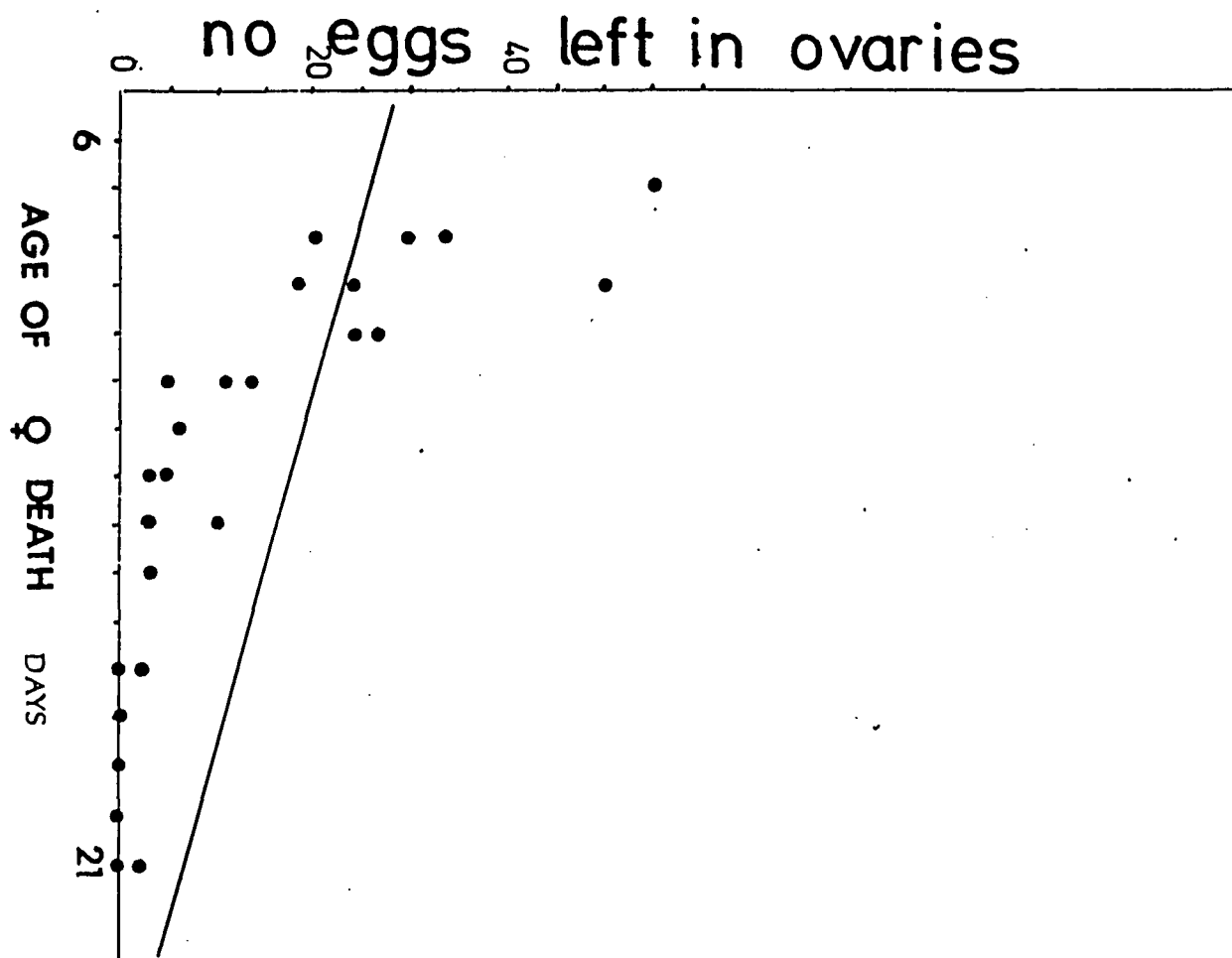


TABLE 22. Life and fertility table for the oviposition rate cohort exposed to D. simulans.

| x    | l(x) | m(x)   | x    | l(x) | m(x)  |
|------|------|--------|------|------|-------|
| 17.5 | 1000 | 21.987 | 30.5 | 467  | 0.000 |
| 18.5 | 1000 | 31.828 | 31.5 | 400  | 0.000 |
| 19.5 | 1000 | 25.241 | 32.5 | 367  | 0.000 |
| 20.5 | 1000 | 21.034 | 33.5 | 367  | 0.000 |
| 21.5 | 1000 | 13.250 | 34.5 | 300  | 0.000 |
| 22.5 | 1000 | 8.130  | 35.5 | 267  | 0.000 |
| 23.5 | 1000 | 4.172  | 36.5 | 167  | 0.000 |
| 24.5 | 967  | 1.759  | 37.5 | 133  | 0.000 |
| 25.5 | 867  | 1.154  |      |      |       |
| 26.5 | 767  | 1.000  |      |      |       |
| 27.5 | 667  | 0.550  |      |      |       |
| 28.5 | 567  | 0.118  |      |      |       |
| 29.5 | 533  | 0.118  |      |      |       |

$$R_0 = 129.81$$

$$T_c = 19.65$$

$$'r' = 0.248$$

TABLE 23.

Oviposition data for L. bouhardi exposed to D. simulans

| Day of<br>exposure | singly                               |       |             | multiply    |      | total<br>hosts | ratio |
|--------------------|--------------------------------------|-------|-------------|-------------|------|----------------|-------|
|                    | parasitized                          | alive | melan. dead | parasitized | dead |                |       |
| 0.5                | 73                                   | 0     | 2           | 0           |      | 86             | 0.87  |
| 1.5                | 52                                   | 0     | 0           | 0           |      | 58             | 0.90  |
| 2.5                | 22                                   | 0     | 0           | 0           |      | 23             | 0.96  |
| 3.5                | 50                                   | 0     | 0           | 0           |      | 54             | 0.93  |
| 4.5                | 33                                   | 2     | 0           | 0           |      | 39             | 0.90  |
| 5.5                | 21                                   | 0     | 0           | 0           |      | 68             | 0.31  |
| 6.5                | 8                                    | 3     | 0           | 0           |      | 65             | 0.17  |
| 7.5                | Female died, 15 eggs left in ovaries |       |             |             |      |                |       |

Adult female L. boulandi hatch with their polytrophic ovaries filled with 250-350 mature eggs, all available for oviposition. The drive to oviposit is assumed to be dependent upon the interaction and neuronal feedback between the eggs, ovarioles, ovaries, ovipositor and various muscles and accessory structures of the female reproductive tract. As ovipositions continue and eggs are depleted, the neuronal feedback between these structures should lessen in intensity and the "drive" to oviposit should decrease.

The phenomena of "predator satiation" and "parasitoid egg depletion" are equivalent in their effects upon the searching behavior of the predator or parasitoid (Hassel, 1978). Satiation due to egg depletion may in fact be one of the responses occurring in L. boulandi. We find that twelve females with post-reproductive periods varying from 2 to 11 days, had anywhere from 1 to 26 eggs left in their ovaries; seven females with extensive post-reproductive periods showed no eggs left in their ovaries, while the rest of the females showed no post-reproductive periods with anywhere from 6 to 55 eggs left. Exhaustion of ovipositor musculature after periods of extensive oviposition (Flanders, 1939) is also a possible factor in the decrease in daily ovipositions.

It is evident that the rate of oviposition decreases with increasing host exposure. We can not, however, rule out the possibility that Streams (1968) was on the right track.

Both phenomena may be occurring and a test of this hypothesis still remains to be made.

#### Summary

An experiment was conducted in an attempt to determine the cause of the decrease in successful progeny production evident in females following five days of extensive oviposition. Two hypotheses were considered, either (1) the actual rate of oviposition (parasitized hosts/available hosts/day), or (2) the adult female's ability to chemically protect her larvae from encapsulation, decreased. A life table experiment was conducted and daily oviposition rates were determined by dissecting host larvae 24 hours after exposure. The number of eggs remaining in each females' ovaries were determined after death.

Progeny production and survivorship schedules followed expected patterns for continuous exposure cohorts. Data from host dissections elicits a pattern consistent with the first hypothesis. The percent of available hosts parasitized per day decreased from an average of 91% (range 87-96%) for the first five exposure periods, to 31% on the sixth period and 17% on the last exposure period. Satiation due to egg depletion, as well as exhaustion of ovipositor musculature are presented as possible factors in the decrease in daily oviposition rate.

Experiments 5 & 6. The Reproductive Strategies  
of L. bouhardi When Exposed to a Sympatric  
Population of D. melanogaster

Part I. Early Experiments, April, 1979

Introduction

The majority of the data on life history tactics presented thus far has been based upon experiments utilizing Drosophila simulans as the source of host larvae. D. simulans is an acceptable host for both L. bouhardi and L. heterotoma, but as Carton (1978) and I have shown, D. melanogaster is a more suitable host for L. bouhardi.

The life table and host availability experiments discussed in this section were performed using sympatric populations of L. bouhardi and D. melanogaster captured in Hampton, Virginia during late August, 1977, only a few miles from the 1975 capture site. It will become evident that the trends seen in the experiments with D. simulans can be effectively replicated with D. melanogaster.

Materials and Methods

Host collection. The same general procedures employed in earlier experiments were employed here. One important difference, however, involved the deposition of a drop of a thick suspension of activated yeast (28g yeast/40ml water) to the surface of the medium prior to introducing the flies. This yeast suspension allowed increased daily oviposition rates and longevities for the flies. In addition, since I

had often observed adult wasps actively feeding on the yeasted Drosophila medium, and since the data from earlier experiments (Series V) indicated that adding yeast to the wasps' honey droplet might have increased their longevity, I expected that the parasitoids might show increased longevity as well.

Host availability schedules. The following schedules were used:

1. Continuous: 24 hours per day for life.
2. Intermittent: 24 hours of exposure, every third day.
3. Limited-1: one hour per day, for life.
4. Limited-2: two hours per day, for life.
5. Delayed: no hosts for the first 6 days, then 24 hours per day for the rest of life.

Each cohort contained 20 pairs of parasitoids. In order to insure against mortality from drowning in bacterial slime, standard medium was replaced by Carolina Instant (Blue) medium in hostless vials. The host and parasitoid strains were derived from sympatric populations of wasps (Ha77 strain) and flies (W0 strain) collected during 1977. All other conditions of temperature, relative humidity and photoperiod were the same as in earlier experiments. Daily survivorship of females and overall daily progeny production were recorded as before.



## Results

### Continuous hosts

Survivorship. This cohort exhibited the typical survivorship distribution for this species (see figure 24). An average female lived  $18.3 \pm 0.4$  days. Figure 24 and table 24 represent the survivorship curve and life table, respectively, for this cohort.

Fertility. Figure 25 and table 24 represent the fertility curve and table for this cohort. Fertility is given as the mean number of female progeny produced per female during each oviposition period. This continuously exposed cohort survived for a total of 20 exposure periods during which, 11 days were spent producing female progeny and 12 days were spent producing male progeny. The peak in daily female progeny production occurred during the first exposure period and the first two days of exposure produced 74% of all female progeny. Between the second and third days of exposure female progeny production dropped 94%, then rose again on the following day and dropped gradually thereafter. Daily male progeny production reached its peak during the second exposure period, then too, dropped significantly (92%) during the third exposure period, and subsequently rose prior to a gradual decline. As in all previous continuously exposed cohorts, the sex ratio of daily progeny production remained female biased early, but changed to male biased after three days. It is important to

Figure 24. Survivorship curve for the continuous exposure cohort (Ha77 strain) exposed to D. melanogaster (W.O. strain), April, 1979.

Survivorship curve for  
the CONTINUOUS cohort, 24 hour exposure  
host, *Drosophila melanogaster*  
WOODS ORCHARD I

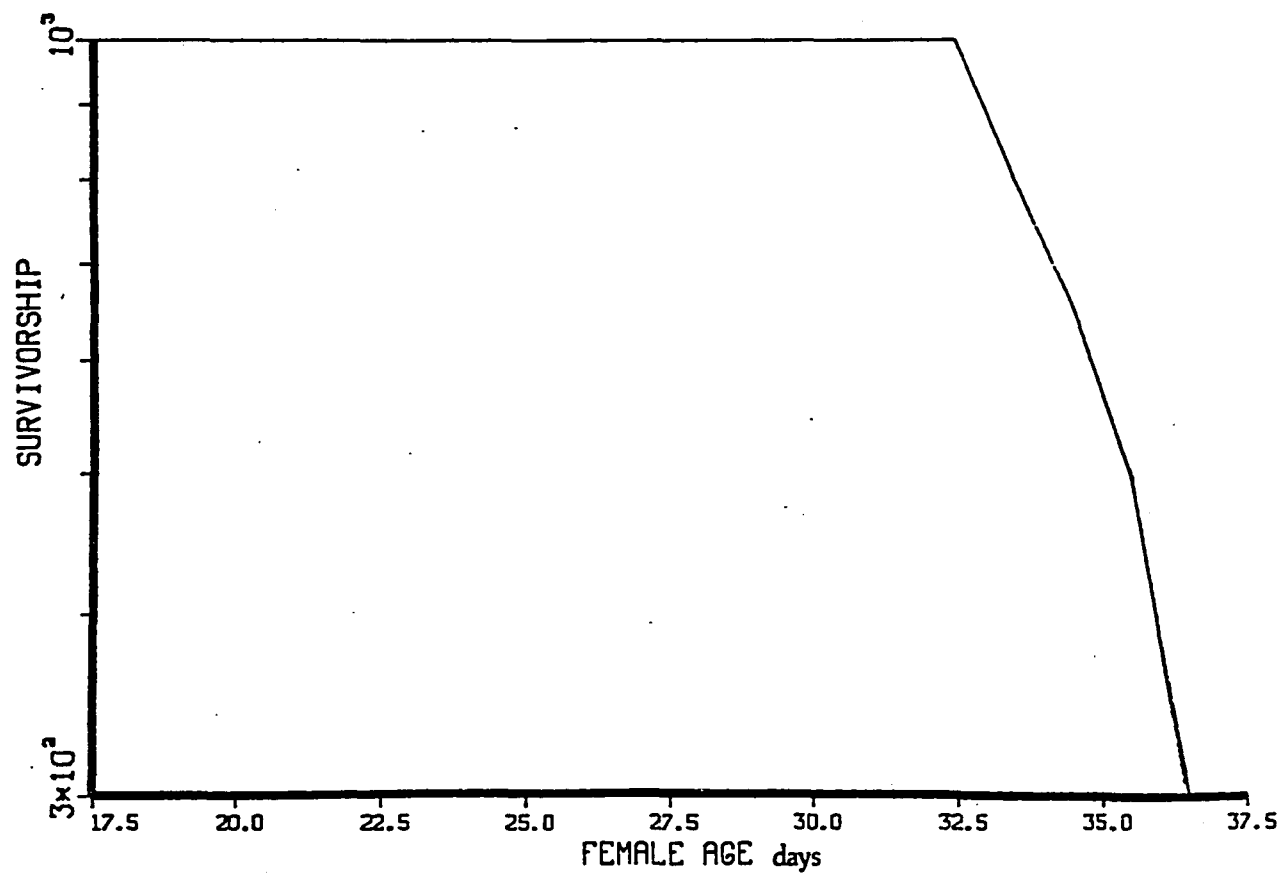


Figure 25. Fertility curve for the continuous exposure cohort (Ha77 strain) exposed to D.\_\_\_\_melanogaster (W.O. strain), April, 1979.

Fertility curve for  
the CONTINUOUS cohort, 24 hour exposure  
host, *Drosophila melanogaster*  
WOODS ORCHARD

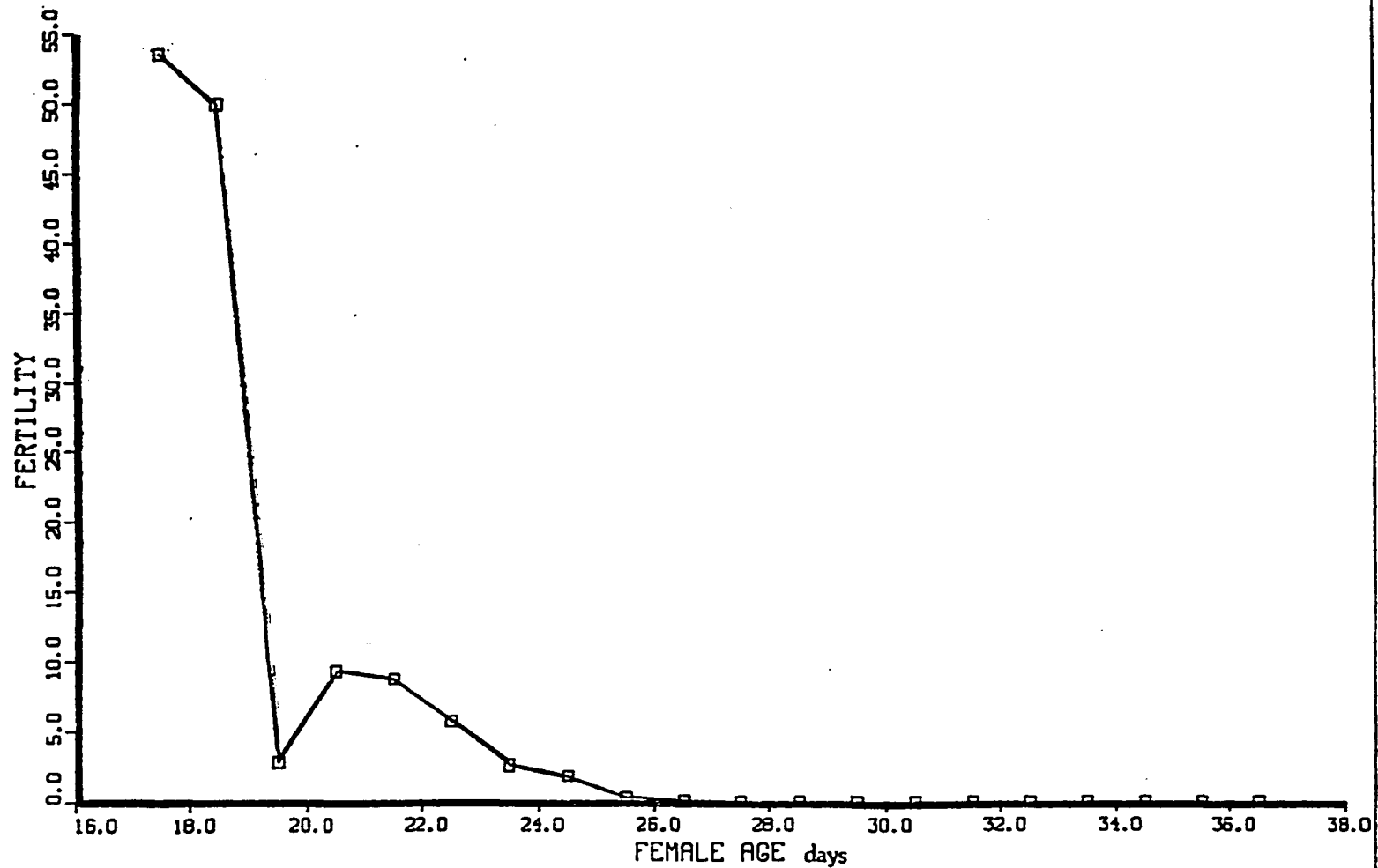


TABLE 24. Life and fertility table for the 24h continuous  
contact cohort, exposed to Drosophila melanogaster,  
Woods Orchard strain, April, 1979.

| x    | l(x) | m(x)  | x    | l(x) | m(x) |
|------|------|-------|------|------|------|
| 17.5 | 1000 | 53.55 | 30.5 | 1000 | 0.00 |
| 18.5 | 1000 | 49.95 | 31.5 | 1000 | 0.00 |
| 19.5 | 1000 | 2.80  | 32.5 | 1000 | 0.00 |
| 20.5 | 1000 | 9.30  | 33.5 | 800  | 0.00 |
| 21.5 | 1000 | 8.75  | 34.5 | 650  | 0.00 |
| 22.5 | 1000 | 5.70  | 35.5 | 500  | 0.00 |
| 23.5 | 1000 | 2.60  | 36.5 | 300  | 0.00 |
| 24.5 | 1000 | 1.85  |      |      |      |
| 25.5 | 1000 | 0.30  |      |      |      |
| 26.5 | 1000 | 0.10  |      |      |      |
| 27.5 | 1000 | 0.05  |      |      |      |
| 28.5 | 1000 | 0.00  |      |      |      |
| 29.5 | 1000 | 0.00  |      |      |      |

$R_0 = 134.95$

$T_c = 18.82$

$'r' = 0.261$

note that female progeny production ceased 5 days prior to the death of any female.

#### Delayed hosts

Survivorship. Here again, we find the typical survivorship curve expected for this species (figure 25 and table 25). The mean length of life of the females in this cohort is  $16.8 \pm 0.6$  days (see table 30).

Fertility. Following the initial 6 day non-host period, female progeny were produced during the next 10 days. 86.2% of the female progeny were produced during the first two days of host exposure and female progeny production decreased thereafter. On the average male progeny were produced during 65.6% of the average cohort exposure time. Female progeny, on the other hand, were produced during only 45.6% of the time (see table 30 and figure 27).

Unlike the previous delayed cohort (Series III), no mortality occurred during the non-host period. The peak in production of both sexes occurred during the first exposure period. The first two oviposition periods produced 63% of the total male progeny; 85% of the total female progeny; and 74% of the total progeny. Again, as in the continuous exposure cohort, the third exposure period produced significantly fewer progeny than previous periods, i.e., there was a 98-99% drop in progeny production. And again, progeny production rose during the next two exposure periods prior to a gradual decline. Tables 25 and 30 give the daily

Figure 26. Survivorship curve for the delayed exposure cohort - (Ha77- strain)--- exposed to D.\_\_\_\_melanogaster (W.O. strain), April, 1979.



Survivorship curve for  
the INTERMITTENT cohort, 24 hour exposure  
host, *Drosophila melanogaster*  
WOODS ORCHARD I

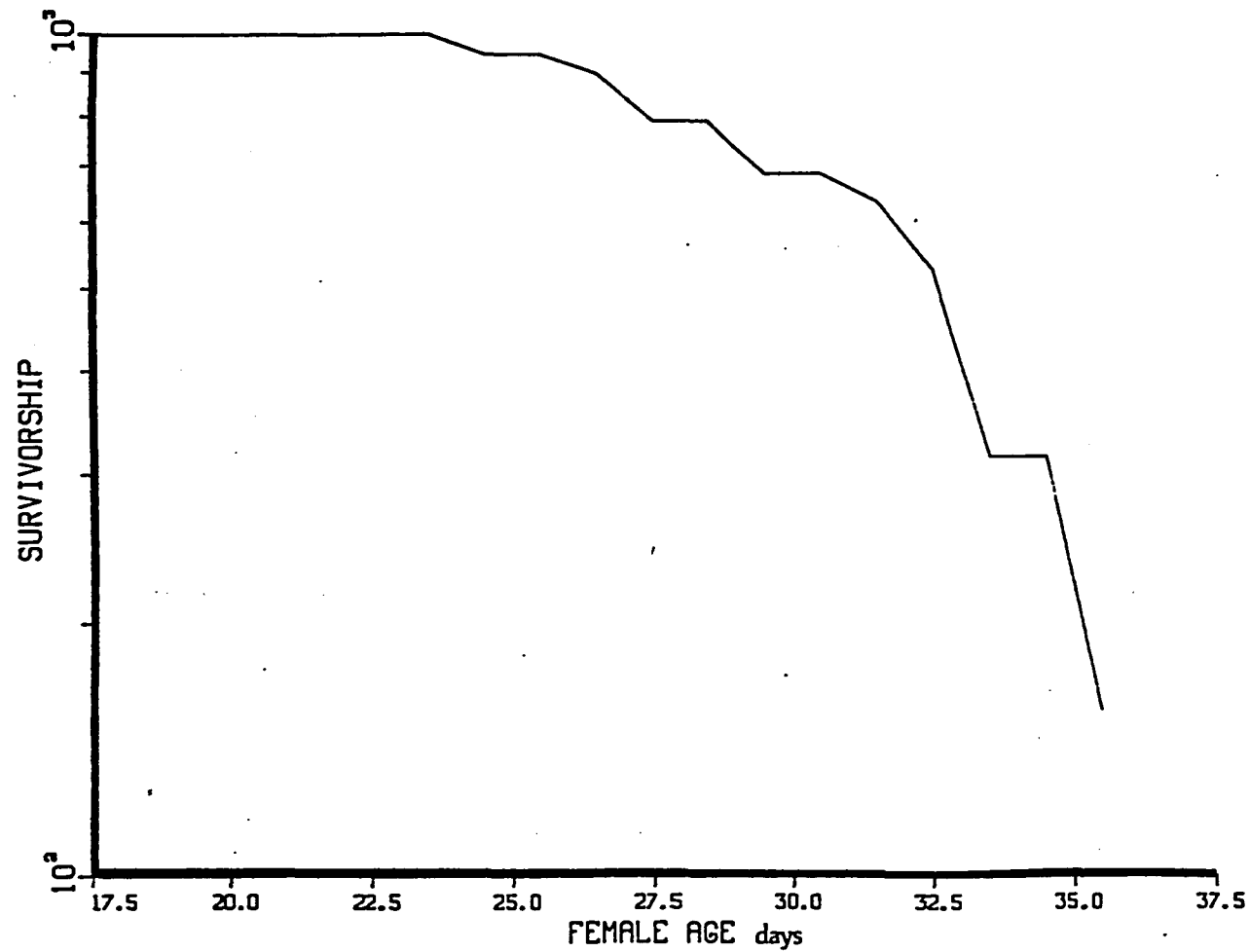


Figure 27. Fertility curve for the delayed exposure cohort (Ha77 strain) exposed to D.\_\_\_\_melanogaster (W.O. strain), April, 1979. .

Fertility curve for  
the INTERMITTENT cohort, 24 hour exposure  
host, *Drosophila melanogaster*  
WOODS ORCHARD

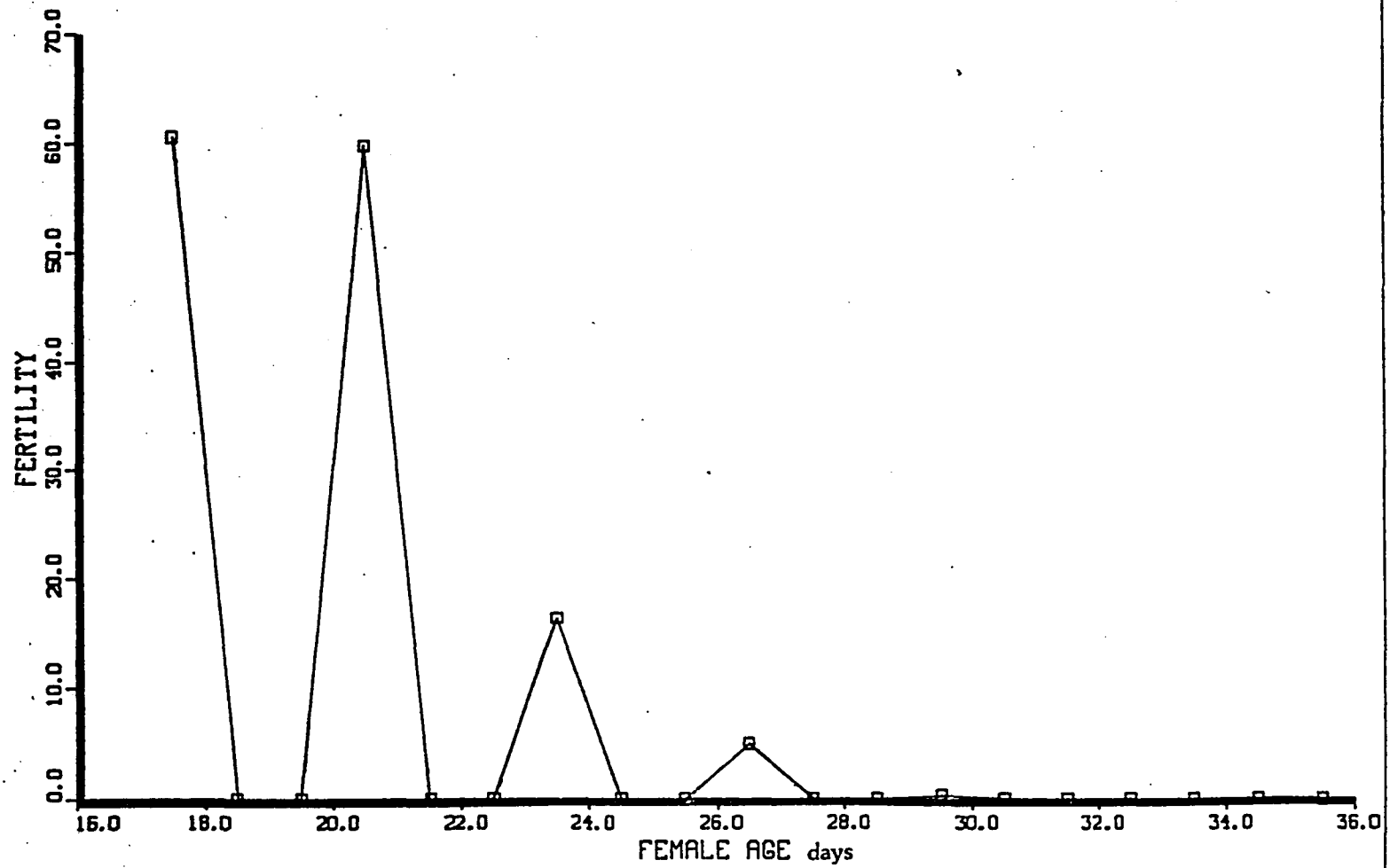


TABLE 25. Life and fertility table for the delayed cohort  
exposed to D. melanogaster, Woods Orchard strain,  
April, 1979.

| x    | l (x)  | m (x) | x    | l (x) | m (x) |
|------|--------|-------|------|-------|-------|
| 17.5 | 1000.0 | 0.0   | 30.5 | 947.4 | 0.8   |
| 18.5 | 1000.0 | 0.0   | 31.5 | 842.1 | 0.3   |
| 19.5 | 1000.0 | 0.0   | 32.5 | 736.8 | 0.2   |
| 20.5 | 1000.0 | 0.0   | 33.5 | 736.8 | 0.0   |
| 21.5 | 1000.0 | 0.0   | 34.5 | 473.7 | 0.0   |
| 22.5 | 1000.0 | 0.0   | 35.5 | 263.2 | 0.0   |
| 23.5 | 1000.0 | 47.9  |      |       |       |
| 24.5 | 1000.0 | 20.7  |      |       |       |
| 25.5 | 1000.0 | 00.3  |      |       |       |
| 26.5 | 1000.0 | 1.1   |      |       |       |
| 27.5 | 947.4  | 4.9   |      |       |       |
| 28.5 | 947.4  | 3.4   |      |       |       |
| 29.5 | 947.4  | 0.1   |      |       |       |

$$R_0 = 79.18$$

$$T_c = 24.36$$

$$'r' = 0.179$$

progeny production schedules and sex ratios. The first two exposure periods were female biased while all subsequent ones were male biased.

#### Intermittent hosts

Survivorship. Figure 28 and table 26 represent the survivorship data for this cohort. Again, as in all other cohorts the survivorship curve is a variation of the Pearl (1928) type 1 curve. The mean length of life of females in this cohort is  $14.7 \pm 1.0$  days.

Fertility. The cohort survived through seven oviposition periods. The first oviposition period (day 0.5) produced 60.6 females per female; the second oviposition yielded 59.9 females per female (day 3.5), while subsequent oviposition periods produced significantly and progressively fewer female progeny. The first two oviposition periods produced 86.6% of the total female progeny (see figure 29 and table 26).

On the average, the females in this cohort spent  $5.3 \pm 0.3$  days exposed to host larvae. 78.9% of this time was spent producing male progeny, while 65.6% of the time was spent producing female progeny (see table 31).

Of the seven exposure periods, male progeny were produced during the first five and female progeny during the first six. The peak in daily female progeny production occurred during the first exposure period, while the peak in daily male progeny production occurred during the second exposure

Figure 28. Survivorship curve for the intermittent exposure cohort (Ha77 strain) exposed to D.\_\_\_\_melanogaster (W.O. strain), April, 1979.

Survivorship curve for  
the DELAYED 6 DAYS cohort  
host, *Drosophila melanogaster*  
WOODS ORCHARD I

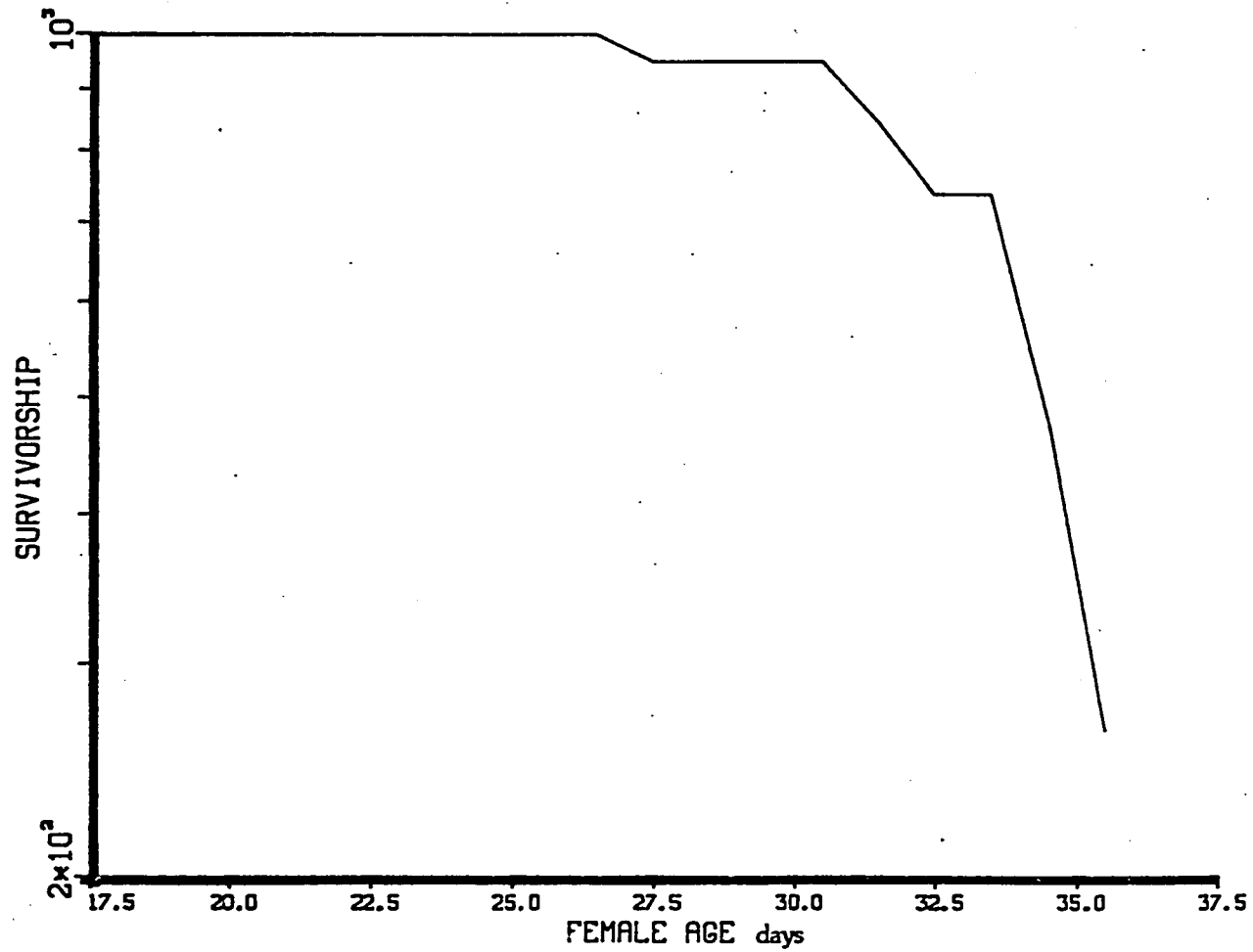


Figure 29. Fertility curve for the intermittent exposure cohort (Ha77 strain) exposed to D. melanogaster (W.O. strain), April, 1979.



Fertility curve for  
the DELAYED 6 DAYS cohort  
host, *Drosophila melanogaster*  
WOODS ORCHARD

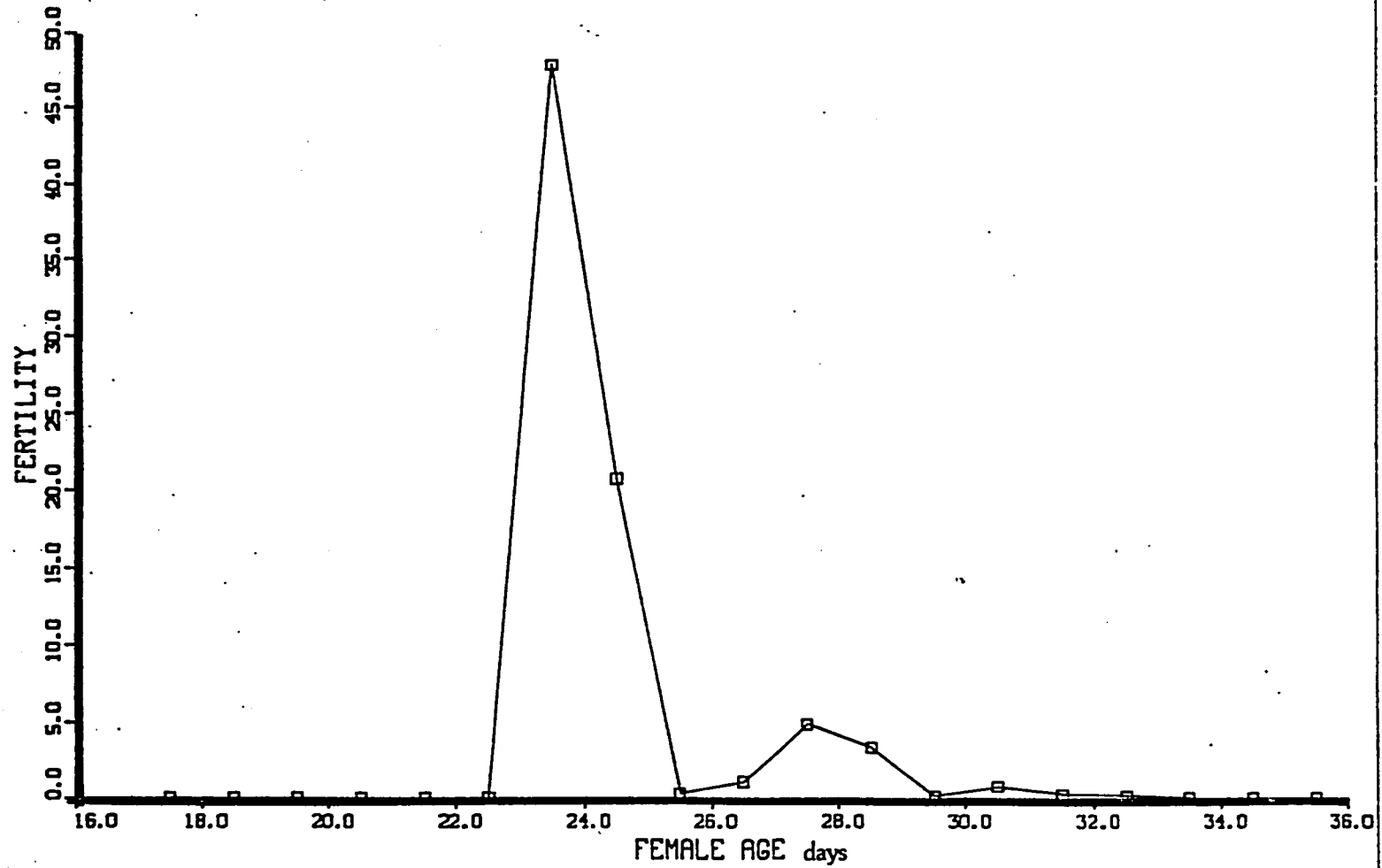


TABLE 26. Life and fertility table for the intermittent cohort, exposed to D. melanogaster, Woods Orchard strain, April, 1979

| x    | l(x)    | m(x)  | x    | l(x)   | m(x) |
|------|---------|-------|------|--------|------|
| 17.5 | 1000.00 | 60.68 | 30.5 | 684.22 | 0.00 |
| 18.5 | 1000.00 | 0.00  | 31.5 | 631.58 | 0.00 |
| 19.5 | 1000.00 | 0.00  | 32.5 | 526.32 | 0.00 |
| 20.5 | 1000.00 | 59.88 | 33.5 | 315.81 | 0.00 |
| 21.5 | 1000.00 | 0.00  | 34.5 | 315.81 | 0.00 |
| 22.5 | 1000.00 | 0.00  | 35.5 | 157.91 | 0.00 |
| 23.5 | 1000.00 | 16.35 |      |        |      |
| 24.5 | 947.36  | 0.00  |      |        |      |
| 25.5 | 947.36  | 0.00  |      |        |      |
| 26.5 | 894.72  | 5.00  |      |        |      |
| 27.5 | 789.47  | 0.00  |      |        |      |
| 28.5 | 789.47  | 0.00  |      |        |      |
| 29.5 | 684.22  | 0.27  |      |        |      |

$$R_0 = 141.57$$

$$T_c = 19.77$$

$$r' = 0.251$$

period. Between the second and third exposure periods female progeny production decreased 73% and male progeny production decreased 46%. Prior to the third exposure period 85% of all female progeny, and 74.4% of the total progeny had been oviposited. The sex ratio (see table 29) was female biased for the first two exposure periods, but again, corresponding to the point at which daily ovipositions decrease, the sex ratio became male biased and remained so until the last oviposition period.

Limited cohort, (daily 1 hr exposure)

Survivorship. The survivorship curve of this cohort also follows the type 1 curve of Pearl (1928), however the mean length of life of the 18 fertilized females ( $10.4 \pm 0.6$ ) is significantly lower than that of all other cohorts (see figure 30, and tables 27 and 32).

Fertility. This cohort produced female progeny during 11 successive daily one hour oviposition periods with 95.7% of all female progeny were being produced during the first 8. The peak in female progeny production occurred on the third day of exposure, followed by a subsequent gradual decrease. The reproductive variables for this cohort are presented in table 33. It is evident that male progeny ( $95.6 \pm 11.8$  per female) were produced during 92% of the exposure periods, and female progeny ( $126.8 \pm 10.6$  per female) were produced during 67.6% of the exposure periods. Unlike the limited cohort discussed earlier, this cohort survived for four days past the last day of successful female progeny production (see figure 31).

Figure 30. Survivorship curve for the limited 1h exposure cohort (Ha77 strain) exposed to D.\_\_\_\_melanogaster (W.O. strain), April, 1979.

Survivorship curve for  
the LIMITED cohort, one hour exposure  
host, *Drosophila melanogaster*  
WOODS ORCHARD I

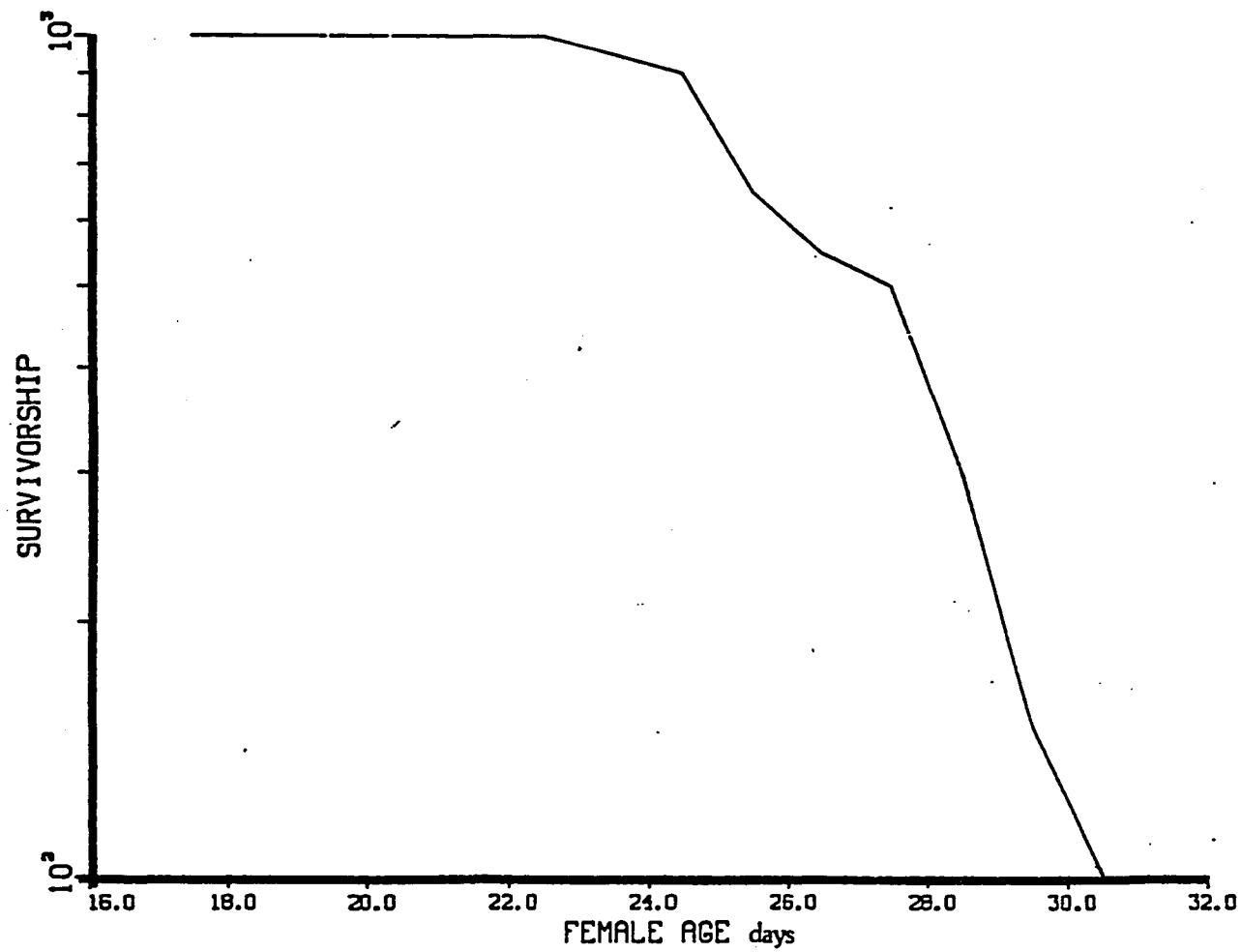


Figure 31. Fertility curve for the limited 1h exposure cohort (Ha77 strain) exposed to D.\_\_\_\_melanogaster (W.O. strain), April, 1979.

Fertility curve for  
the LIMITED cohort, one hour exposure  
host, Drosophila melanogaster  
WOODS ORCHARD

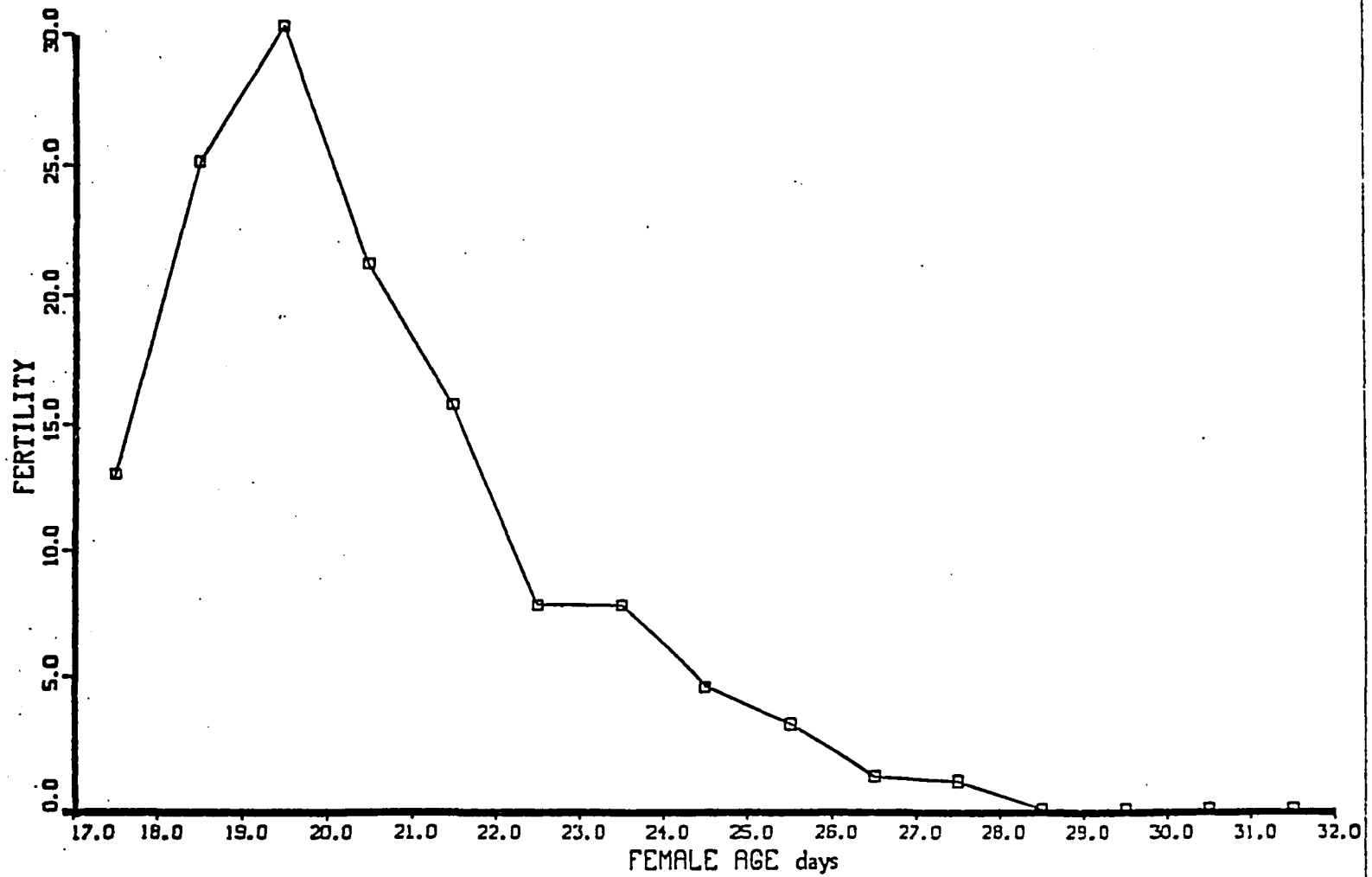


TABLE 27. Life and fertility table for the 1 hour limited contact cohort, exposed to D. melanogaster, Woods Orchard strain, April, 1979.

| x              | l (x)         | m (x)         |
|----------------|---------------|---------------|
| 17.5           | 1000          | 12.999        |
| 18.5           | 1000          | 25.167        |
| 19.5           | 1000          | 30.278        |
| 20.5           | 1000          | 21.220        |
| 21.5           | 1000          | 15.720        |
| 22.5           | 1000          | 7.780         |
| 23.5           | 950           | 7.770         |
| 24.5           | 900           | 4.625         |
| 25.5           | 650           | 3.231         |
| 26.5           | 550           | 1.273         |
| 27.5           | 500           | 1.100         |
| 28.5           | 300           | 0.000         |
| 29.5           | 150           | 0.000         |
| 30.5           | 100           | 0.000         |
| 31.5           | 100           | 0.000         |
| -----          |               |               |
| $R_0 = 128.06$ | $T_c = 20.26$ | $'r' = 0.240$ |



Limited cohort, (daily 2 hr exposure)

Survivorship. This cohort also shows the typical survivorship curve for this species, with an average length of life for females of  $15.5 \pm 0.8$  days (see figure 32, tables 28 and 33).

Fertility. Female progeny were produced over a period of 12 days, while 95.1% of the female progeny were produced during the first 7 exposure periods. Fecundity peaked on the second day, decreased gradually for 5 more days and then decreased sharply thereafter.  $90.4 \pm 6.0$  male progeny, on the average, were produced during 68.1 % of the average female life span (see table 33).  $139.4 \pm 6.0$  females per female were produced during 55.6% of the life span (figure 33).

Daily progeny production sex ratios are given in table 29. Both male and female progeny distributions reached their peaks during the second oviposition period. Following these peaks both male and female production decreased gradually until the period between the seventh and eighth days of exposure. At this point female progeny production decreased 73% while male progeny production did not decrease as sharply. Hence the sex ratio became male biased at that point and remained so throughout the rest of the cohort's existence. Progeny production was effectively spread throughout much of the life span of this cohort.

Figure 32. Survivorship curve for the limited 2h exposure cohort (Ha77 strain) exposed to D.\_\_\_\_melanogaster (W.O. strain), April, 1979.

Survivorship curve for  
the LIMITED cohort, two hour exposure  
host, Drosophila melanogaster  
WOODS ORCHARD I

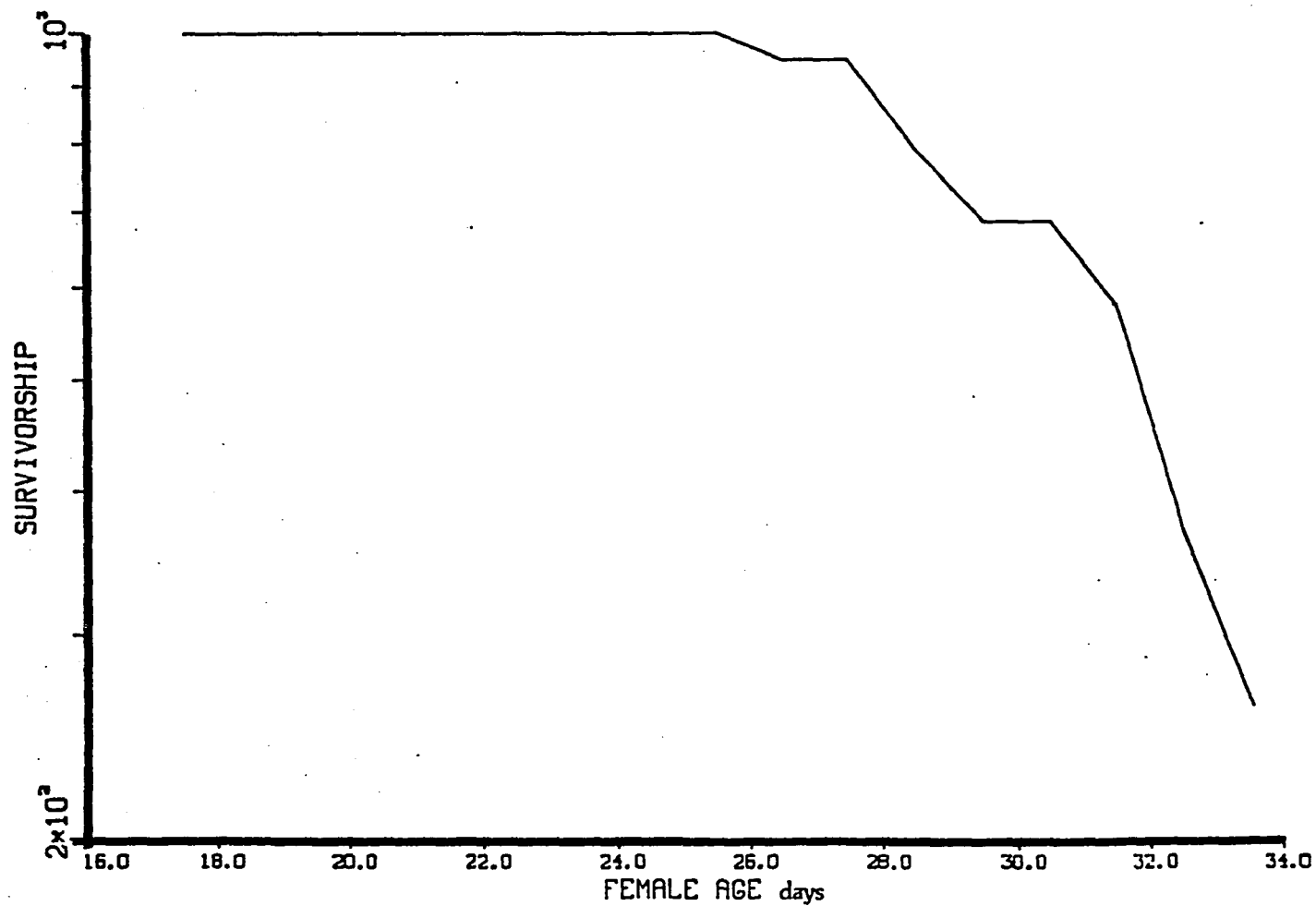


Figure 33. Fertility curve for the limited 2h exposure cohort (Ha77 strain) exposed to D. melanogaster (W.O. strain), April, 1979.

Fertility curve for  
the LIMITED cohort, two hour exposure  
host, Drosophila melanogaster  
WOODS ORCHARD

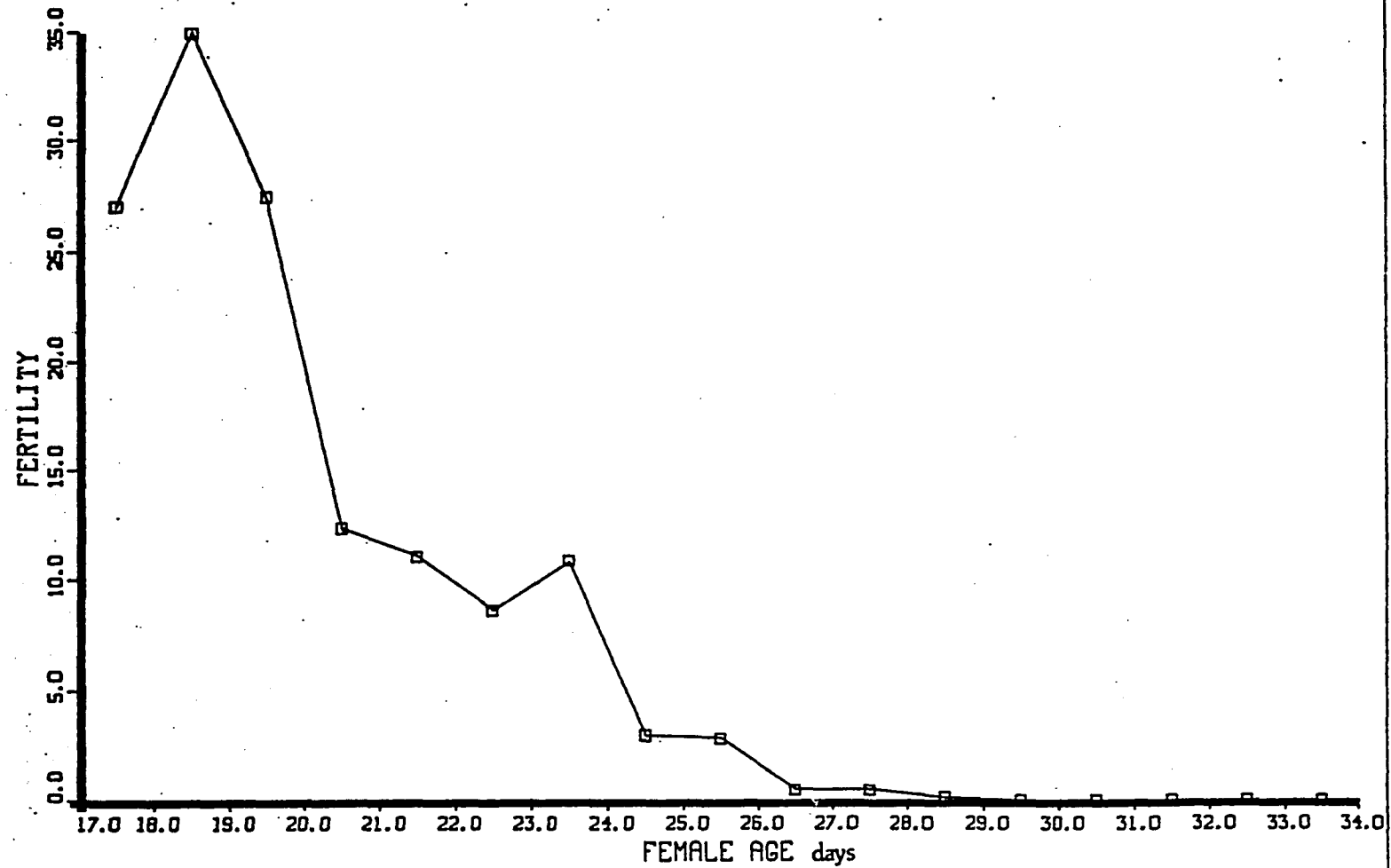


TABLE 28. Life and fertility table for the 2 hour limited contact cohort, exposed to D. melanogaster, Woods Orchard strain, April, 1979.

---

| x    | l (x)   | m (x)  |
|------|---------|--------|
| 17.5 | 1000.00 | 27.050 |
| 18.5 | 1000.00 | 34.950 |
| 19.5 | 1000.00 | 27.500 |
| 20.5 | 1000.00 | 12.350 |
| 21.5 | 1000.00 | 11.050 |
| 22.5 | 1000.00 | 8.579  |
| 23.5 | 1000.00 | 10.842 |
| 24.5 | 1000.00 | 2.943  |
| 25.5 | 1000.00 | 2.789  |
| 26.5 | 947.36  | 0.500  |
| 27.5 | 947.36  | 0.500  |
| 28.5 | 789.47  | 0.133  |
| 29.5 | 684.21  | 0.000  |
| 30.5 | 684.21  | 0.000  |
| 31.5 | 578.95  | 0.000  |
| 32.5 | 368.42  | 0.000  |
| 33.5 | 263.14  | 0.000  |

---

$R_0 = 139.11$

$T_c = 19.89$

$'r' = 0.248$

TABLE 29. Daily sex ratio changes for the five cohorts  
of L. boucardi exposed to D. melanogaster larvae  
(Woods Orchard strain), April, 1979.

| Age  | Continuous | Intermittent | Delayed | Limited |      |
|------|------------|--------------|---------|---------|------|
|      |            |              |         | 1h      | 2h   |
| 17.5 | 0.24       | 0.21         | ----    | 0.34    | 0.31 |
| 18.5 | 0.39       | ----         | ----    | 0.32    | 0.30 |
| 19.5 | 0.48       | ----         | ----    | 0.28    | 0.33 |
| 20.5 | 0.54       | 0.37         | ----    | 0.40    | 0.39 |
| 21.5 | 0.58       | ----         | ----    | 0.44    | 0.36 |
| 22.5 | 0.67       | ----         | ----    | 0.60    | 0.46 |
| 23.5 | 0.76       | 0.54         | 0.36    | 0.53    | 0.39 |
| 24.5 | 0.82       | ----         | 0.48    | 0.61    | 0.68 |
| 25.5 | 0.94       | ----         | 0.50    | 0.73    | 0.75 |
| 26.5 | 0.94       | 0.79         | 0.65    | 0.79    | 0.91 |
| 27.5 | 0.92       | ----         | 0.60    | 0.82    | 0.85 |
| 28.5 | 1.00       | ----         | 0.70    | 1.00    | 0.78 |
| 29.5 | ----       | 0.89         | 0.79    | ----    | ---- |
| 30.5 | ----       | ----         | 0.76    | ----    | 1.00 |
| 31.5 | ----       | ----         | 0.85    | ----    | ---- |
| 32.5 | ----       | ----         | 0.80    | ----    | ---- |
| 33.5 | ----       | ----         | ----    | ----    | 1.00 |

## Discussion

### Survivorship

All cohorts exhibited the expected survivorship curves. The mean length of life values show some of the same trends seen earlier. The longest lived cohort is the 24 hours continuous exposure cohort; its average  $18.3 \pm 0.3$  day length of life is significantly longer than that of all other cohorts. Interestingly, the next longest-lived cohort is the delayed cohort, in which females were held for six days prior to host exposure. In retrospect, we can see that the short length of life of the Series III cohort could readily be attributed to poor handling procedures and limited sample size. As Birch (1953) pointed out in his life-history studies of Calandra and Rhizopertha, a larger sample size would necessarily include more, longer-lived individuals. The trend seen in earlier experiments, of lower lengths of life for cohorts with discontinuous host exposure is also seen here. The shortest length of life ( $10.4 \pm 0.6$  days) was exhibited by the limited (1 hour) cohort; the intermittent exposure cohort exhibited the next shortest length of life ( $14.6 \pm 1.0$  days), followed by the 2 hour limited cohort ( $15.5 \pm 0.8$  days), and the delayed cohort ( $16.8 \pm 0.6$  days).

### Progeny production schedules

All cohorts, with the exception of the delayed cohort showed no statistically significant differences in the mean



numbers of male, female, or total progeny produced (see tables 30-34 and 64-68 in the appendix).

The continuous cohort was the most successful in the production of total and female progeny per female ( $249.9 \pm 12.0$ , and  $140.3 \pm 8.6$ , respectively). The two hour limited, one hour limited, and intermittent cohorts produced, on the average,  $229.8 \pm 7.3$ ,  $222.3 \pm 8.0$ , and  $227.7 \pm 8.9$  total progeny per female, respectively. The delayed cohort produced the lowest mean number of total offspring per female ( $152.9 \pm 9.8$ ), perhaps attributable to aging prior to host exposure.

If we consider the continuous, intermittent, and delayed cohorts together as cohorts in which host exposure periods were 24 hours long, we can find similarities in their schedules of progeny production. In all cases the fertility values peaked during the first exposure period, with the next exposure period also high. In the continuous cohort, 76.7% of the female progeny were produced by the second day, with 96.4% produced by the sixth day. In the intermittent cohort, the first day's ovipositions produced 42.65% of the total female progeny and by the third exposure period 96.3% had been produced. In the delayed cohort, 86.1% of the female progeny had been produced during the first two oviposition periods, with 94% being produced by the end of the fifth period (see figure 34).

Figure 34. Fertility curves for all cohorts exposed to D.  
melanogaster (April, 1979).

Fertility curves for  
cohorts exposed to  
Drosophila melanogaster  
WOODS ORCHARD

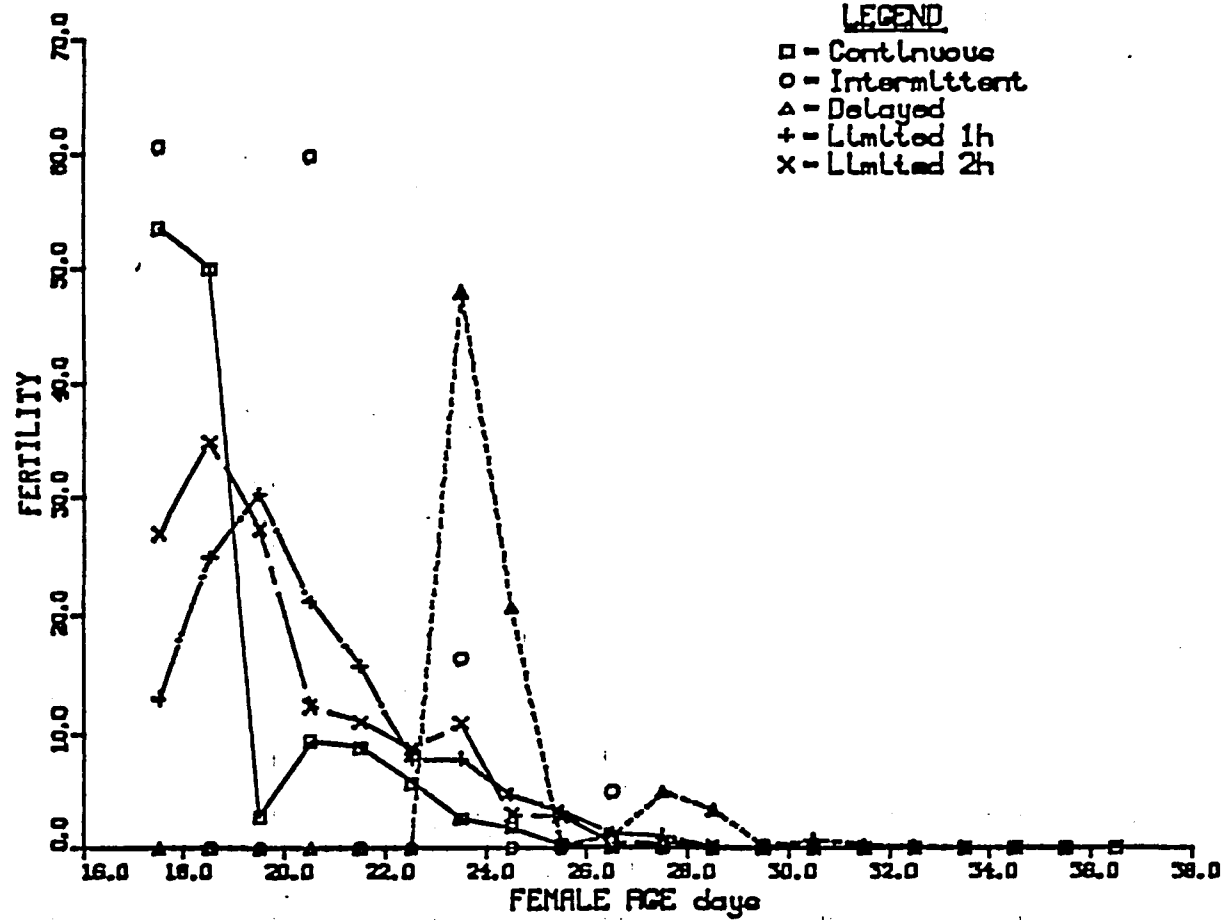


TABLE 30. Reproductive variables for the continuous and delayed cohorts exposed to D. melanogaster (Woods Orchard strain), April, 1979 (mean  $\pm$  SE).

| Variable                                        | Continuous<br>(20) | Delayed<br>(18)    |
|-------------------------------------------------|--------------------|--------------------|
| Length of life                                  | 18.3 $\pm$ 0.3     | 16.8 $\pm$ 0.6 *   |
| Days of male production                         | 9.6 $\pm$ 0.3      | 7.1 $\pm$ 0.3 @    |
| Days of female production                       | 6.1 $\pm$ 0.5      | 4.9 $\pm$ 0.5 @    |
| Total male progeny                              | 109.6 $\pm$ 12.1   | 72.3 $\pm$ 7.8 *   |
| Total female progeny                            | 140.3 $\pm$ 8.6    | 80.7 $\pm$ 5.5 **  |
| Total progeny                                   | 249.9 $\pm$ 12.0   | 152.9 $\pm$ 9.8 ** |
| Post reproductive period<br>for fertilized eggs | 11.9 $\pm$ 0.7     | 5.9 $\pm$ 0.8 **   |
| Total post reproductive<br>period               | 8.5 $\pm$ 0.4      | 3.5 $\pm$ 0.5 **   |

Symbols: \*=  $p < .05$ , \*\*=  $p < .01$ , @= not comparable

TABLE 31. Reproductive variables for the continuous and intermittent cohorts exposed to D. melanogaster (Woods Orchard strain), April, 1979 (mean  $\pm$  SE).

| Variable                                        | Continuous<br>(20) | Intermittent<br>(17) |
|-------------------------------------------------|--------------------|----------------------|
| Length of life                                  | 18.3 $\pm$ 0.3     | 14.6 $\pm$ 1.0 **    |
| Days of male production                         | 9.6 $\pm$ 0.3      | 4.2 $\pm$ 0.2 @      |
| Days of female production                       | 6.1 $\pm$ 0.5      | 3.5 $\pm$ 0.3 @      |
| Total male progeny                              | 109.6 $\pm$ 12.1   | 88.0 $\pm$ 10.1      |
| Total female progeny                            | 140.3 $\pm$ 8.6    | 139.7 $\pm$ 10.3     |
| Total progeny                                   | 249.9 $\pm$ 12.0   | 227.7 $\pm$ 8.9      |
| Post reproductive period<br>for fertilized eggs | 11.9 $\pm$ 0.7     | 1.9 $\pm$ 0.4 **     |
| Total post reproductive<br>period               | 8.5 $\pm$ 0.4      | 1.1 $\pm$ 0.2 **     |

Symbols: \* =  $p < .05$ , \*\* =  $p < .01$ , @ = not comparable

TABLE 32. Reproductive variables for the continuous and 1 hr limited cohorts exposed to D. melanogaster (Woods Orchard strain), April, 1979 (mean  $\pm$  SE).

| Variable                                        | Continuous<br>(20) | 1 hr Limited<br>(18) |
|-------------------------------------------------|--------------------|----------------------|
| Length of life                                  | 18.3 $\pm$ 0.3     | 10.4 $\pm$ 0.6 **    |
| Days of male production                         | 9.6 $\pm$ 0.3      | 9.6 $\pm$ 0.5        |
| Days of female production                       | 6.1 $\pm$ 0.5      | 7.1 $\pm$ 0.7        |
| Total male progeny                              | 109.6 $\pm$ 12.1   | 95.6 $\pm$ 11.8      |
| Total female progeny                            | 140.3 $\pm$ 8.6    | 126.8 $\pm$ 10.6     |
| Total progeny                                   | 249.9 $\pm$ 12.0   | 222.3 $\pm$ 8.0      |
| Post reproductive period<br>for fertilized eggs | 11.9 $\pm$ 0.7     | 4.1 $\pm$ 1.1 **     |
| Total post reproductive<br>period               | 8.5 $\pm$ 0.4      | 0.9 $\pm$ 0.4 **     |

Symbols: \* =  $p < .05$ , \*\* =  $p < .01$ , @ = not comparable

TABLE 33. Reproductive variables for the continuous and 2 hr limited cohorts exposed to D. melanogaster (Woods Orchard strain), April, 1979 (mean  $\pm$  SE).

| Variable                                        | Continuous<br>(20) | 2 hr Limited<br>(19) |
|-------------------------------------------------|--------------------|----------------------|
| Length of life                                  | 18.3 $\pm$ 0.3     | 15.5 $\pm$ 0.8 **    |
| Days of male production                         | 9.6 $\pm$ 0.3      | 10.6 $\pm$ 0.3 *     |
| Days of female production                       | 6.1 $\pm$ 0.5      | 8.6 $\pm$ 0.4 **     |
| Total male progeny                              | 109.6 $\pm$ 12.1   | 90.4 $\pm$ 6.0       |
| Total female progeny                            | 140.3 $\pm$ 8.6    | 139.4 $\pm$ 6.0      |
| Total progeny                                   | 249.9 $\pm$ 12.0   | 229.8 $\pm$ 7.3      |
| Post reproductive period<br>for fertilized eggs | 11.9 $\pm$ 0.7     | 6.8 $\pm$ 0.8 **     |
| Total post reproductive<br>period               | 8.5 $\pm$ 0.4      | 4.8 $\pm$ 0.8 **     |

Symbols: \*=  $p < .05$ , \*\*=  $p < .01$ , @= not comparable

TABLE 34. Reproductive variables for the 1 hr limited and 2 hr limited cohorts exposed to D. melanogaster (Woods Orchard strain), April, 1979 (mean  $\pm$  SE).

| Variable                                        | 1 hr Limited<br>(18) | 2 hr Limited<br>(19) |
|-------------------------------------------------|----------------------|----------------------|
| Length of life                                  | 10.4 $\pm$ 0.6       | 15.5 $\pm$ 0.8 **    |
| Days of male production                         | 9.6 $\pm$ 0.5        | 10.6 $\pm$ 0.3       |
| Days of female production                       | 7.1 $\pm$ 0.7        | 8.6 $\pm$ 0.4        |
| Total male progeny                              | 95.6 $\pm$ 11.8      | 90.4 $\pm$ 6.0       |
| Total female progeny                            | 126.8 $\pm$ 10.6     | 139.4 $\pm$ 6.0      |
| Total progeny                                   | 222.3 $\pm$ 8.0      | 229.8 $\pm$ 7.3      |
| Post reproductive period<br>for fertilized eggs | 4.1 $\pm$ 1.1        | 6.8 $\pm$ 0.8        |
| Total post reproductive<br>period               | 0.9 $\pm$ 0.4        | 4.8 $\pm$ 0.8 **     |

Symbols: \* =  $p < .05$ , \*\* =  $p < .01$ , @ = not comparable



The overall effects obtained by delaying host exposure for six days are (1) decrease in total progeny production, and (2) right shift in the fertility schedule. The first five oviposition periods in the continuous and delayed cohorts exhibit a similar distribution presumably due to the equivalent lengths of exposure periods. This pattern can also be seen in the intermittent cohort. Here too we find a right handed shift in the fertility distribution and daily oviposition rates comparable to rates in other 24 hour exposure cohorts. In fact, in all earlier cases of 24 hour exposure the same phenomenon occurs. Thus we see that the overall effect of delaying or staggering oviposition periods of equal length is to introduce a lag or gap in the distribution of successful female progeny corresponding to the periods of non-exposure.

In the limited cohorts the efficiency of females in producing successful progeny per unit time is remarkable. The two hour per day cohort produced  $139.4 \pm 6.0$  female progeny per female during a total of 32 hours of exposure. This corresponds to more than a 12 fold increase in efficiency in comparison to the continuous cohort. We see in both limited cohorts a trend that was suggested earlier, that is, that females when exposed to hosts for a short period of time on a daily basis will spread their production of successful progeny through time, producing successful progeny later in life and producing more or as many female

progeny per female as females exposed to hosts on a continuous daily basis.

The data presented in this section support my conclusions, based on earlier experiments utilizing D. simulans, that L. boulandi exhibits a very highly plastic reproductive strategy. One further set of experiments were conducted to test the replicability of the trends in reproductive schedules in D. melanogaster, as well as to employ an entirely new analytical technique.

Part II. L. boulandi and D. melanogaster  
a New Analytical Approach, January, 1980

### Introduction

Chabora et al., (1979) published the results of an experiment on a strain of L. boulandi from Chapel Hill, North Carolina, that introduced a novel and preferred means of data collection and calculation of life table characteristics.

Life tables are based upon the interactions of two important population parameters, the age-specific survivorship distribution, and the age-specific fertility distribution. While the meaning of "age-specific survivorship" is straightforward, the meaning of "age-specific fertility", at least in this species, is not and leads to problems in data collection and interpretation. Age-specific fertility may be defined as the number of

females produced per female per unit time. Problems arise in applying this definition; does production refer to oviposition or natality? The enormous variability in development rate of eggs deposited during the same oviposition period, which can produce up to a 10 day spread in hatching time, makes this distinction meaningful. Plasticity in development rate has been proposed by Giesel (1976), Masaki (1980), and Stearns (1976, 1977) as a successful strategy for hedging bets against the risk of the total failure of a brood, by limiting the probability of all progeny hatching during periods of environmental severity and uncertainty.

In the case of these experiments one of the environmental components of the variance in development rate is host density. This is evident in the significant decreases in size of many late hatching adults. Peters and Barbosa (1977) have reviewed the effects of density on insects in culture and show that among many variables, high densities during development of drosophilids can lead to either increased or decreased size, depending upon the species. It is not hard to conceive of this same phenomenon being carried over from host development to parasitoid development. My own observations indicate that those parasitoids that hatch late and are of normal size can be assumed to hatch late because of genetic rather than density effects.

It became necessary to incorporate this variability into the life table. Age-specific fertility distributions used in all previous experiments were based upon the mean number of females produced per female per oviposition period and had to be supplanted by a new fertility distribution based upon the age-specific natality of female progeny (i.e., the mean number of female progeny per female that hatch on a particular day). The increased experimental effort allowed for a more realistic and informative view of the life-history tactics of this species.

The overall effect of lumping the progeny production data together based upon the day of exposure should be to shift the fecundity distribution to the left and thereby produce an overestimate of 'r', and as I will show below, this has indeed been the case.

#### Materials and Methods

Four cohorts of 20 females each were presented with hosts according to the following schedules:

- a) 24 hour continuous exposure daily;
- b) Intermittent exposure (as before);
- c) Delayed exposure (3 day delay prior to host contact);
- d) Limited exposure (1 hour per day ).

Survivorship data was taken daily and following the initial emergence of progeny (day 16.5 for males; 17.5 for females), daily natality was recorded per vial. Vials were discarded following 72 hours of non-emergence.

## Results

### Survivorship

As in all previous experiments, the survivorship curves for each cohort follow the typical "type 1" distribution of Pearl (1928) (see figures 35-38 and tables 35-38). The continuous cohort, exposed to hosts for 24 hour periods daily, exhibited the longest mean length of life ( $17.4 \pm 0.7$  days). This value, however, did not differ significantly from the mean length of life values for any of the other three cohorts (see tables 41-43).

### Daily natality and daily oviposition rates

The continuous exposure cohort. In this cohort and in all the others, the life and fertility table data (tables 35-38, figure 44) have been tabulated based upon the two methods discussed above.

The peak natality for the cohort occurs on day 20.5 (17.2 females/female) followed by an initially steep but subsequently gradual decline until day 30.5 after which no female progeny hatch. Female natality was spread over a 14 day period. Approximately 50% of the natality occurred between days 18.5 and 20.5, while an additional 30% occurred between days 21.5 and 22.5, and the rest occurred over the next 8 days (see table 35). The life-history and population growth parameters calculated using age-specific natality rates are given in table 35, as are the same parameters calculated using the daily oviposition data.

TABLE 35. Life and fertility table for the 24h continuous contact cohort exposed to Drosophila melanogaster, Woods Orchard strain, January, 1980.

---

| x                     | l(x) | m(x) - N      | m(x) - O      | x           | l(x) | m(x) - N | m(x) - O |
|-----------------------|------|---------------|---------------|-------------|------|----------|----------|
| <hr/>                 |      |               |               |             |      |          |          |
| 17.5                  | 1000 | 0.211         | 49.579        | 30.5        | 850  | 0.211    | 0.000    |
| 18.5                  | 1000 | 8.053         | 14.842        | 31.5        | 800  | 0.000    | 0.000    |
| 19.5                  | 1000 | 11.421        | 2.947         | 32.5        | 750  | 0.000    | 0.000    |
| 20.5                  | 1000 | 17.158        | 5.684         | 33.5        | 650  | 0.000    | 0.000    |
| 21.5                  | 1000 | 16.105        | 4.000         | 34.5        | 550  | 0.000    | 0.000    |
| 22.5                  | 1000 | 7.053         | 1.421         | 35.5        | 450  | 0.000    | 0.000    |
| 23.5                  | 1000 | 6.158         | 1.316         | 36.5        | 300  | 0.000    | 0.000    |
| 24.5                  | 1000 | 3.474         | 0.579         |             |      |          |          |
| 25.5                  | 1000 | 2.579         | 0.053         |             |      |          |          |
| 26.5                  | 1000 | 1.632         | 0.000         |             |      |          |          |
| 27.5                  | 950  | 0.684         | 0.000         |             |      |          |          |
| 28.5                  | 950  | 0.579         | 0.000         |             |      |          |          |
| 29.5                  | 950  | 0.158         | 0.000         |             |      |          |          |
| <hr/>                 |      |               |               |             |      |          |          |
| For natality data:    |      | $R_0 = 75.37$ | $T_c = 21.42$ | 'r' = 0.202 |      |          |          |
| For oviposition data: |      | $R_0 = 74.42$ | $T_c = 18.47$ | 'r' = 0.234 |      |          |          |

---

In order to adequately compare the results with those of previous experiments the data was also evaluated on the basis of age-specific ovipositional success (tables 35,41-43, and figure 39). The first exposure period produced the peak in daily ovipositions of female eggs (44.6). This value decreased rapidly thereafter and by day 26.5, no further female progeny were produced. The first oviposition period produced 59.1% of all the female progeny and by the fifth oviposition period, 95% of all female progeny had been produced.

The average female in this cohort lived  $17.4 \pm 0.7$  days during which time she produced male progeny during  $9.2 \pm 0.3$  days (53.5% of the average life span). Female progeny were produced during  $4.7 \pm 0.5$  days (27.2% of the average life span). The average progeny production per female is given in table 41, and the population growth parameters are given in table 35.

The\_\_\_delayed\_\_\_cohort. The age-specific natality distribution is presented in table 36 and figure 45. The peak in this distribution occurs during the second day of emergence (day 19.5), at 27.00 female per female. Female natality then drops rapidly during the next three days, rises again and then falls gradually until day 34.5, when no female progeny hatch. Female progeny hatches over a total of 14 days. The first three days of emergence produced 47.8% of all female emergences. The following four days of

TABLE 36. Life and fertility tables for the delayed cohort, exposed to D. melanogaster, Woods Orchard strain, January, 1980.

| x    | l(x) | m(x)-N | m(x)-O | x    | l(x) | m(x)-N | m(x)-O |
|------|------|--------|--------|------|------|--------|--------|
| 17.5 | 1000 | 0.000  | 0.000  | 30.5 | 600  | 1.274  | 0.000  |
| 18.5 | 1000 | 0.000  | 0.000  | 31.5 | 550  | 1.781  | 0.000  |
| 19.5 | 1000 | 0.000  | 0.000  | 32.5 | 450  | 0.421  | 0.000  |
| 20.5 | 950  | 2.947  | 76.158 | 33.5 | 450  | 0.431  | 0.000  |
| 21.5 | 950  | 27.000 | 4.789  | 34.5 | 400  | 0.000  | 0.000  |
| 22.5 | 950  | 20.842 | 1.579  | 35.5 | 250  | 0.000  | 0.000  |
| 23.5 | 950  | 13.842 | 6.632  | 36.5 | 200  | 0.000  | 0.000  |
| 24.5 | 950  | 5.895  | 9.579  |      |      |        |        |
| 25.5 | 950  | 8.421  | 3.842  |      |      |        |        |
| 26.5 | 950  | 7.684  | 2.579  |      |      |        |        |
| 27.5 | 800  | 6.842  | 0.750  |      |      |        |        |
| 28.5 | 700  | 5.162  | 0.214  |      |      |        |        |
| 29.5 | 600  | 3.521  | 0.000  |      |      |        |        |

For natality data:  $R_0 = 96.18$   $T_c = 23.71$   $'r' = 0.193$

For oviposition data:  $R_0 = 100.65$   $T_c = 21.51$   $'r' = 0.214$



emergence produced 33.9% more females and the subsequent seven days produced all further female emergences. Population growth and life history parameters calculated from the natality data are given in table 36.

Table 36 and figure 40 present the daily oviposition data. The first oviposition period (day 19.5) produced the peak value in female eggs laid per female (76.2) and production of female progeny dropped off sharply after that, to 0.00 at day 29.5. 72% of all female progeny were oviposited during the first day of host exposure while additional 13% were produced during the next three days and the rest were produced during the subsequent five days. The average female survived for  $15.4 \pm 0.9$  days and  $12.4 \pm 0.9$  oviposition periods. Male progeny and female progeny were produced for 59.6% and 48.9% of exposure time, respectively (see table 41 for the reproductive variables). Population growth and life history parameters calculated from the daily oviposition data are given in table 36.

The intermittent exposure cohort. The female natality of this cohort extends over a period of 17 days, with a peak of 27.6 females per female on the third day of emergence. This peak in age-specific natality was followed by a sharp decrease to 11.8 females per female on the following day, then a slight increase to 13.3 females per female on the fifth day of emergence. Female natality decreased regularly thereafter (see figure 46 and table 37). Approximately 61%

TABLE 37. Life and fertility table for the intermittent cohort exposed to D. melanogaster (Woods Orchard strain), January, 1980.

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| x    | l(x) | m(x) -N | m(x) -O | x    | l(x) | m(x) -N | m(x) -O |
|------|------|---------|---------|------|------|---------|---------|
| 17.5 | 1000 | 0.579   | 59.526  | 30.5 | 800  | 0.857   | 0.000   |
| 18.5 | 1000 | 14.632  | 0.000   | 31.5 | 800  | 0.859   | 0.000   |
| 19.5 | 1000 | 27.632  | 0.000   | 32.5 | 800  | 0.214   | 0.000   |
| 20.5 | 1000 | 11.789  | 34.316  | 33.5 | 550  | 0.325   | 0.000   |
| 21.5 | 1000 | 13.316  | 0.000   | 34.5 | 550  | 0.000   | 0.000   |
| 22.5 | 1000 | 12.632  | 0.000   | 35.5 | 450  | 0.000   | 0.000   |
| 23.5 | 1000 | 8.789   | 14.789  | 36.5 | 250  | 0.000   | 0.000   |
| 24.5 | 1000 | 5.368   | 0.000   | 37.5 | 100  | 0.000   | 0.000   |
| 25.5 | 1000 | 5.737   | 0.000   |      |      |         |         |
| 26.5 | 950  | 3.579   | 3.167   |      |      |         |         |
| 27.5 | 900  | 2.842   | 0.000   |      |      |         |         |
| 28.5 | 900  | 1.503   | 0.000   |      |      |         |         |
| 29.5 | 850  | 1.147   | 0.000   |      |      |         |         |

---

For natality data:  $R_0 = 110.48$   $T_c = 21.71$  'r' = 0.217

For oviposition data:  $R_0 = 111.64$   $T_c = 19.46$  'r' = 0.242

of all natality occurred within the first five days of emergence, 24% more occurred within the next three days and the other 15% occurred over the subsequent nine days. Interestingly, this long emergence period is based upon eggs laid during only 4 oviposition periods. Life history parameters based upon natality data are given in table 37.

Of the seven oviposition periods available to the cohort, only the first four produced female progeny. The first oviposition period produced the highest number of female eggs laid per female (59.5), which accounted for 53.24% of all the female progeny. The second oviposition period produced 34.3 successful female eggs per female, while the third and fourth periods produced 14.8 and 3.2 successful female eggs per female, respectively (see table 37 and figure 41). Females survived for  $17.0 \pm 0.8$  days with an average number of oviposition periods of  $6.1 \pm 0.3$  days. 66.9% and 52% of the total exposure time was spent producing male and female progeny, respectively. Table 45 presents the reproductive variables for this cohort. Life history parameters based upon age-specific oviposition data are given in table 37 and daily sex ratios for oviposition and natality are given in tables 39 and 40, respectively.

The limited exposure cohort. The female progeny of this cohort emerged over a 17 day period with a peak of 12.3 females per female on the fourth day of emergence (see table 38 and figure 47). Natality decreased gradually and

TABLE 38.

Life and fertility table for the 1 hour limited contact cohort, exposed to D. melanogaster, (Woods Orchard strain), January, 1980.

| x    | l(x) | m(x)-N | m(x)-O | x    | l(x) | m(x)-N | m(x)-O |
|------|------|--------|--------|------|------|--------|--------|
| 17.5 | 1000 | 0.278  | 11.556 | 30.5 | 750  | 0.457  | 0.000  |
| 18.5 | 1000 | 5.222  | 15.833 | 31.5 | 650  | 0.189  | 0.000  |
| 19.5 | 1000 | 5.222  | 17.333 | 32.5 | 600  | 0.063  | 0.000  |
| 20.5 | 1000 | 12.272 | 9.556  | 33.5 | 550  | 0.189  | 0.000  |
| 21.5 | 1000 | 11.278 | 8.611  | 34.5 | 500  | 0.000  | 0.000  |
| 22.5 | 1000 | 8.889  | 4.278  | 35.5 | 150  | 0.000  | 0.000  |
| 23.5 | 950  | 9.000  | 5.176  | 36.5 | 100  | 0.000  | 0.000  |
| 24.5 | 900  | 7.166  | 1.813  |      |      |        |        |
| 25.5 | 900  | 6.009  | 1.375  |      |      |        |        |
| 26.5 | 850  | 4.130  | 0.667  |      |      |        |        |
| 27.5 | 800  | 2.174  | 0.429  |      |      |        |        |
| 28.5 | 800  | 2.043  | 0.071  |      |      |        |        |
| 29.5 | 800  | 1.504  | 0.000  |      |      |        |        |

For natality data:  $R_0 = 72.26$   $T_c = 22.64$  'r' = 0.189

For oviposition data:  $R_0 = 75.92$   $T_c = 20.07$  'r' = 0.216

TABLE 39.

Daily sex ratio of ovipositions in the four cohorts  
of L. boulandi exposed to D. melanogaster larvae  
(Woods Orchard strain), January, 1980.

| Day of<br>exposure | Cohort     |              |         |         |
|--------------------|------------|--------------|---------|---------|
|                    | Continuous | Intermittent | Delayed | Limited |
| 0.5                | 0.56       | 0.34         | ----    | 0.46    |
| 1.5                | 0.64       | ----         | ----    | 0.38    |
| 2.5                | 0.71       | ----         | ----    | 0.43    |
| 3.5                | 0.80       | 0.53         | 0.41    | 0.54    |
| 4.5                | 0.80       | ----         | 0.51    | 0.58    |
| 5.5                | 0.90       | ----         | 0.62    | 0.63    |
| 6.5                | 0.87       | 0.60         | 0.57    | 0.65    |
| 7.5                | 0.93       | ----         | 0.55    | 0.82    |
| 8.5                | 0.98       | ----         | 0.64    | 0.85    |
| 9.5                | 1.00       | 0.67         | 0.68    | 0.90    |
| 10.5               | 1.00       | ----         | 0.82    | 0.90    |
| 11.5               | ----       | ----         | 0.63    | 0.96    |
| 12.5               | ----       | 1.00         | 1.00    | 1.00    |
| 13.5               | ----       | ----         | ----    | 1.00    |
| 14.5               | ----       | ----         | ----    | ----    |

TABLE 40. Daily natality sex ratio for the four cohorts of L. boucardi exposed to D. melanogaster larvae (Woods Orchard strain), January, 1980.

| Parental<br>age | Cohort     |              |         |         |
|-----------------|------------|--------------|---------|---------|
|                 | Continuous | Intermittent | Delayed | Limited |
| 16.5            | 1.00       | 1.00         | ----    | 1.00    |
| 17.5            | 0.99       | 0.96         | ----    | 0.94    |
| 18.5            | 0.80       | 0.39         | ----    | 0.39    |
| 19.5            | 0.67       | 0.23         | 1.00    | 0.67    |
| 20.5            | 0.58       | 0.54         | 0.88    | 0.49    |
| 21.5            | 0.53       | 0.37         | 0.36    | 0.49    |
| 22.5            | 0.64       | 0.31         | 0.25    | 0.47    |
| 23.5            | 0.67       | 0.53         | 0.23    | 0.52    |
| 24.5            | 0.74       | 0.66         | 0.56    | 0.57    |
| 25.5            | 0.76       | 0.43         | 0.54    | 0.57    |
| 26.5            | 0.70       | 0.51         | 0.55    | 0.61    |
| 27.5            | 0.78       | 0.49         | 0.42    | 0.66    |
| 28.5            | 0.76       | 0.58         | 0.46    | 0.64    |
| 29.5            | 0.90       | 0.50         | 0.47    | 0.63    |
| 30.5            | 0.67       | 0.36         | 0.56    | 0.67    |
| 31.5            | 1.00       | 0.43         | 0.30    | 0.89    |
| 32.5            | 1.00       | 0.56         | 0.58    | 0.90    |
| 33.5            | 1.00       | 0.40         | 0.31    | 0.80    |

regularly thereafter. Life history parameters based upon age-specific natality are also given in table 38.

The first three oviposition periods produced 58.3% of all total female offspring. The first period produced an average of 11.6 female eggs per female; the second, 15.8 female eggs per female; and the third produced the peak value, 17.3 female eggs per female. Successful female ovipositions decreased sharply to 9.6 on the following day and decreased gradually over the following 8 days (see table 38 and figure 42). The average female survived  $15.1 \pm 1.0$  days, and during her life produced male progeny and female progeny during 73.5% and 47.4% of her life span, respectively. Reproductive variables are given in table 43.

## Discussion

### Survivorship

As in all previous experiments, the survivorship curves for all cohorts follow the typical 'type 1' distribution of Pearl (1928). The continuous cohort exhibited the longest mean length of life ( $17.4 \pm 0.7$  days). This value, however, did not differ significantly from the mean length of life values for any of the other three cohorts (see tables 41-43, and 69-71 in the appendix) The fertility distributions

### Fertility

Male progeny production schedule. As before, we must look at DOMP in two ways. We can compare the numerical value of the variable directly between daily exposed cohorts

Figure 35. Survivorship curve for the continuous exposure cohort (Ha77 strain) exposed to D.\_\_\_\_melanogaster (W.O. strain), January, 1980.



Survivorship curve for  
the CONTINUOUS cohort, 24 hour exposure  
host, Drosophila melanogaster  
WOODS ORCHARD II

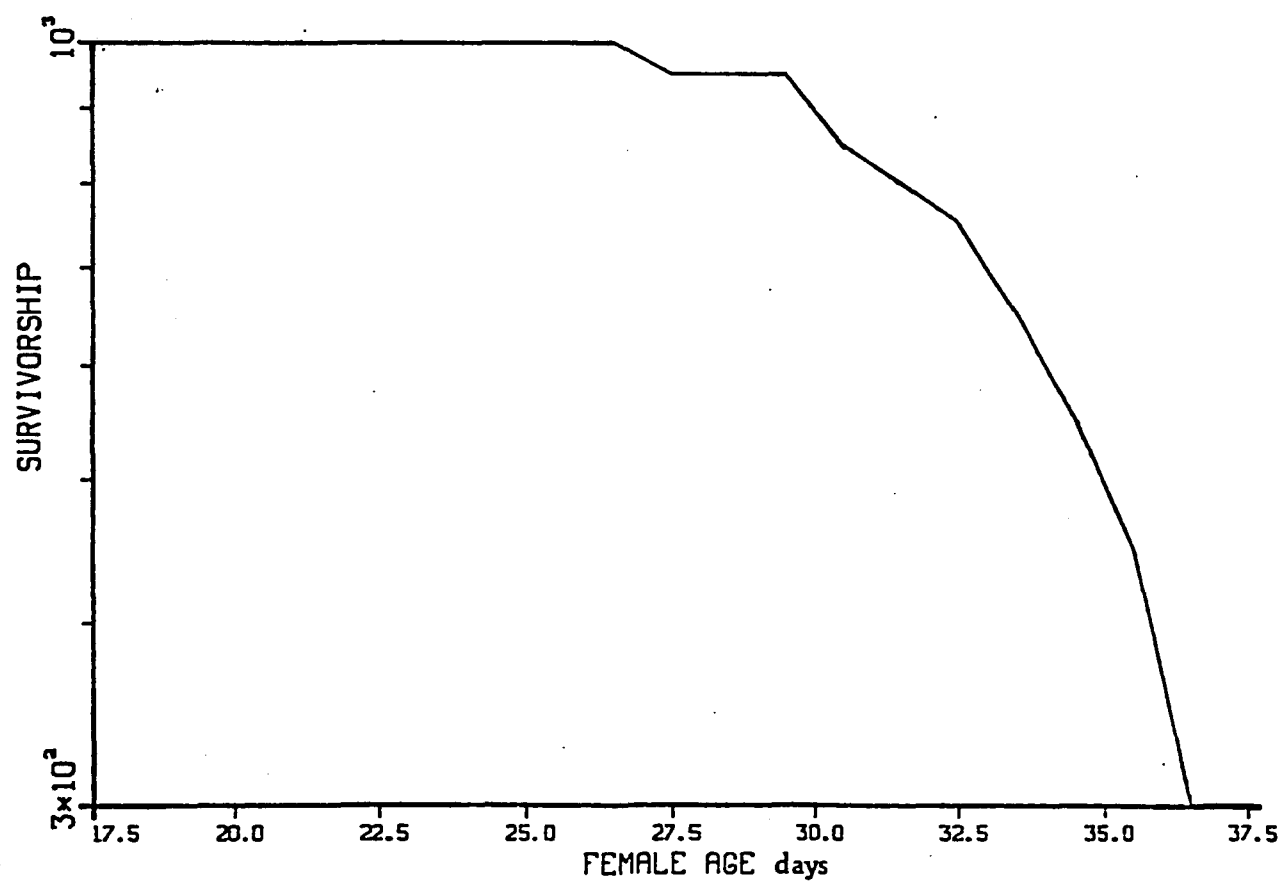


Figure 36. Survivorship curve for the delayed exposure cohort (Ha77 strain) exposed to D. melanogaster (W.O. strain), January, 1980.

Survivorship curve for  
the INTERMITTENT cohort, 24 hour exposure  
host, Drosophila melanogaster  
WOODS ORCHARD II

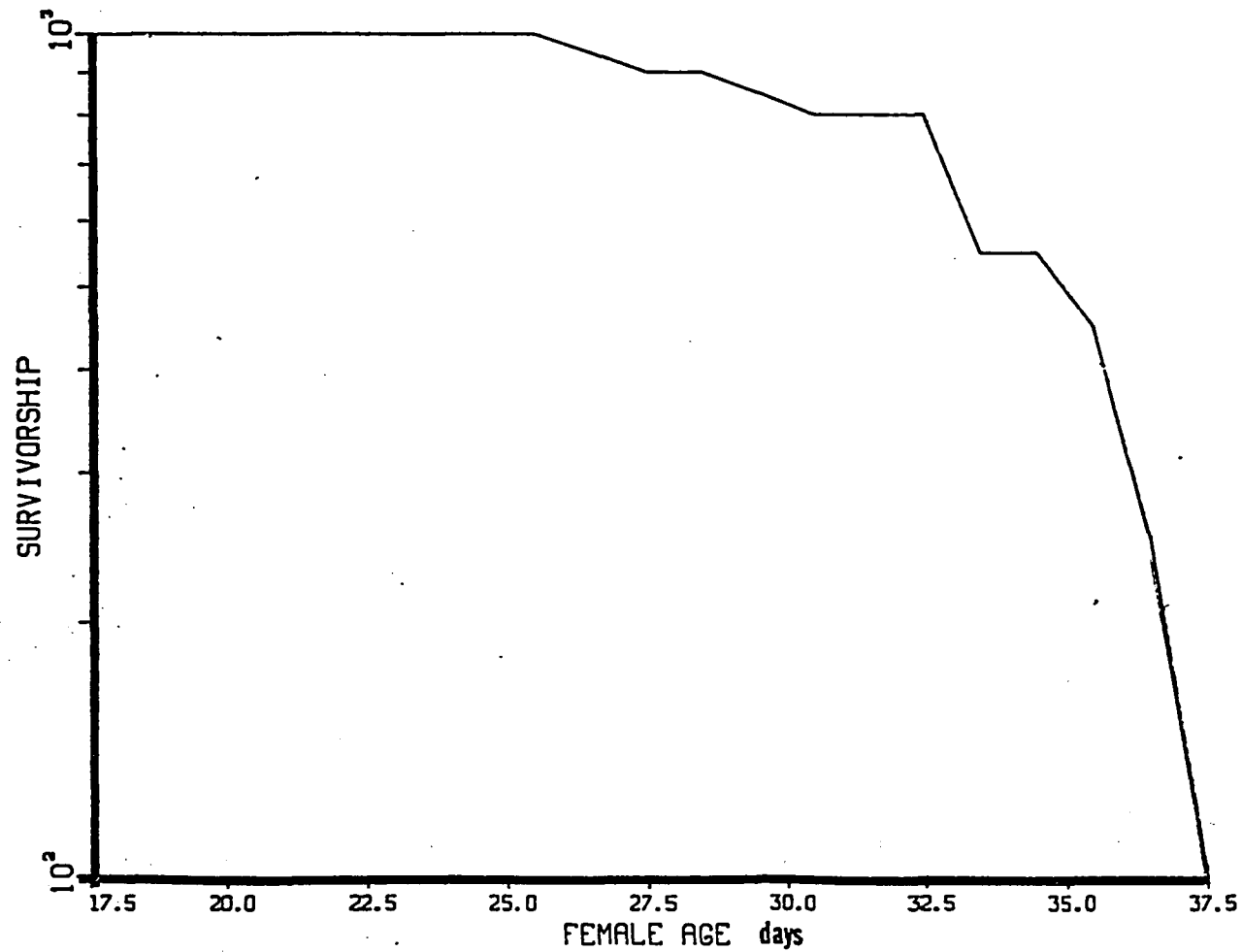


Figure 37. Survivorship curve for the intermittent exposure cohort (Ha77 strain) exposed to D.\_\_\_\_melanogaster (W.O. strain), January, 1980.

Survivorship curve for  
the DELAYED cohort, 24 hour exposure  
host, *Drosophila melanogaster*  
WOODS ORCHARD II

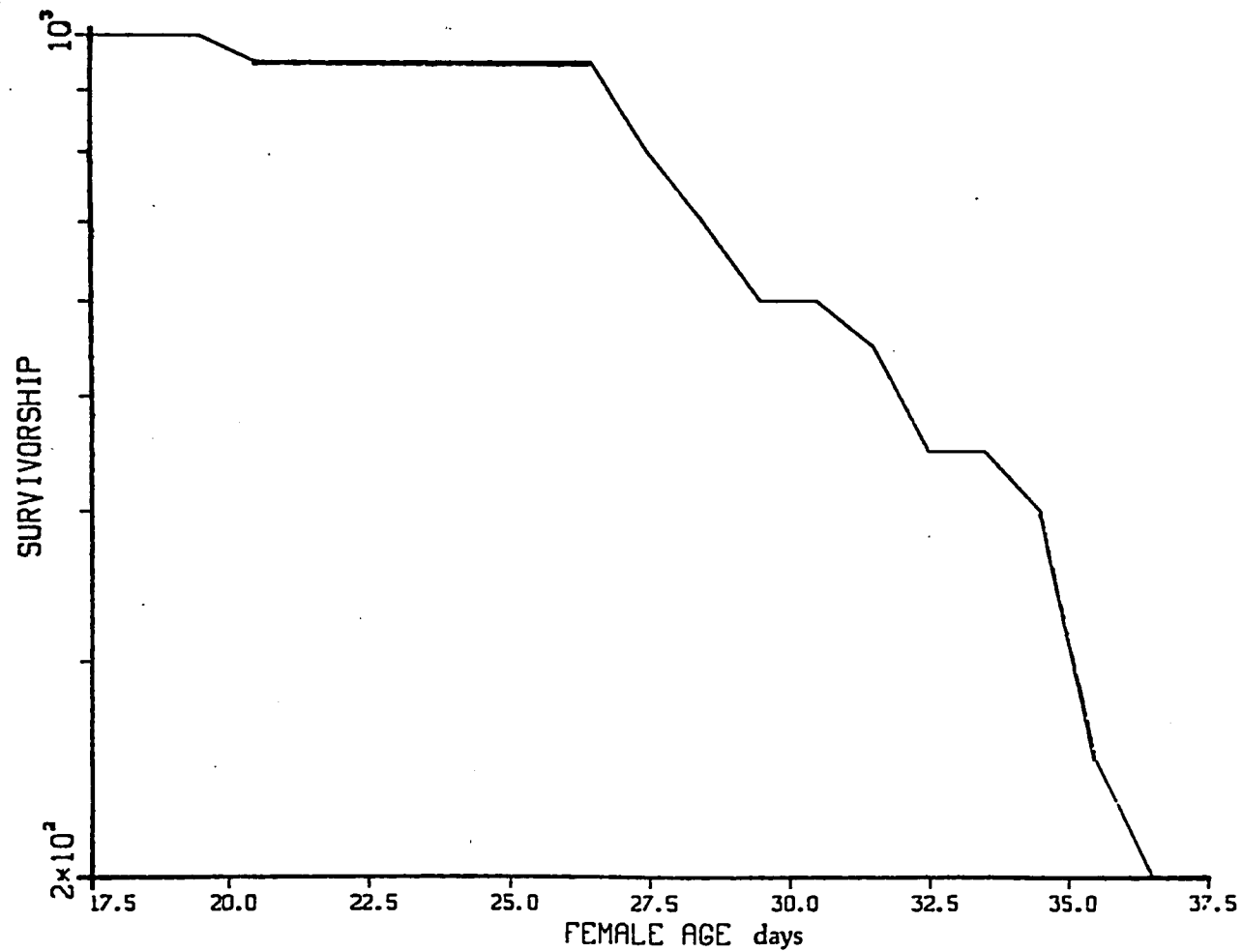


Figure 38. Survivorship curve for the limited 1h exposure cohort (Ha77 strain) exposed to D.\_\_\_\_\_melanogaster (W.O. strain), January, 1980.

Survivorship curve for  
the LIMITED cohort, 1 hour exposure  
host, *Drosophila melanogaster*  
WOODS ORCHARD II

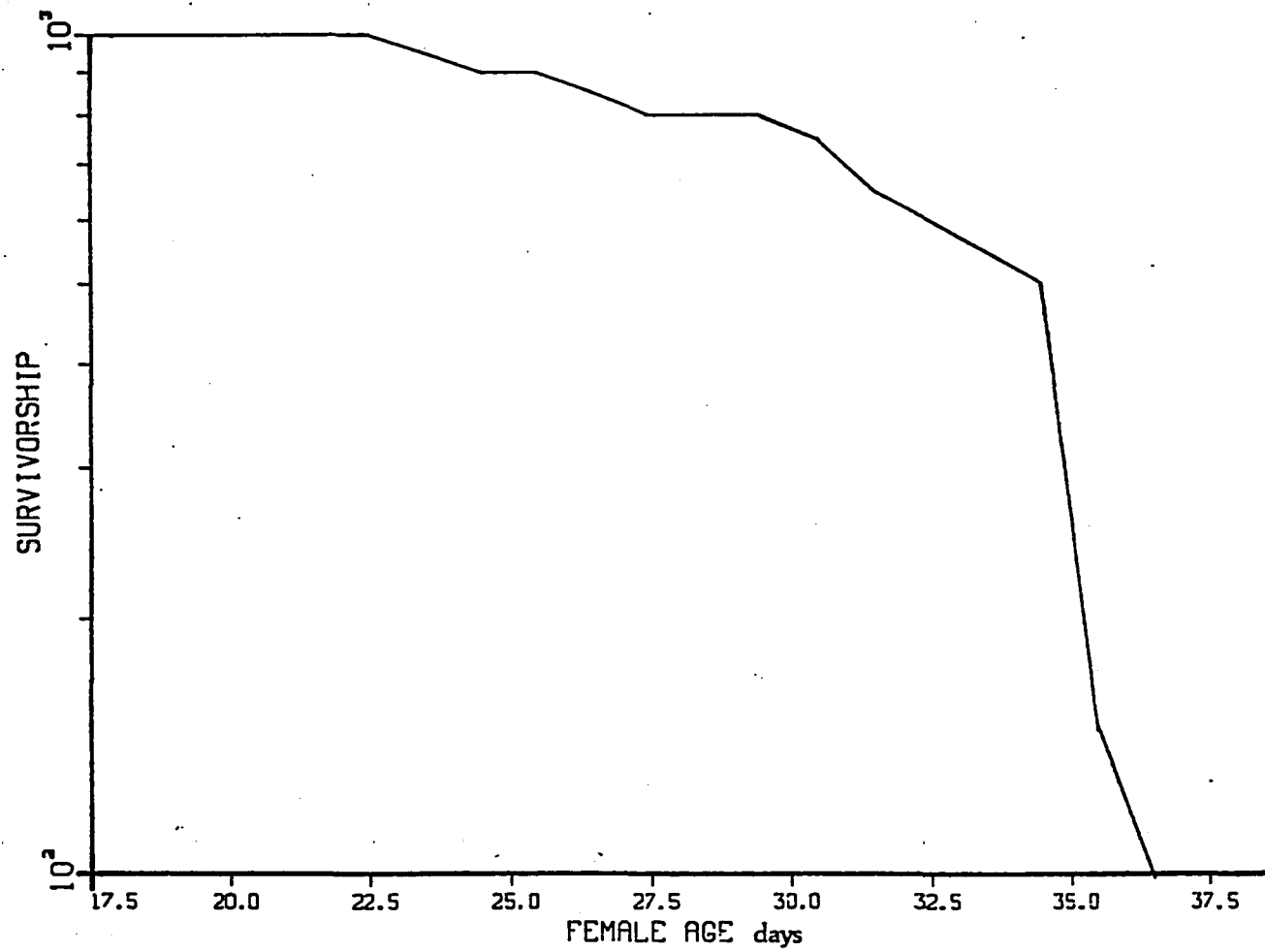


Figure 39. Oviposition curve for the continuous exposure cohort (Ha77 strain) exposed to D. melanogaster (W.O. strain), January, 1980.



Oviposition curve for  
the CONTINUOUS cohort, 24 hour exposure  
host, Drosophila melanogaster  
WOODS ORCHARD II

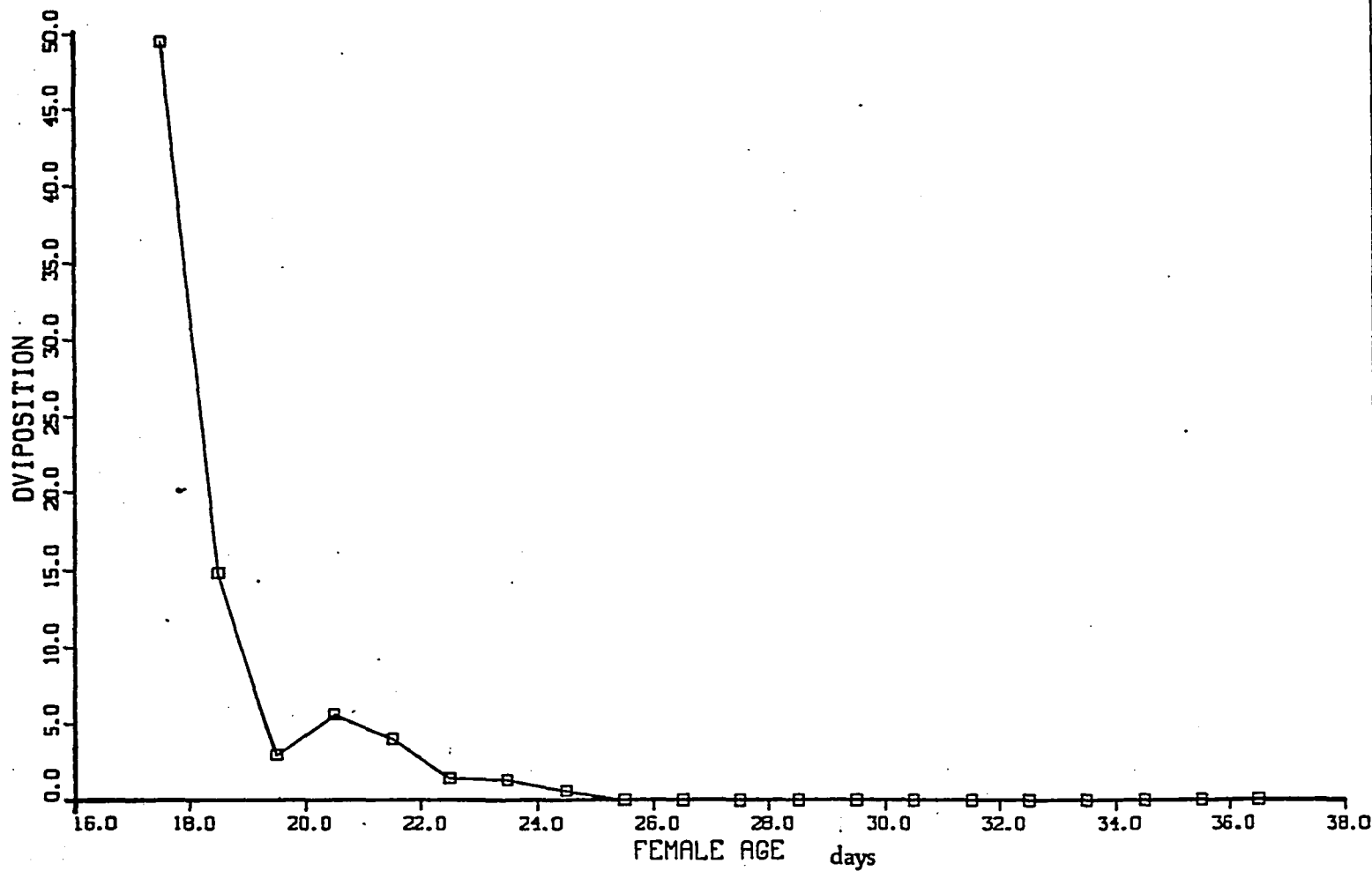


Figure 40. Oviposition curve for the delayed exposure cohort (Ha77 strain) exposed to D. melanogaster (W.O. strain), January, 1980.

Oviposition curve for  
the INTERMITTENT cohort, 24 hour exposure  
host, *Drosophila melanogaster*  
WOODS ORCHARD II

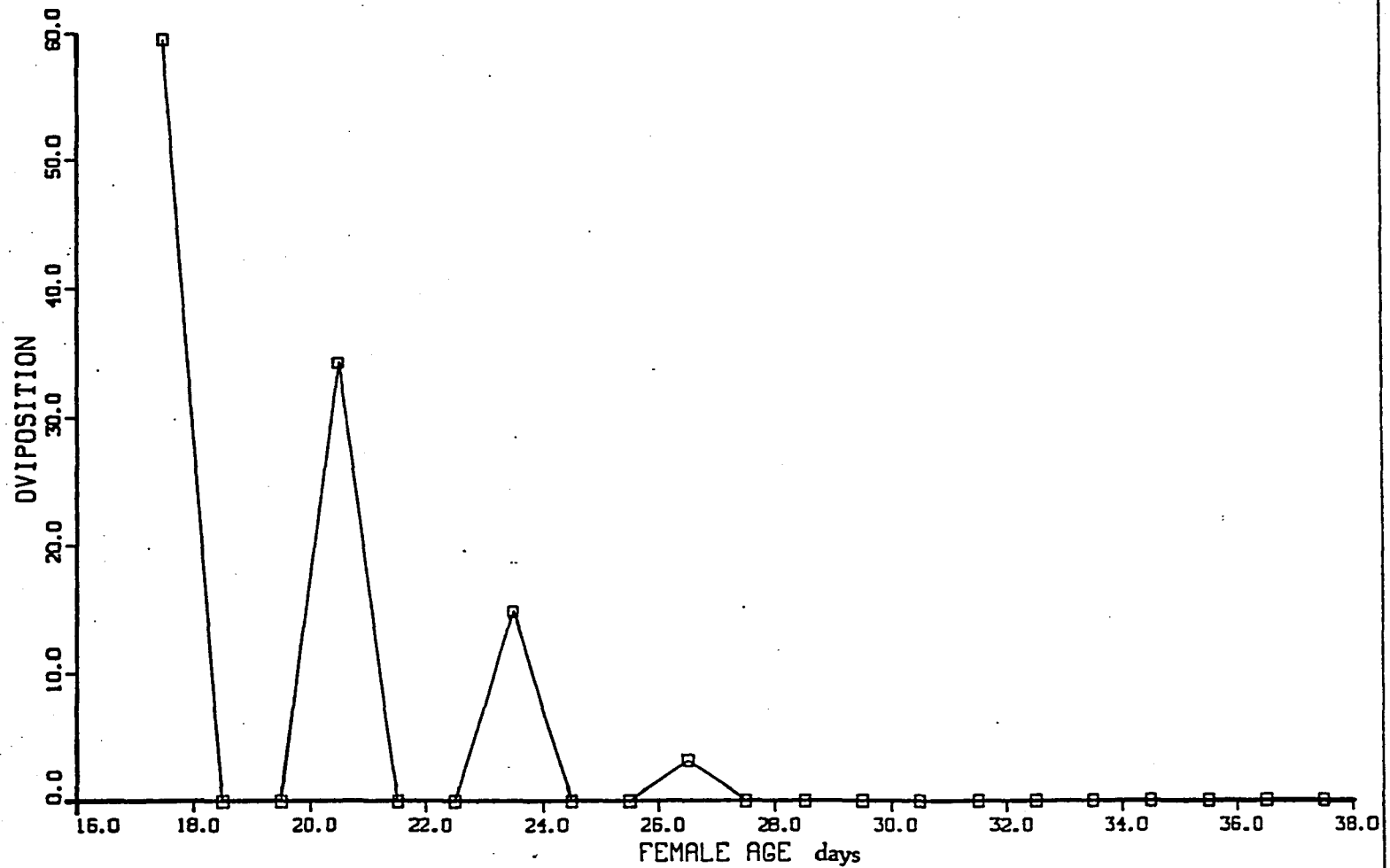


Figure 41. Oviposition curve for the intermittent exposure cohort (Ha77 strain) exposed to D. melanogaster (W.O. strain), January, 1980.

Oviposition curve for  
the DELAYED cohort, 24 hour exposure  
host, *Drosophila melanogaster*  
WOODS ORCHARD II

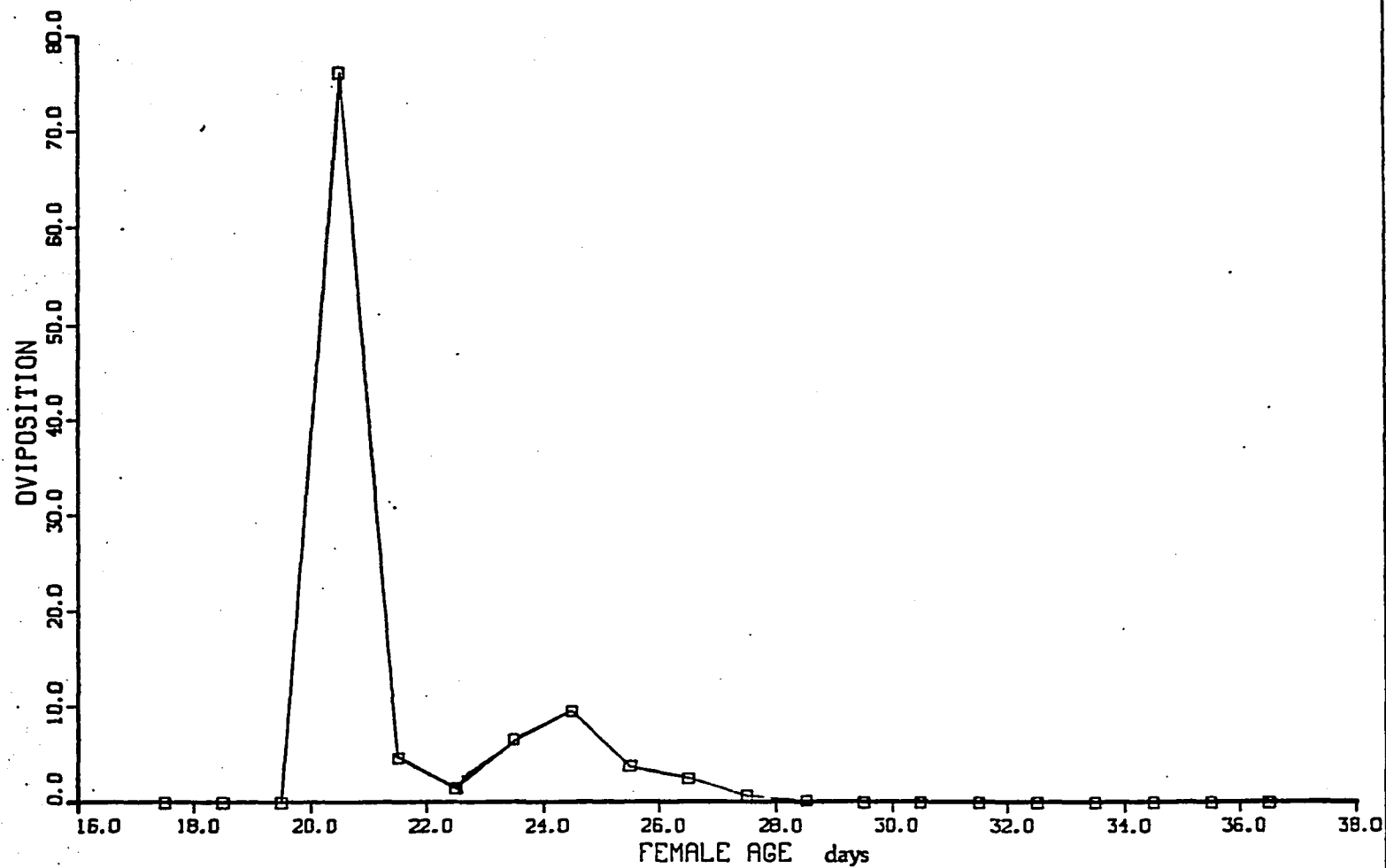


Figure 42. Oviposition curve for the limited 1h exposure cohort (Ha77 strain) exposed to D. melanogaster (W.O. strain), January, 1980.

Oviposition curve for  
the LIMITED cohort, 1 hour exposure  
host, *Drosophila melanogaster*  
WOODS ORCHARD II

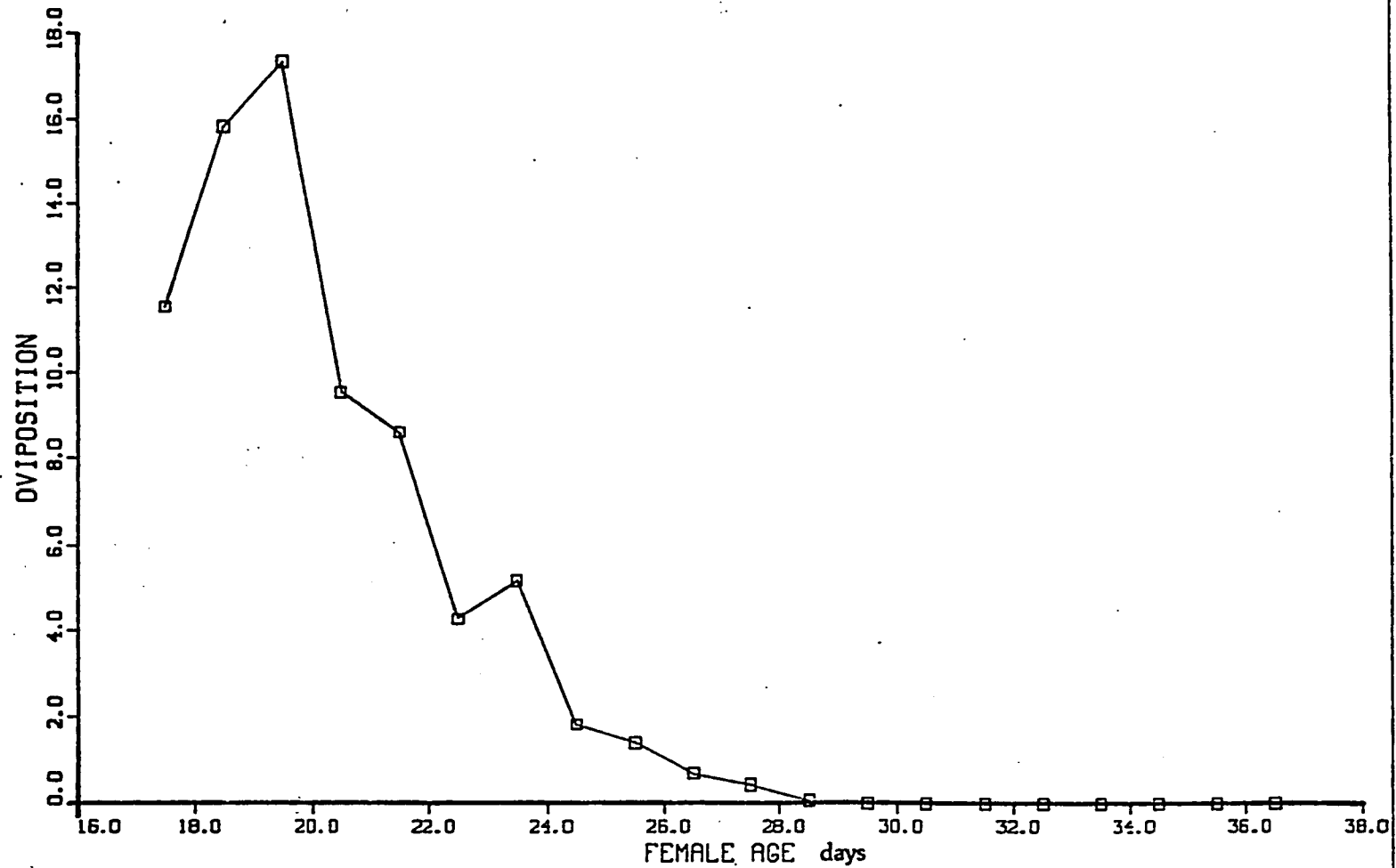


Figure 43. Oviposition curves for all cohorts exposed to D.  
melanogaster, (January, 1980).



Oviposition curves for  
 cohorts exposed to  
Drosophila melanogaster  
 WOODS ORCHARD II

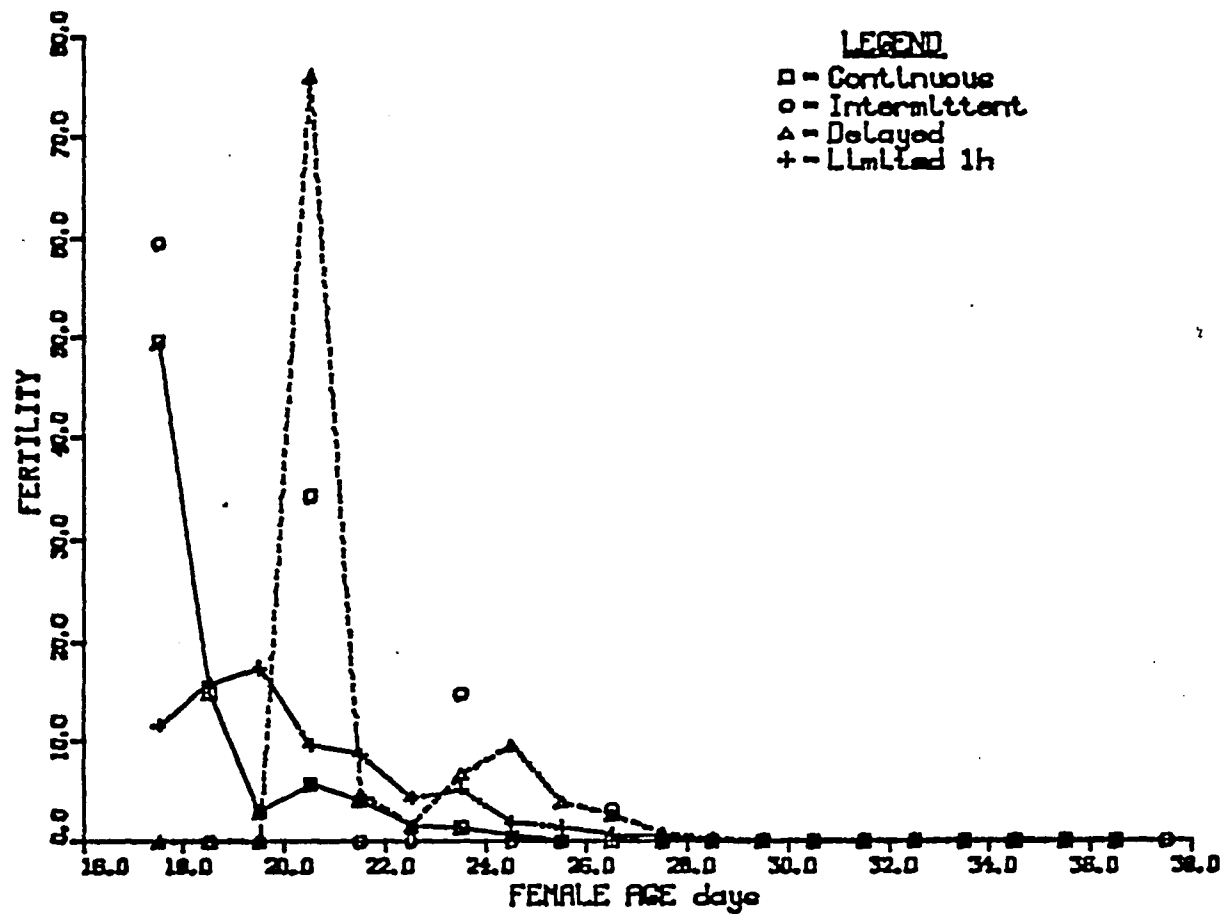


Figure 44.      Natality    curve for the   continuous   exposure  
cohort   (Ha77· strain)· exposed - - to · D. . . melanogaster (W.O.  
strain) , January, 1980.

Natality curve for  
the CONTINUOUS cohort, 24 hour exposure  
host, Drosophila melanogaster  
WOODS ORCHARD II

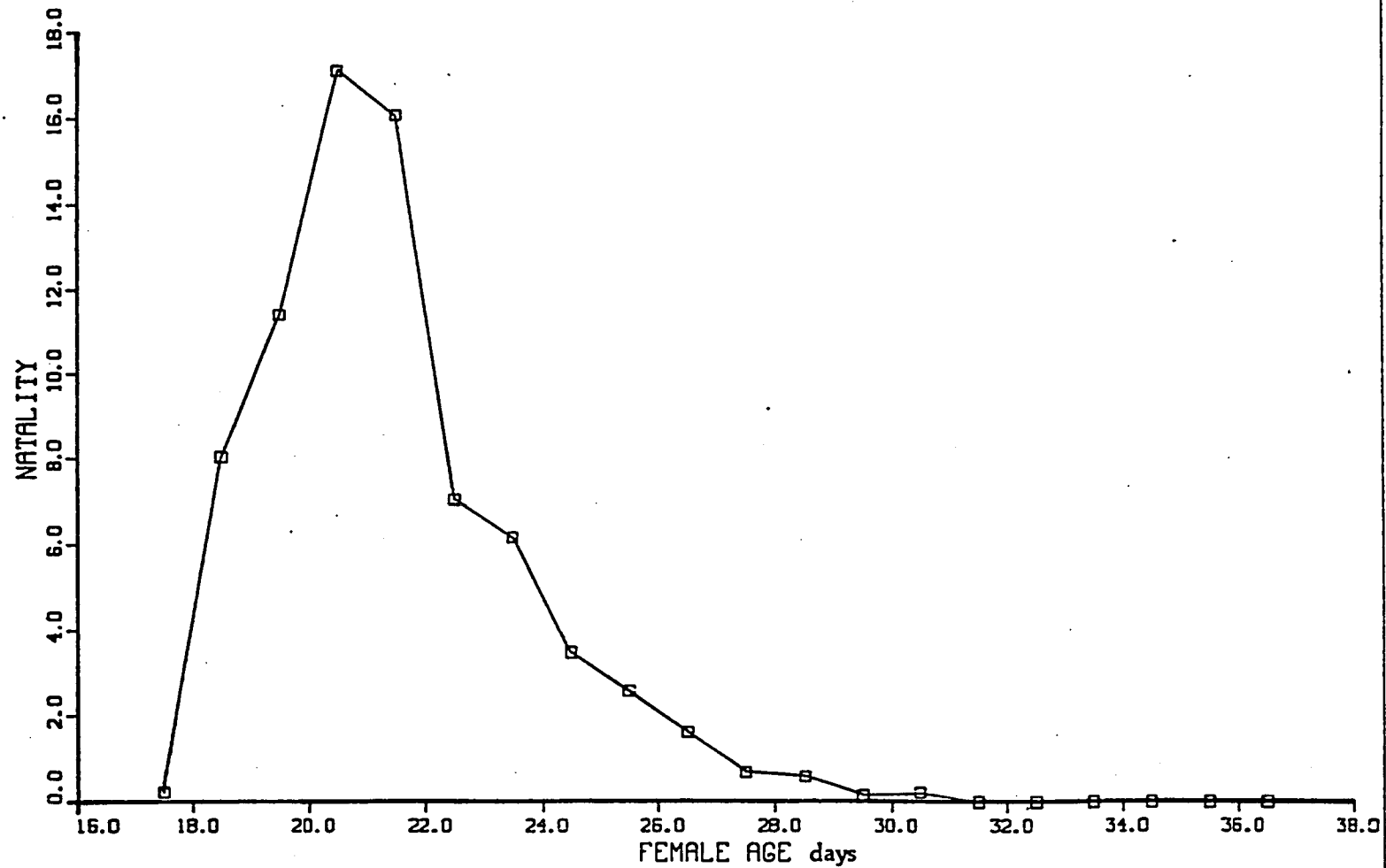


Figure 45.     Natality     curve for the     delayed     exposure  
cohort     (Ha77     strain)     exposed     to     D.\_\_\_\_\_melanogaster (W.O.  
strain), January, 1980.

Natality curve for  
the INTERMITTENT cohort, 24 hour exposure  
host, *Drosophila melanogaster*  
WOODS ORCHARD II

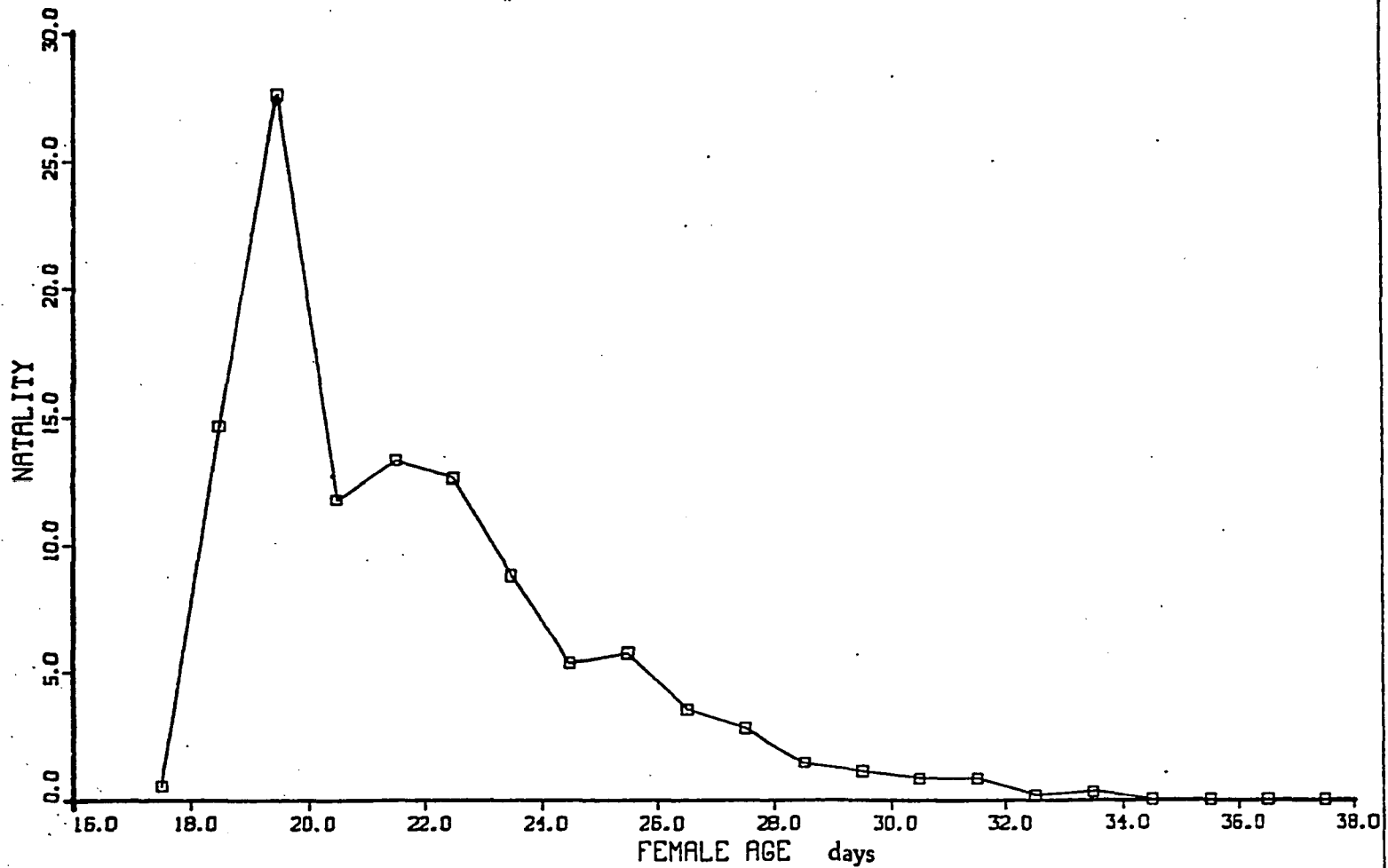


Figure 46. Natality curve for the intermittent exposure cohort (Ha77 strain) exposed to D.\_\_\_\_melanogaster (W.O. strain), January, 1980.

Natality curve for  
the DELAYED cohort, 24 hour exposure  
host, *Drosophila melanogaster*  
WOODS ORCHARD II

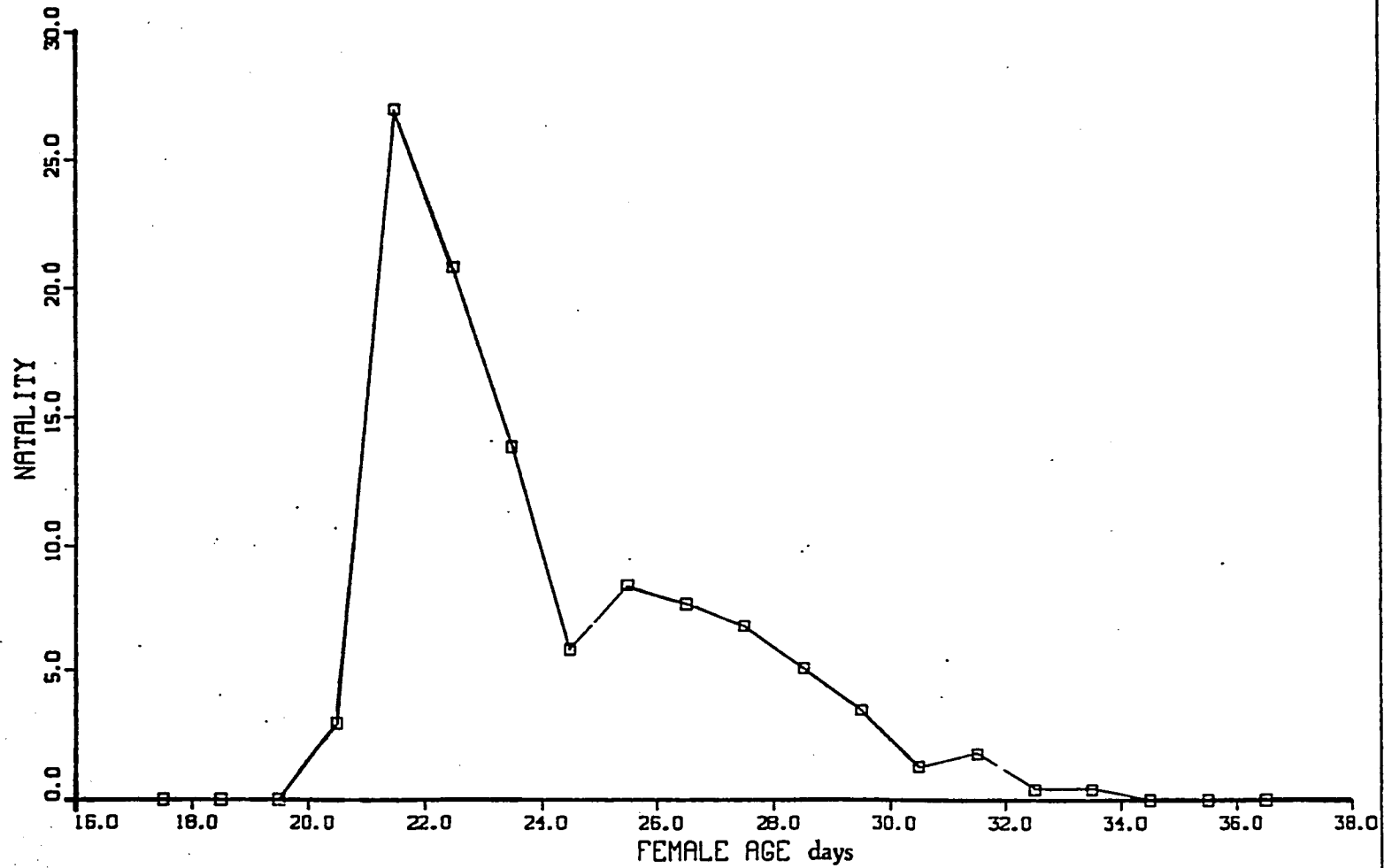


Figure 47.    Natalty    curve for the limited 1h exposure cohort (Ha77 strain) exposed to D.\_\_\_\_melanogaster (W.O. strain), January, 1980.



Natality curve for  
the LIMITED cohort, 1 hour exposure  
host, *Drosophila melanogaster*  
WOODS ORCHARD II

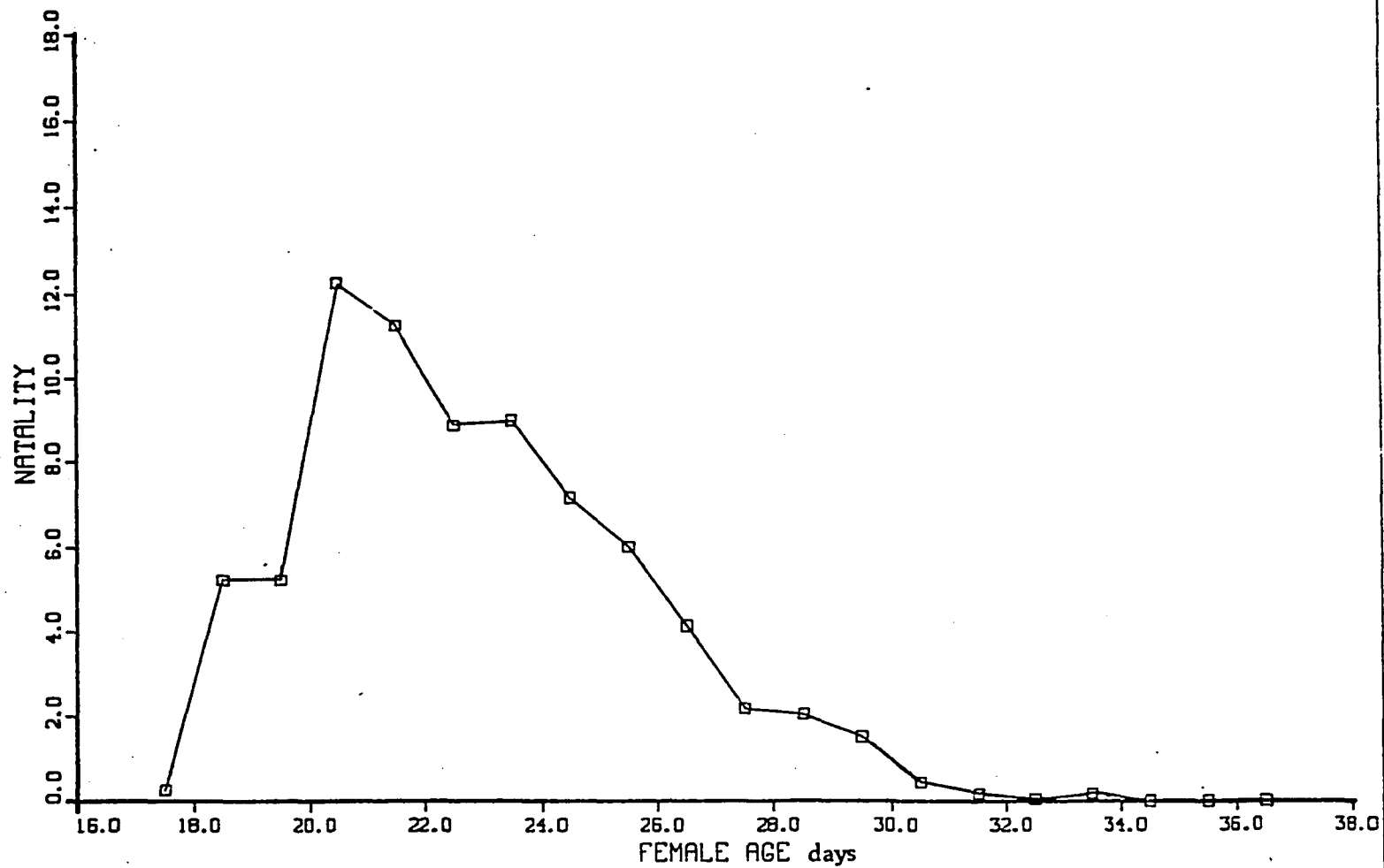
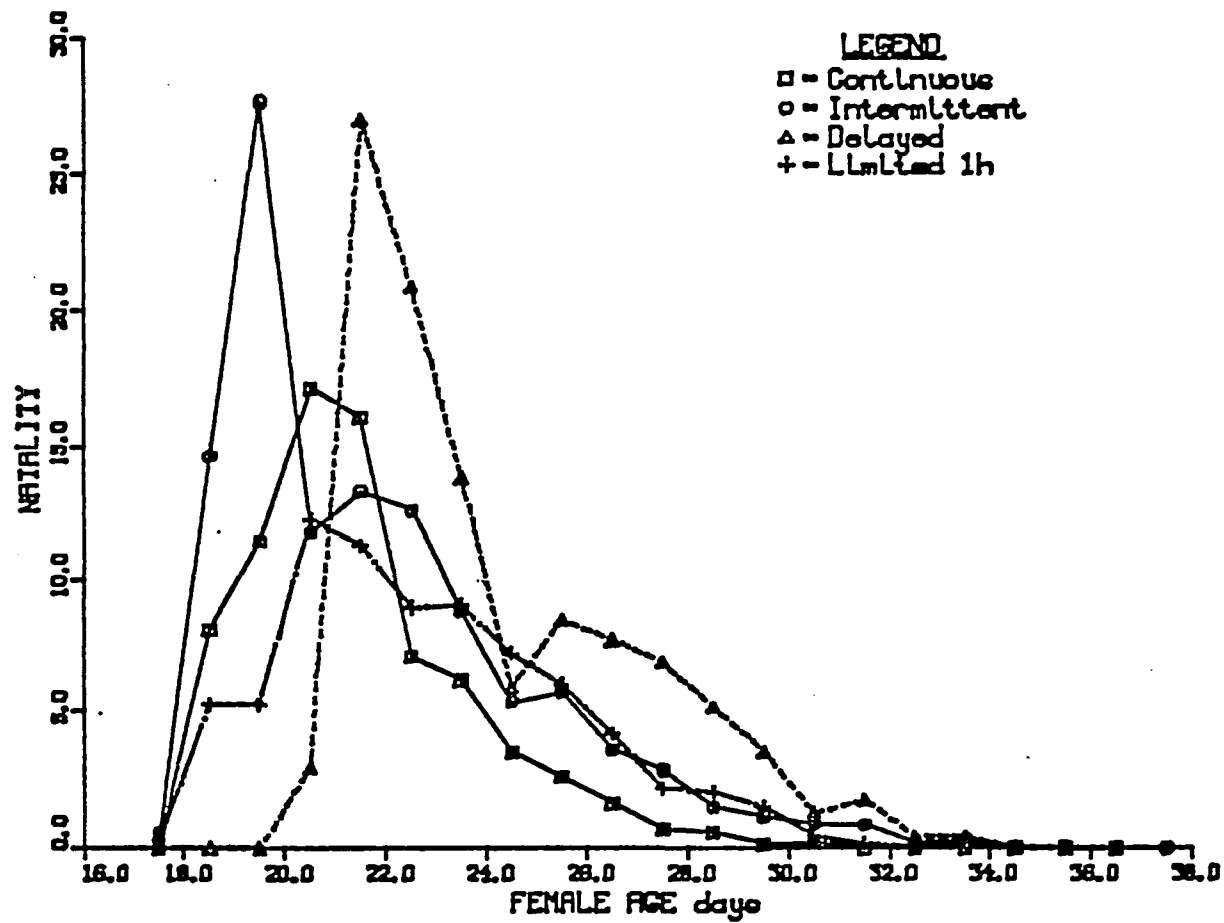


Figure 48. Natality curves for all cohorts exposed to Dx  
melanogaster, (January, 1980).

Natality curves for  
cohorts exposed to  
Drosophila melanogaster  
WOODS ORCHARD II



and we can compare it as a ratio of the number of exposure periods spent in male production divided by the total. The females in the limited cohort had a significantly higher mean value for DOMP than their continuously exposed counterparts (see tables 41-43). The females in the continuous cohort produced male progeny during 53.4% of their life span. Females in the delayed cohort produced males during 59.6% of their oviposition periods; the intermittent cohort, during 67% of their oviposition periods, and the limited cohort, for 73.5% of their oviposition periods.

Female progeny production schedule. The continuous cohort, following the trend in all other experiments produced successful female progeny during only 27.2% of their total exposure time and their  $4.7 \pm 0.5$  days of female production was significantly lower than that of both the limited and delayed cohorts (see tables 41-43). It was the intermittent cohort, though, that was most successful in the use of exposure periods to produce female offspring, i.e., 53%. Whereas the limited and delayed cohorts spent 47.4% and 48.9% of their exposure periods producing female eggs, respectively.

In terms of the efficiency of ovipositing successful female eggs per hour of exposure, the limited cohort was 27.5 times more efficient than the continuous cohort; 13.8 times more efficient than the delayed cohort, and 6.4 times more efficient than the intermittent cohort.

The number of progeny produced. The continuous cohort produced significantly more male progeny per fertilized female than did any other cohort, and produced significantly fewer female progeny per female than the intermittent or the delayed cohorts. No significant difference could be found between the continuous and limited cohorts in the mean number of total females produced per female. The continuous cohort did produce significantly more total offspring per female than did any other cohort (see tables 41-43). Here again, we seem to be observing the sometimes pervasive effects of stress produced by continuous exposure to high density host patches, on the successful production of female progeny.

The average total egg compliment of this parasitoid strain is  $286.34 \pm 2.0$  eggs at hatching. We can calculate the efficiency of egg utilization for each cohort, and assuming, as we did before, that all eggs are laid, we can also use this data to assess the developmental mortality of *L. bouhardi* larvae. In this set of experiments the "continuous" cohort produced a mean of  $239.3 \pm 14.3$  total progeny, utilizing on the average, 83.6% of all available eggs. In the previous *D. melanogaster* experiment, the analogous cohort utilized  $249.9 \pm 12.0$  eggs, or 87.3% of its egg compliment, but produced significantly more female progeny than this latter counterpart (see tables 11 and 45).

Intermittently exposed cohorts utilized 71.8% and 79.5% of their available eggs, on the average, in this and the previous experiment, respectively. The one hour limited cohorts utilized 60.5% and 72.6% of their available eggs, and the previous two hour limited exposure cohort utilized 80.3% of its available eggs to produce progeny. The six day delayed cohort utilized only 53.4% of its available eggs, while the three day delayed cohort, here, utilized 70.5% of its egg complement.

The trends in host utilization are quite clear and repeatable. Long and continuous exposure to hosts generally yields the greatest success in total host utilization. Limiting the availability or, in effect the density, of hosts decreases the overall success of host utilization and increases the efficiency of searching. In addition, the period of post-reproductive survival is decreased and the sex ratio of ovipositions per unit time is modified. This is achieved by increasing the number of oviposition periods later in life during which females have sufficient eggs for oviposition and an effective sperm supply for their fertilization.

Post-reproductive periods. As in all previous experiments, females in the continuously exposed cohort exhibited, on the average, significantly longer total and female post-reproductive periods than females in than any other cohort. The intermittent cohort exhibited the

shortest post-reproductive periods. Interestingly, the post-reproductive periods for the limited cohort were markedly longer than expected based upon previous experiments (see tables 41-43).

### Summary

This new analytical approach to the study of parasitoid life-histories is well worth the considerable effort involved. Not only is the information content of the data doubled, but life tables are produced that more closely reflect the patterns of replacement in the population. It is obvious, that for a given insect species or population, age-specific oviposition and age-specific natality rates jointly determine their reproductive strategy. As Giesel (1976) has pointed out, variability in natality rates is an important adaptive strategy for an organism living in a temporally heterogeneous environment. In L. boucardi and other species, variability in emergence time acts as an additional hedge against environmental uncertainty.

Plasticity in emergence rates in L. boucardi are affected by both environmental and non-environmental components. Larval density and competition for food have been shown to significantly affect the development of drosophilids and other insects (Peters and Barbosa, 1977), and are indeed affecting their development and the development of their parasitoids in these experiments. Although not quantified here, there is a marked decrease in size in most (but not

all) adults that hatch later than their sibs produced during the same oviposition period. This size difference must be an indication of severe competition between host larvae. However, not all late hatching adults are small, reflecting a non-environmental, or density-independent component. Indeed, larval development experiments to be described later, in which densities were limited to 25 larvae per vial, show up to a five day variability in the development rate of parasitoids that were given hosts of the same age during the same 1 hour period.

There are four basic meaningful concepts that can be gleaned from the natality data. First, is the obvious effect of daily oviposition rates. The first few "explosive" oviposition periods in cohorts presented hosts for 24 hour periods account for the majority of the natality of the cohort. For any particular natality period, one can observe the amount of emergence due to each oviposition period. Highly productive oviposition periods account for the greatest amount of emergences. Second, it is evident that the overall natality period greatly outstrips the total progeny production period. Third, we find that the eggs deposited by older females take longer to develop than eggs of younger females. Finally, when considering the different methods of calculating life-history parameters it is obvious that the previous calculations produced overestimates of 'r' by shifting the fertility distribution to the left. To look



for any further patterns in natality from this data would be misleading.

TABLE 41. Reproductive variables for the continuous and delayed cohorts exposed to D. melanogaster (Woods Orchard strain), January, 1980 (mean  $\pm$  SE).

| Variable                                        | Continuous<br>(19) | Delayed<br>(19)    |
|-------------------------------------------------|--------------------|--------------------|
| Length of life                                  | 17.4 $\pm$ 0.7     | 15.4 $\pm$ 1.0     |
| Days of male production                         | 9.3 $\pm$ 0.3      | 7.4 $\pm$ 0.3 @    |
| Days of female production                       | 4.7 $\pm$ 0.5      | 6.1 $\pm$ 0.5 @    |
| Total male progeny                              | 163.4 $\pm$ 13.1   | 94.1 $\pm$ 8.3 **  |
| Total female progeny                            | 75.9 $\pm$ 13.4    | 107.8 $\pm$ 10.2   |
| Total progeny                                   | 239.3 $\pm$ 14.3   | 201.8 $\pm$ 12.4 * |
| Post reproductive period<br>for fertilized eggs | 12.7 $\pm$ 0.6     | 6.3 $\pm$ 0.7 **   |
| Total post reproductive<br>period               | 8.1 $\pm$ 0.7      | 4.7 $\pm$ 0.9 **   |

Symbols: \* =  $p < .05$ , \*\* =  $p < .01$ , @ = not comparable

TABLE 42. Reproductive variables for the continuous and intermittent cohorts exposed to D. melanogaster (Woods Orchard strain), January, 1980 (mean  $\pm$  SE).

| Variable                                        | Continuous<br>(19) | Intermittent<br>(19) |
|-------------------------------------------------|--------------------|----------------------|
| Length of life                                  | 17.4 $\pm$ 0.7     | 16.9 $\pm$ 0.8       |
| Days of male production                         | 9.3 $\pm$ 0.3      | 4.1 $\pm$ 0.1 @      |
| Days of female production                       | 4.7 $\pm$ 0.5      | 3.2 $\pm$ 0.2 @      |
| Total male progeny                              | 163.4 $\pm$ 13.1   | 92.7 $\pm$ 8.2 **    |
| Total female progeny                            | 75.9 $\pm$ 13.4    | 112.9 $\pm$ 8.0 *    |
| Total progeny                                   | 239.3 $\pm$ 14.3   | 205.6 $\pm$ 6.8 *    |
| Post reproductive period<br>for fertilized eggs | 12.7 $\pm$ 0.6     | 2.9 $\pm$ 0.4 **     |
| Total post reproductive<br>period               | 8.1 $\pm$ 0.7      | 2.0 $\pm$ 0.3 **     |

Symbols: \* =  $p < .05$ , \*\* =  $p < .01$ , @ = not comparable

TABLE 43. Reproductive variables for the continuous and 1 hr limited cohorts exposed to D. melanogaster (Woods Orchard strain), January, 1980 (mean  $\pm$  SE).

| Variable                                        | Continuous<br>(19) | 1 hr Limited<br>(18) |
|-------------------------------------------------|--------------------|----------------------|
| Length of life                                  | 17.4 $\pm$ 0.7     | 15.1 $\pm$ 0.6       |
| Days of male production                         | 9.3 $\pm$ 0.3      | 11.1 $\pm$ 0.5 **    |
| Days of female production                       | 4.7 $\pm$ 0.5      | 7.2 $\pm$ 0.6 **     |
| Total male progeny                              | 163.4 $\pm$ 13.1   | 97.6 $\pm$ 8.3 **    |
| Total female progeny                            | 75.9 $\pm$ 13.4    | 75.7 $\pm$ 11.1      |
| Total progeny                                   | 239.3 $\pm$ 14.3   | 173.3 $\pm$ 13.7 **  |
| Post reproductive period<br>for fertilized eggs | 12.7 $\pm$ 0.6     | 7.9 $\pm$ 1.1 **     |
| Total post reproductive<br>period               | 8.1 $\pm$ 0.7      | 4.0 $\pm$ 0.8 **     |

Symbols: \* =  $p < .05$ , \*\* =  $p < .01$ , @ = not comparable

## CHAPTER 3

### THE PRODUCTIVITY OF FERTILIZED AND UNFERTILIZED FEMALES OF LEPTOPLILINA BOULARDI AND L. HETEROTOMA

#### Introduction

Throughought the data collection period in the life table experiments described earlier it became evident that unfertilized L. boulardi females, generally produced more offspring than their fertilized sisters. The consistency of this pattern led me to believe that it should be examined experimentally and experiments were conducted to compare the survivorship and overall reproductive success of fertilized and unfertilized cohorts of L. boulardi and L. heterotoma.

Fisher (1930) proposed that selection in diplodiploid organisms acts such that parents invest equally in the sexes. It follows that when there is inequality in the cost of raising the sexes, the parents producing fewer of the more expensive sex will be selected for (Hoogland, 1981). Since Fisher (1930) proposed his theory an enormous body of litterature has amassed pertaining to the existence and evolution of differing sex ratios in populations of diploid organisms (Bodmer and Edwards, 1960; Kalmus and Smith, 1960;

Kimura and Crow, 1965, 1969; Caughley, 1971; Speith, 1974), and haplodiploid organisms (Trivers and Hare, 1976; Hamilton, 1967; Crozier, 1976). The highly variable sex ratios of arrhenotokous parasitic wasps have also enjoyed theoretical and experimental treatment (Flanders, 1939, 1942, 1969; Doutt, 1959; Jackson, 1966; Schwartz and Gerling, 1974; Bar and Gerling, 1971; Wilkes, 1964; Hartl, 1971; and others).

All available life table studies of hymenopterous parasitoids include data concerning the progeny of fertilized females. However, an important aspect of the reproductive biology of arrhenotokous species is often neglected or treated cavalierly, that is, the reproductive output of unfertilized females. In these instances, since unfertilized females produce only male progeny, it is impossible to construct a fertility table (s.s), but it is nonetheless important to compare the total productivity of fertilized and unfertilized females. This type of data is available for Telenomus remus (Schwartz and Gerling, 1974), Pteroptrix smithi (Bar and Gerling, 1971), Eucoila trichopsila (Sychevskya, 1974), and L. heterotoma (Nostvik, 1954).

Nostvik (1954) states:

"In order to compare the rate of infection by unfertilised females with fertilised females, two

series of cultures, each containing 50 Drosophila eggs, were started. When the larvae were three days old, the first series of 20 cultures was infected by a fertilised female placed in each culture, and the other series of 20 cultures by an unfertilized female for each culture. All Pseudeucoila used were seven days old and the experiments were carried out at a temperature of 23 °C."

Nostvik's results were listed as follows:

|                               | Fertilized | Unfertilized |
|-------------------------------|------------|--------------|
|                               | females    | females      |
| Developed <u>Pseudeucoila</u> |            |              |
| Adults                        | 638        | 695          |

He concludes that, "It seems as if the infection is a trifle more effective in the case of parthenogenesis, though this difference can be attributed to normal variation." Neither his experimental design, nor his results or conclusions are informative enough to shed any light on the topic at hand.

Sychevskya (1974) states:

"Fertilization does not affect the number of eggs laid by a female; both groups lay approximately the same

number of eggs on average. This was clarified as a result of two series of experiments with 100 fertilized and unfertilized females. In both instances the females each laid 400 eggs. Similar data have also been obtained by Nostvik (1954)."

Again the information content regarding the productivity of unfertilized females is wanting. The experiments discussed below are not lacking in information content, and the trend they establish, of higher productivity in unfertilized females can be of major importance to many biological control programs.

#### Materials and Methods

##### The hosts

Hosts from the HA strain of D. simulans (from Hampton, Virginia) were used. Procedures for host collection discussed in the previous life table experiments were followed.

##### The parasitoids

Two cohorts of 20 females each were employed for each host species. L. bouhardi individuals belonging to the Ha75 strain (sympatric to the host strain) and L. heterotoma individuals belonging to the "Storrs" strain (graciously supplied to me by A.J. Nappi) were used.

To guard against unwanted matings, all females were procured from pupae separated into individual vials several



days prior to emergence. Twenty females of each species were allowed to mate prior to host exposure, constituting the "fertilized cohorts." Twenty other females per parasitoid species were exposed to hosts without matings, constituting the "unfertilized cohorts."

Daily survivorship and emergence were recorded as in earlier experiments. Daily productivity is given as the mean number of successful progeny produced during each oviposition period. All experiments and stock maintenance were conducted at 25 °C, 60% RH, and 16L/8d photoperiod.

## Results

### L. boulandi

#### Survivorship

The survivorship distributions for the fertilized and unfertilized cohorts, respectively, are presented in figures 49 and 50, and tables 44 and 55. The average female in the fertilized cohort survived for  $18.4 \pm 0.6$  days, while the average female in the unfertilized cohort survived 1.5 days longer, i.e., for  $19.9 \pm 0.6$  days (table 48).

#### Productivity

The females in the unfertilized cohort oviposited successful eggs for an average of  $10.4 \pm 0.2$  days, or 52.1% of their average life span. During this period, an average of  $239.5 \pm 7.2$  progeny were produced per female (table 48).

The females in the fertilized cohort oviposited unfertilized (male) eggs for  $9.9 \pm 0.2$  days, during which

Figure 49. Survivorship curve for the fertilized cohort of L.\_\_\_\_boulardi exposed to D.\_\_\_\_simulans on a continuous schedule.

Survivorship curve for  
L. boulandi  
host, Drosophila simulans  
FERTILIZED COHORT

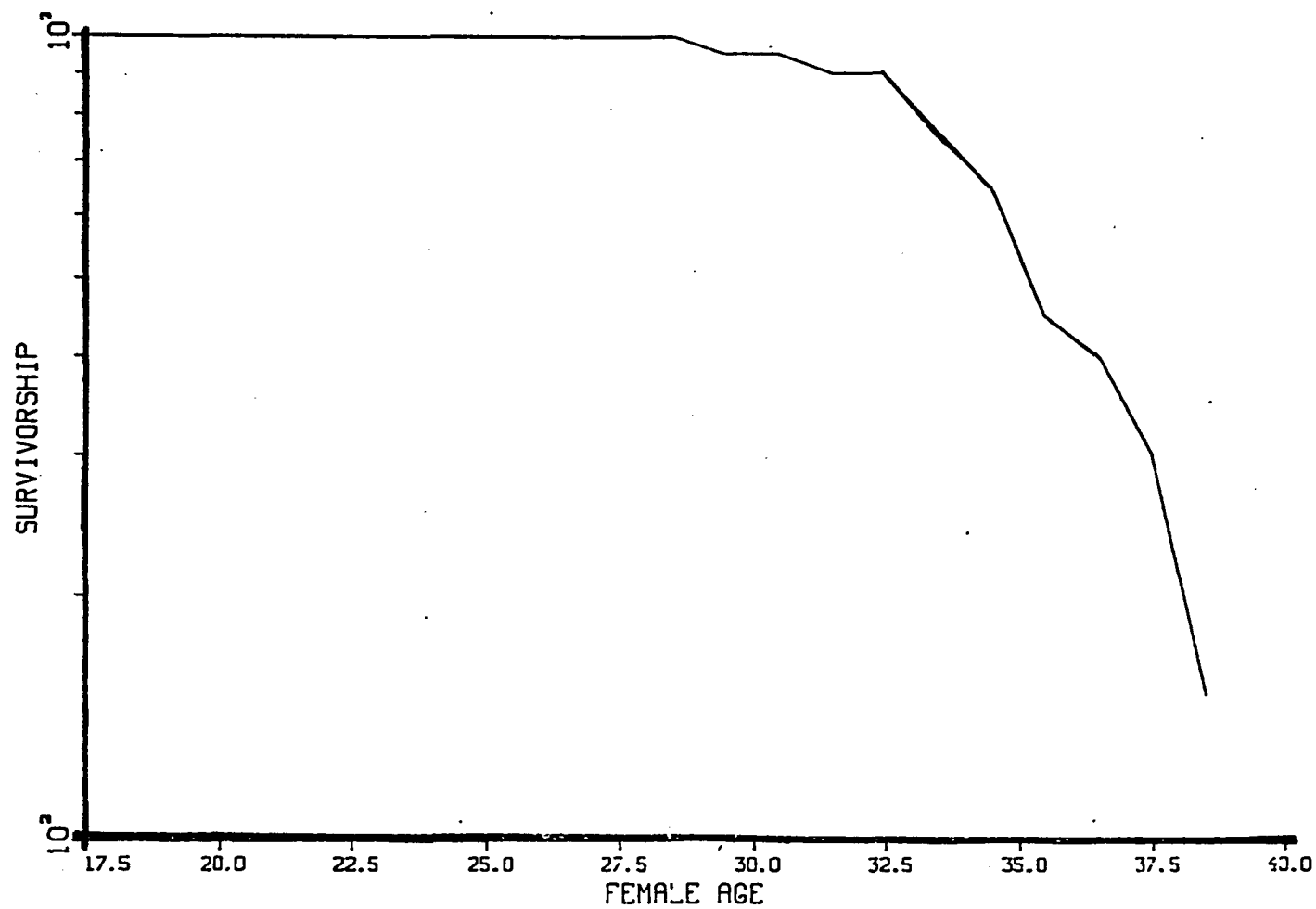


Figure 50. Survivorship curve for the unfertilized cohort of L.\_\_\_\_boulardi exposed to D.\_\_\_\_simulans on a continuous schedule.

Survivorship curve for  
L. boulandi  
host, *Drosophila simulans*  
UNFERTILIZED COHORT

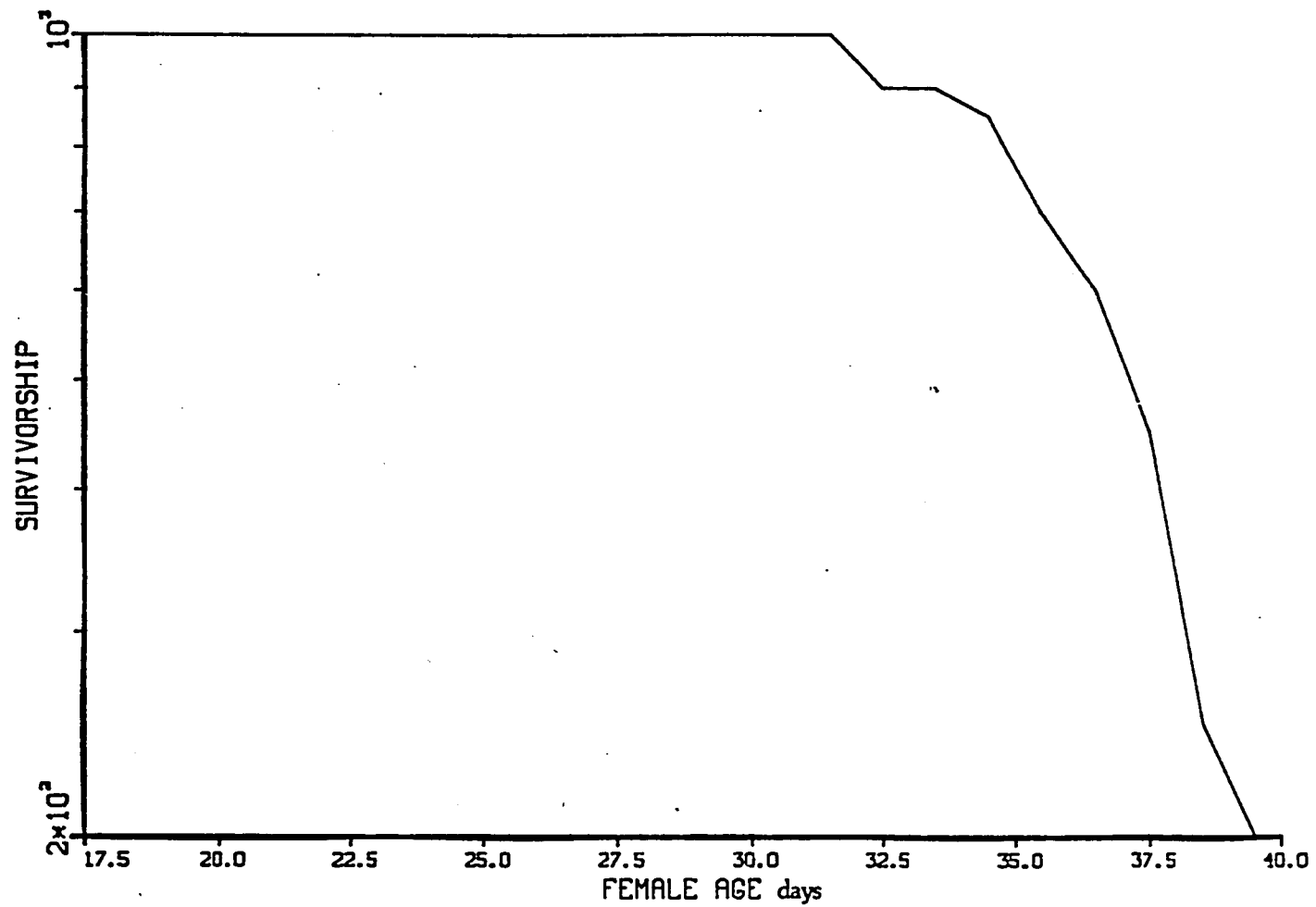


TABLE 44.

Life table, progeny production schedule and daily sex ratio of the fertilized cohort of L. \_\_boulardi exposed to D. simulans larvae on a continuous schedule.

TABLE 44, (continued)

| x    | l(x) | m(x)  | mean no.<br>male prog. | mean no.<br>total prog. | sex<br>ratio |
|------|------|-------|------------------------|-------------------------|--------------|
| 17.5 | 1000 | 23.90 | 8.8                    | 32.70                   | 0.27         |
| 18.5 | 1000 | 54.55 | 36.6                   | 91.15                   | 0.40         |
| 19.5 | 1000 | 3.10  | 3.3                    | 6.40                    | 0.52         |
| 20.5 | 1000 | 2.50  | 4.3                    | 6.80                    | 0.63         |
| 21.5 | 1000 | 4.10  | 6.4                    | 10.50                   | 0.61         |
| 22.5 | 1000 | 6.05  | 9.6                    | 15.65                   | 0.61         |
| 23.5 | 1000 | 3.15  | 8.9                    | 12.05                   | 0.74         |
| 24.5 | 1000 | 0.65  | 5.7                    | 6.35                    | 0.90         |
| 25.5 | 1000 | 0.90  | 3.3                    | 4.20                    | 0.79         |
| 26.5 | 1000 | 0.05  | 2.8                    | 2.85                    | 0.98         |
| 27.5 | 1000 | 0.00  | 0.7                    | 0.7                     | 1.00         |
| 28.5 | 1000 | 0.00  | 0.1                    | 0.1                     | 1.00         |
| 29.5 | 950  | 0.00  | 0.1                    | 0.1                     | 1.00         |
| 30.5 | 950  | 0.00  | 0.0                    | 0.0                     | 0.00         |
| 31.5 | 900  | 0.00  |                        |                         |              |
| 32.5 | 900  | 0.00  |                        |                         |              |
| 33.5 | 750  | 0.00  |                        |                         |              |
| 34.5 | 650  | 0.00  |                        |                         |              |
| 35.5 | 450  | 0.00  |                        |                         |              |
| 36.5 | 400  | 0.00  |                        |                         |              |
| 37.5 | 300  | 0.00  |                        |                         |              |
| 38.5 | 150  | 0.00  |                        |                         |              |

R = 98.95  
0

T = 18.98  
c

'r' = 0.242

TABLE 45.

Life and productivity table for the unfertilized cohort of L. boulandi exposed to D. simulans for 24h daily.

---

| progeny/female |      |        | progeny/female |      |        |
|----------------|------|--------|----------------|------|--------|
| x              | l(x) | (mean) | x              | l(x) | (mean) |
| 17.5           | 1000 | 43.20  | 30.5           | 1000 | 0.00   |
| 18.5           | 1000 | 114.15 | 31.5           | 1000 | 0.00   |
| 19.5           | 1000 | 8.05   | 32.5           | 900  | 0.00   |
| 20.5           | 1000 | 8.25   | 33.5           | 900  | 0.00   |
| 21.5           | 1000 | 11.45  | 34.5           | 850  | 0.00   |
| 22.5           | 1000 | 16.95  | 35.5           | 700  | 0.00   |
| 23.5           | 1000 | 11.50  | 36.5           | 600  | 0.00   |
| 24.5           | 1000 | 8.65   | 37.5           | 450  | 0.00   |
| 25.5           | 1000 | 13.55  | 38.5           | 250  | 0.00   |
| 26.5           | 1000 | 8.10   | 39.5           | 200  | 0.00   |
| 27.5           | 1000 | 1.15   |                |      |        |
| 28.5           | 1000 | 0.30   |                |      |        |
| 29.5           | 1000 | 0.05   |                |      |        |



time  $90.0 \pm 6.7$  males per female, on the average, were produced. The average female oviposited  $99.0 \pm 7.7$  fertilized eggs during  $5.4 \pm 0.6$  days (29.1% of the average life span) yielding a mean of  $188.9 \pm 8.5$  total progeny per female (table 48).

Table 45 and figure 52 present the progeny production schedule for the unfertilized cohort. Production reached a peak of  $114.2 \pm 5.0$  males during the second exposure period and subsequently dropped to  $8.1 \pm 1.6$  during the next day's ovipositions. The first two exposure periods account for 64% of the total progeny production for this cohort. Production rose gradually again to a secondary peak on day 22.5, followed by two days of decrease, another peak on day 25.5, and then decreased to 0.0 on day 30.5.

Table 44 and figure 51 present the data for daily male, female, and total progeny production for the fertilized cohort. Male, female, and total progeny production peaked during the second day of exposure, followed in all cases by a significant decrease in mean daily production; 91% reduction in males; 94% reduction in females; 93% reduction in total. As in the unfertilized cohort, progeny production rose again gradually to a secondary peak on day 22.5, but unlike the other cohort, progeny production decreased continually thereafter. 50% of all male eggs and 79% of all female eggs were oviposited during the first two exposure

Figure 51. Daily production of male, female, and total offspring in the fertilized cohort of L. boulandi.

Progeny production for  
L. boulandi  
FERTILIZED COHORT  
host, Drosophila simulans

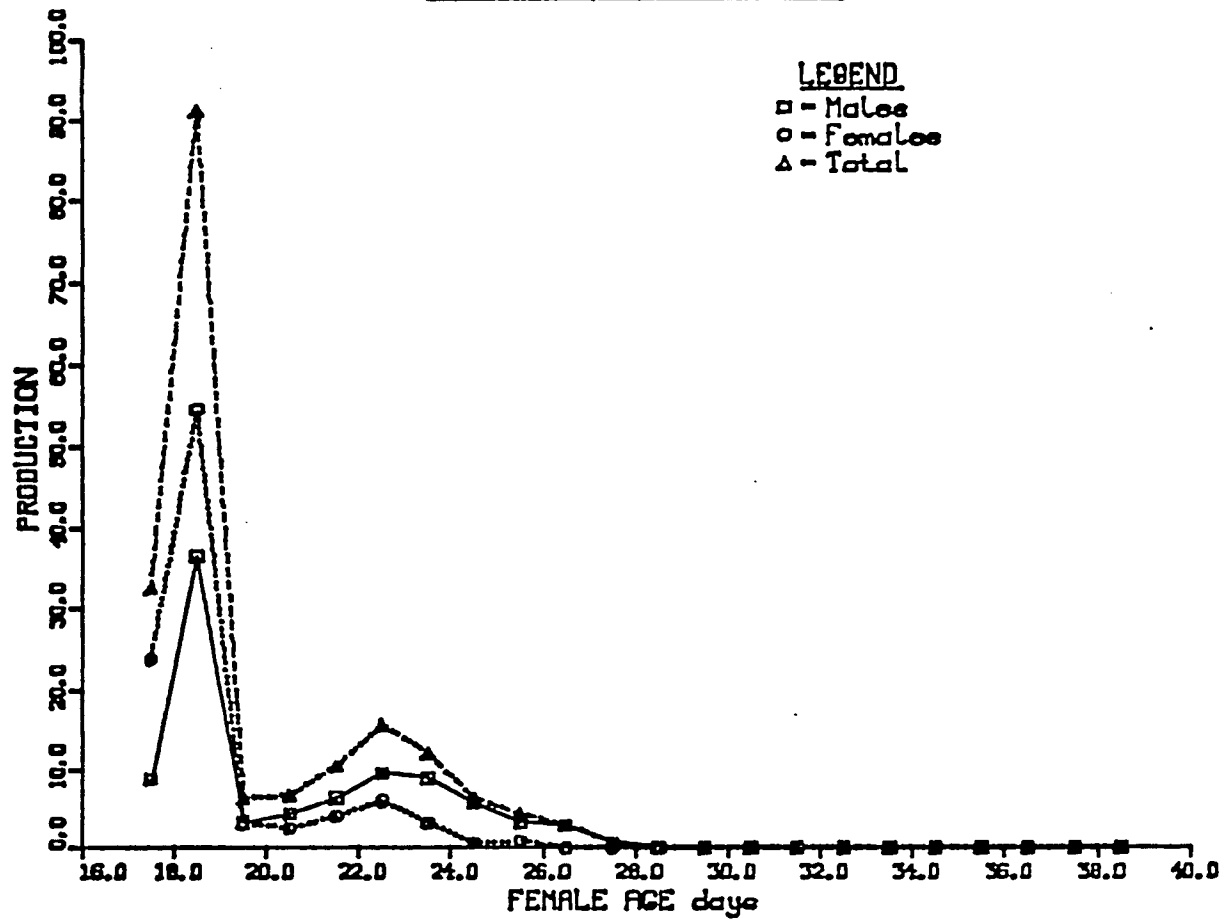
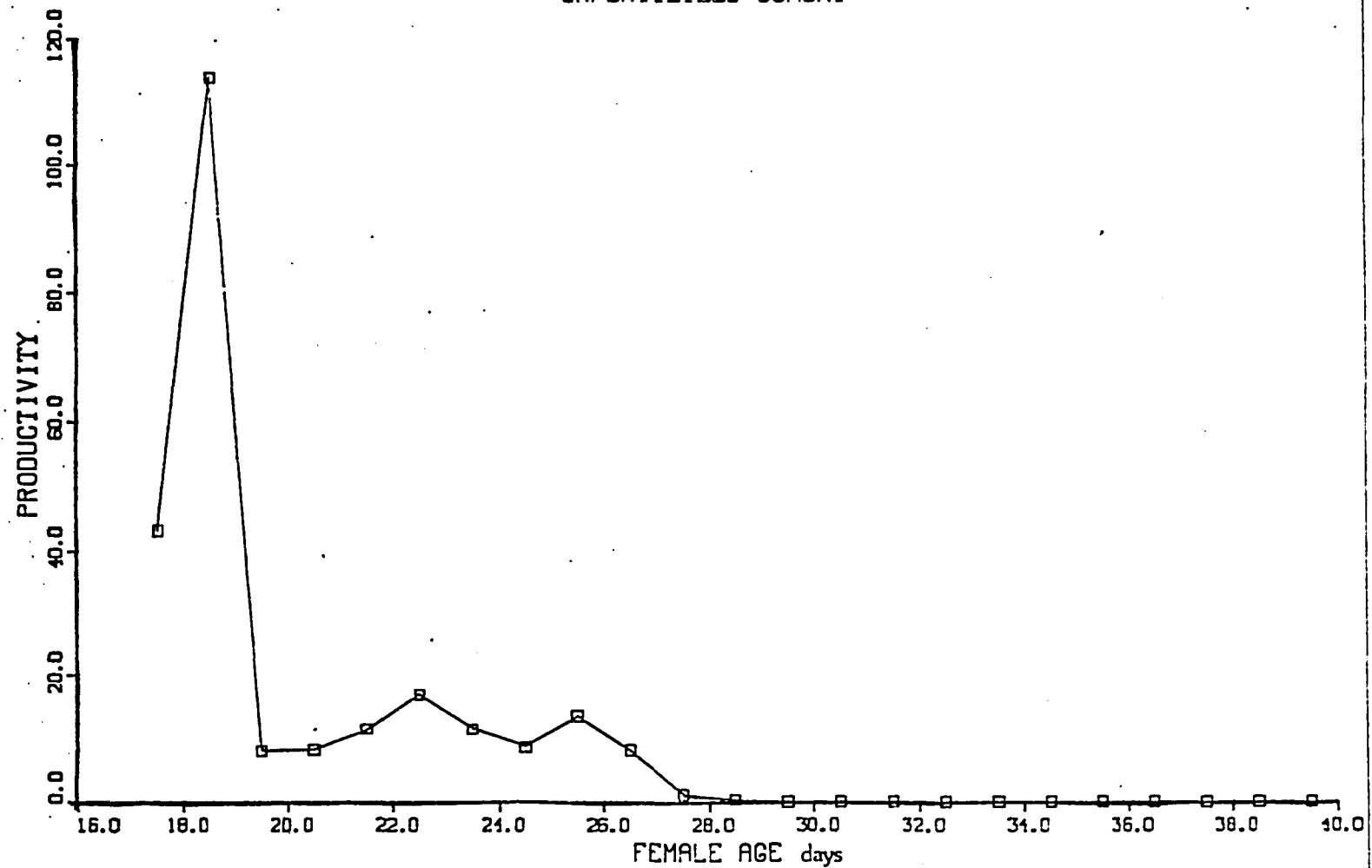


Figure 52. Daily mean production of total offspring in the unfertilized cohort of L. boulandi.

DAILY MEAN TOTAL PROGENY  
PRODUCTION for L. boulandi  
host, Drosophila simulans  
UNFERTILIZED COHORT



periods. As in most previous experiments, the daily sex ratio of progeny production was initially female biased but became male biased following the significant drop in daily oviposition. Table 44 also presents the life history parameters for this cohort. One should note that successful progeny production ceased two days prior to the deaths of any females.

#### L. heterotoma

Two females from the fertilized cohort were not mated successfully and one female was not productive. Therefore, the data presented below, unless otherwise specified, is based upon 17 replicates for the fertilized cohort, and 22 replicates for the unfertilized cohort.

#### Survivorship

The survivorship distributions for the fertilized and unfertilized cohorts, respectively, are presented in figures 53 and 54, and tables 46 and 47. The average fertilized female survived  $17.2 \pm 0.4$  days, while the average unfertilized female survived  $18.8 \pm 0.5$  days.

#### Productivity

The females of the unfertilized cohort oviposited  $160.5 \pm 13.3$  total progeny per female during 52.2% of her average life span (table 49). The average female in the fertilized cohort oviposited  $79.2 \pm 7.0$  male eggs and  $78.2 \pm 8.4$  female eggs during 60.8% and 45.7% of her average life span, respectively. The fertilized cohort yielded an average of

Figure 53. Survivorship curve for the fertilized cohort of L. heterotoma exposed to D. simulans on a continuous schedule.

Survivorship curve for  
L. heterotoma  
host, Drasophila simulans  
FERTILIZED COHORT

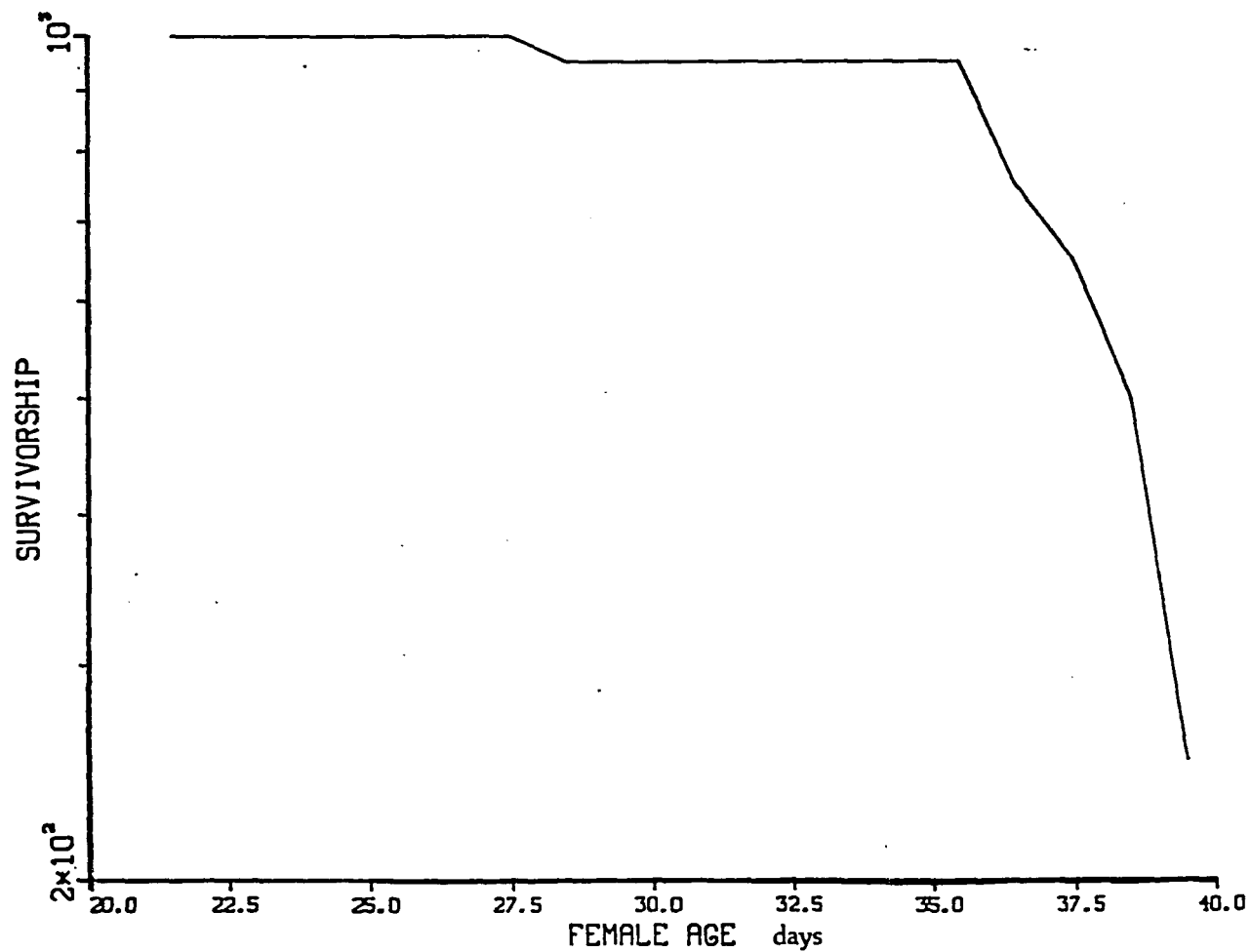




Figure 54. Survivorship curve for the unfertilized cohort of L. heterotoma exposed to D. simulans on a continuous schedule.

Survivorship curve for  
L. heterotoma  
host, Drosophila simulans  
UNFERTILIZED COHORT

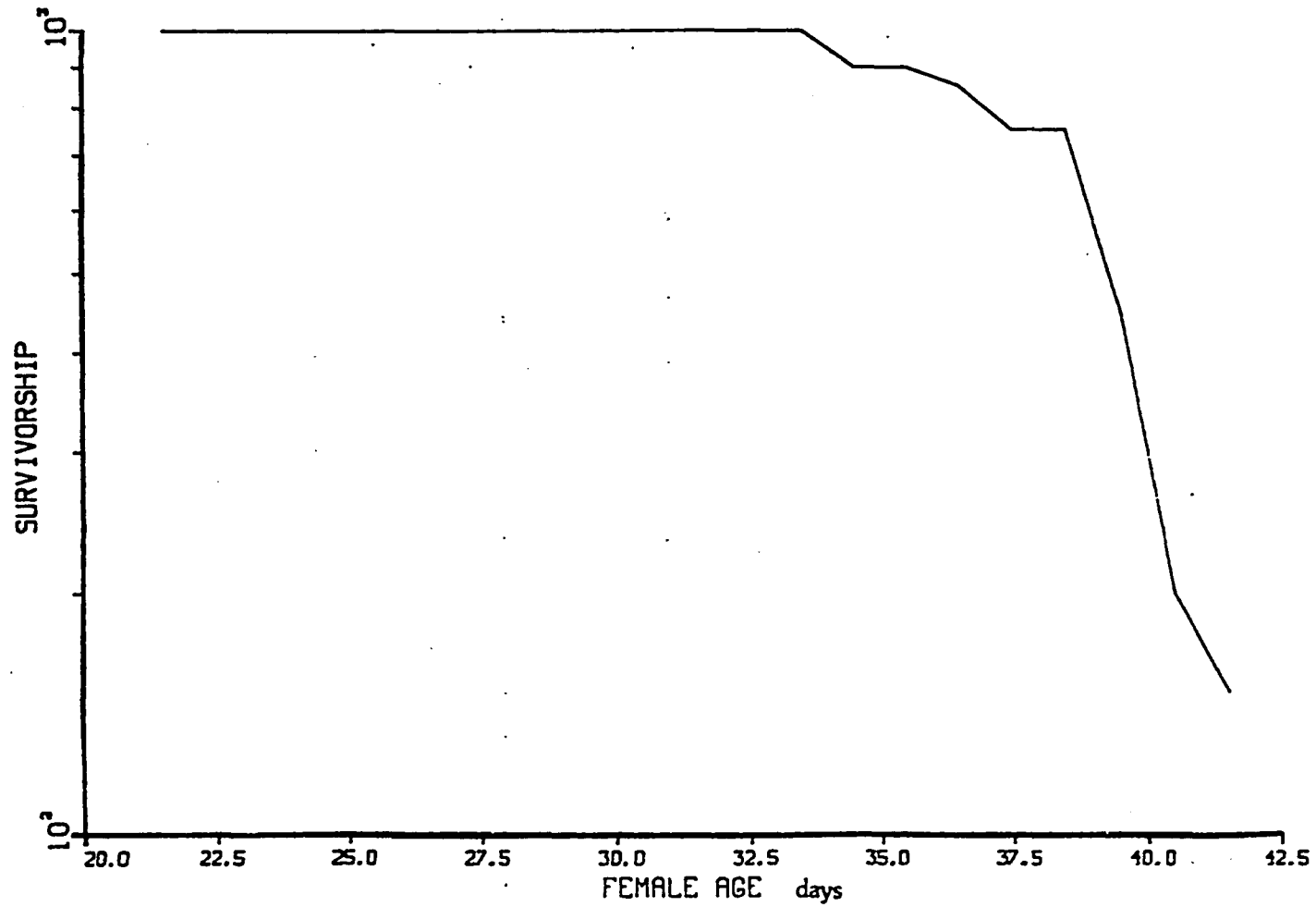


TABLE 46.

Life table, progeny production schedule and daily sex ratio of the fertilized cohort of L. heterotoma exposed to D. simulans larvae on a continuous schedule.

TABLE 46, (continued)

| x                      | l(x)                   | m(x)  | mean no.<br>male prog. | mean no.<br>total prog. | sex<br>ratio |
|------------------------|------------------------|-------|------------------------|-------------------------|--------------|
| 21.5                   | 1000                   | 3.18  | 5.94                   | 9.12                    | 0.65         |
| 22.5                   | 1000                   | 13.29 | 10.00                  | 23.29                   | 0.43         |
| 23.5                   | 1000                   | 20.59 | 16.88                  | 37.41                   | 0.45         |
| 24.5                   | 1000                   | 17.82 | 10.12                  | 27.94                   | 0.36         |
| 25.5                   | 1000                   | 14.65 | 18.06                  | 32.71                   | 0.55         |
| 26.5                   | 1000                   | 2.35  | 5.06                   | 7.41                    | 0.68         |
| 27.5                   | 1000                   | 1.53  | 2.65                   | 4.18                    | 0.63         |
| 28.5                   | 950                    | 0.65  | 1.77                   | 2.41                    | 0.73         |
| 29.5                   | 950                    | 1.77  | 4.59                   | 6.35                    | 0.72         |
| 30.5                   | 950                    | 0.53  | 1.82                   | 2.35                    | 0.70         |
| 31.5                   | 950                    | 0.77  | 1.82                   | 2.59                    | 0.55         |
| 32.5                   | 950                    | 0.29  | 0.35                   | 0.65                    | 0.79         |
| 33.5                   | 950                    | 0.18  | 0.65                   | 0.82                    | 0.67         |
| 34.5                   | 950                    | 0.06  | 0.12                   | 0.18                    | 0.33         |
| 35.5                   | 950                    | 0.12  | 0.06                   | 0.18                    | 0.67         |
| 36.5                   | 750                    | 0.08  | 0.15                   | 0.23                    | ----         |
| 37.5                   | 650                    | 0.00  | 0.00                   | 0.00                    | ----         |
| 38.5                   | 500                    | 0.00  | 0.00                   | 0.00                    | ----         |
| 39.5                   | 250                    | 0.00  | 0.00                   | 0.00                    | ----         |
| <hr/>                  |                        |       |                        |                         |              |
| R <sub>0</sub> = 77.62 | T <sub>c</sub> = 24.44 |       | 'r' = 0.178            |                         |              |

TABLE 47. Life and productivity table for the unfertilized cohort of L. heterotoma exposed to D. simulans larvae on a continuous schedule.

---

| progeny/female |       |        | progeny/female |       |        |
|----------------|-------|--------|----------------|-------|--------|
| x              | l (x) | (mean) | x              | l (x) | (mean) |
| 21.5           | 1000  | 15.86  | 35.5           | 900   | 0.05   |
| 22.5           | 1000  | 21.00  | 36.5           | 850   | 0.15   |
| 23.5           | 1000  | 32.46  | 37.5           | 750   | 0.24   |
| 24.5           | 1000  | 31.00  | 38.5           | 750   | 0.00   |
| 25.5           | 1000  | 34.14  | 39.5           | 450   | 0.00   |
| 26.5           | 1000  | 9.55   | 40.5           | 200   | 0.00   |
| 27.5           | 1000  | 1.96   | 41.5           | 150   | 0.00   |
| 28.5           | 1000  | 2.41   |                |       |        |
| 29.5           | 1000  | 6.64   |                |       |        |
| 30.5           | 1000  | 1.41   |                |       |        |
| 31.5           | 1000  | 1.73   |                |       |        |
| 32.5           | 1000  | 1.18   |                |       |        |
| 33.5           | 1000  | 0.45   |                |       |        |
| 34.5           | 900   | 0.36   |                |       |        |

157.4  $\pm$  10.0 total progeny per female (table 49).

Table 47 and figure 56 present the progeny production schedule for the unfertilized cohort. Daily progeny production equaled 15.9 offspring per female during the first exposure period and then rose to its peak value (34.14) on the fifth day of exposure. Production subsequently decreased to 1.96 progeny per female on the seventh day of exposure, but rose again on the ninth day, prior to a gradual decline over the ensuing 8 days. The first five days of exposure account for 83.7% of all successful ovipositions.

Table 46 and figure 55 present the daily male, female, and total progeny production schedule and daily progeny sex ratio for the fertilized cohort. As in the unfertilized cohort, the production of male progeny reached its peak on day 25.5, with an interim but lower peak two days earlier. Male progeny production decreased 72% between days 25.5 and 26.5 and generally decreased thereafter with a slight peak in production on day 29.5, prior to a continually gradual decline over the next seven days. The female and total progeny production distributions reached their respective peak values on the third day of exposure with a secondary peak two days later. The first five days of exposure accounted for 83.7% of all successful ovipositions. The sex ratio of successful ovipositions was male biased for the first exposure period but became female biased for the

Figure 55. Daily production of male, female, and total offspring in the fertilized cohort of L. heterotoma.

Progeny production for  
L. heterotoma  
 FERTILIZED COHORT  
 host, Drosophila simulans

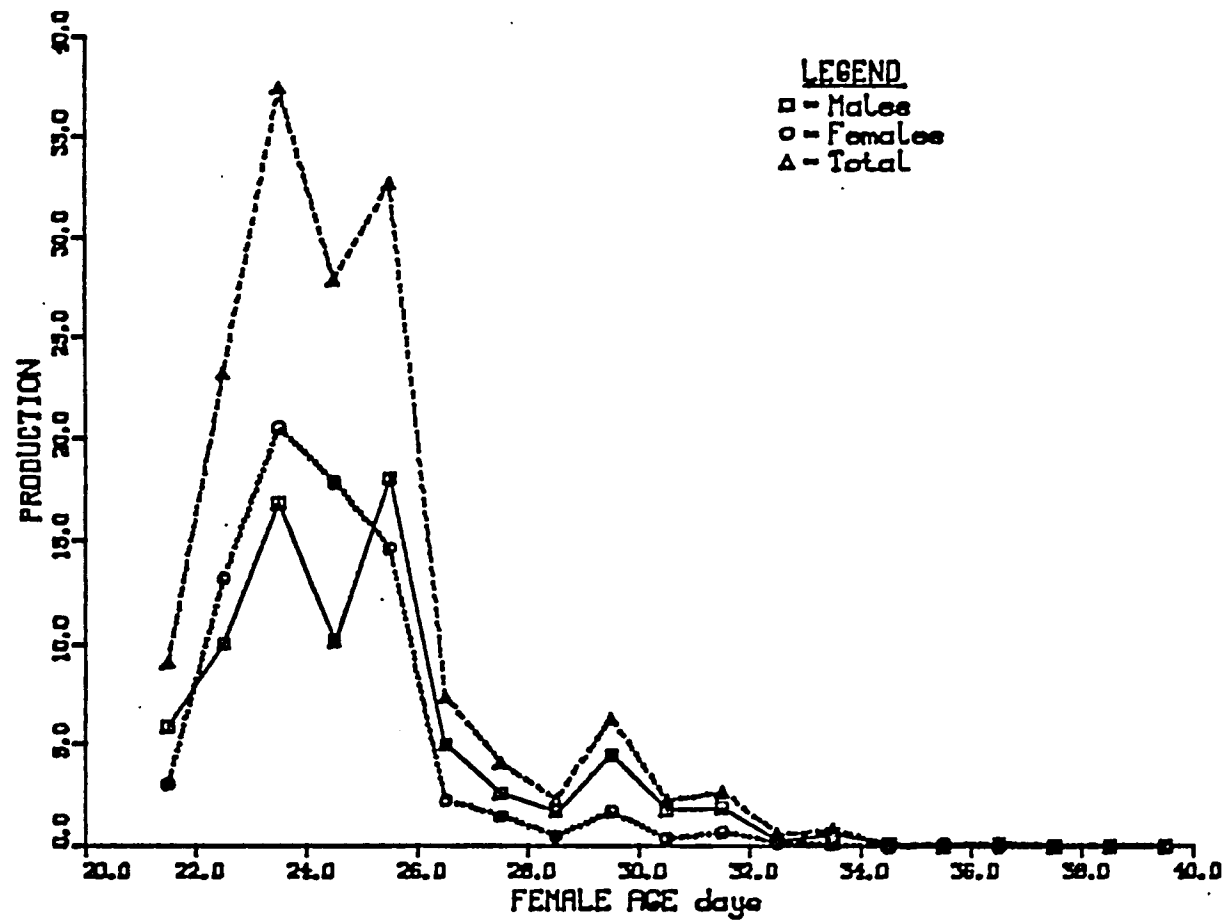
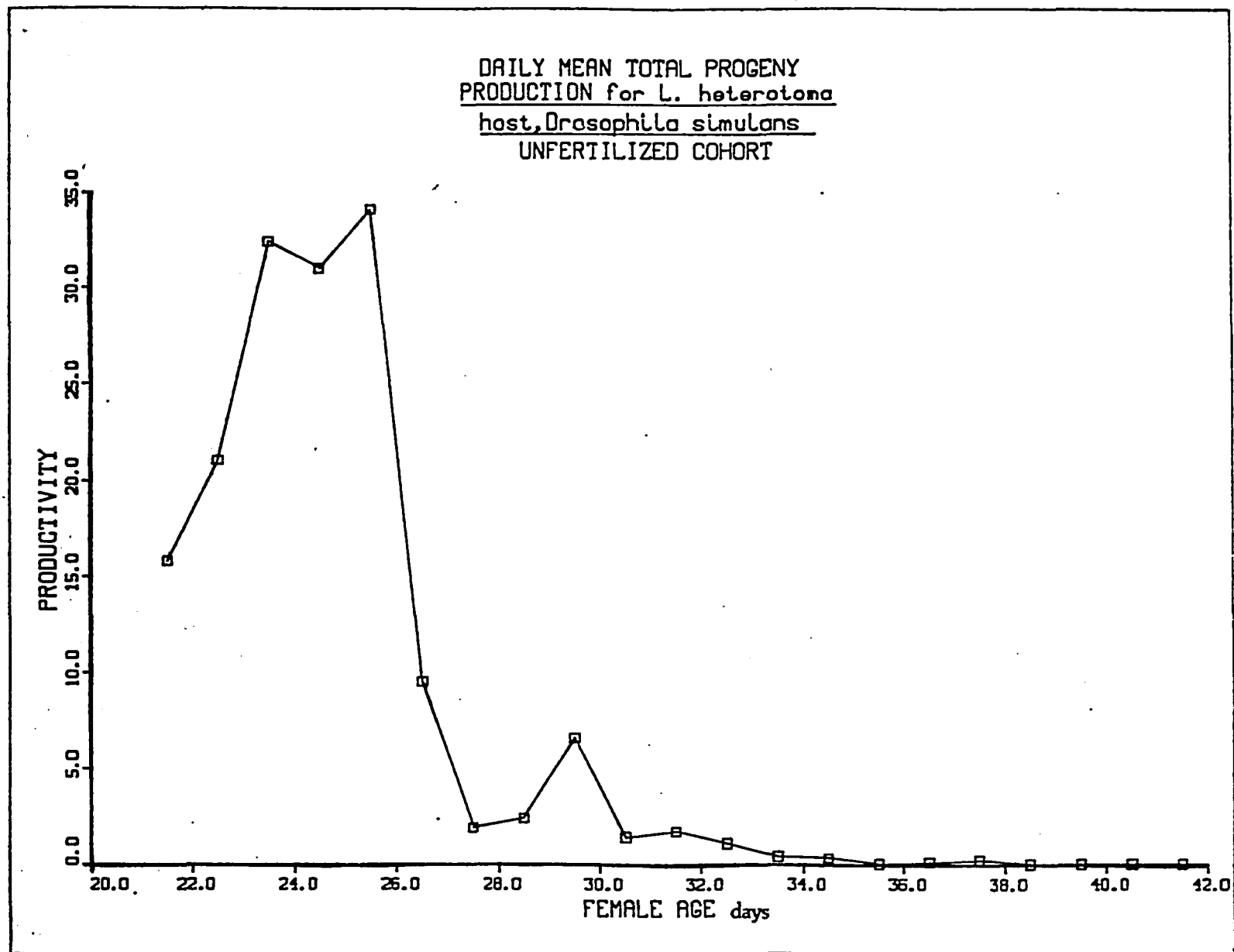




Figure 56. Daily mean production of total offspring in the unfertilized cohort of L. heterotoma.



following three days. The sex ratio then returned to its male bias for all but the penultimate exposure period. The overall sex ratio, for all successful progeny is 0.503, nearly 1:1. The life history parameters for the fertilized cohort are given in table 51, note that the fertility distribution is based upon daily ovipositions.

#### Discussion

The most meaningful method of analyzing the data would be to compare the reproductive variables through analyses of variance. Comparisons are made between conspecific cohorts and between fertilized cohorts in both species (see tables 48-49, and 72-74 in the appendix).

#### L. boulandi

Table 48 compares the mean length of life and mean number of total progeny produced per female in each cohort of *L. boulandi*. Unfertilized females lived longer, on the average, than their fertilized counterparts, but the difference is not significant. More interestingly, the unfertilized cohort produced significantly more total progeny than did the fertilized cohort. This difference is highly significant ( $p < .01$ ) and confirms the trends observed earlier. In fact, the unfertilized cohort produced approximately 1.3 times as many total offspring as the fertilized cohort.

TABLE 48. Reproductive variables for the fertilized and unfertilized cohorts of L.\_\_\_\_boulardi exposed to D. simulans.

| Variable                  | Fertilized     | Unfertilized   |
|---------------------------|----------------|----------------|
|                           | Cohort<br>(20) | Cohort<br>(20) |
| Length of life            | 18.4 ± 0.6     | 19.9 ± 0.6     |
| Days of male production   | 9.0 ± 0.2      | 10.4 ± 0.2     |
| Days of female production | 5.4 ± 0.6      |                |
| Total male progeny        | 90.0 ± 6.7     | 239.5 ± 7.13   |
| Total female progeny      | 99.0 ± 7.7     |                |
| Total progeny             | 190.0 ± 8.5    | 239.5 ± 7.1 ** |

Symbols: \*= p<.05, \*\*= p<.01, @= not comparable

TABLE 49. Reproductive variables for the fertilized and unfertilized cohorts of L. heterotoma exposed to D. simulans.

| Variable                  | Fertilized     | Unfertilized   |   |
|---------------------------|----------------|----------------|---|
|                           | Cohort<br>(20) | Cohort<br>(22) |   |
| Length of life            | 17.2 ± 0.4     | 18.8 ± 0.5     | * |
| Days of male production   | 10.5 ± 0.6     | 9.8 ± 0.6      |   |
| Days of female production | 7.9 ± 0.7      |                |   |
| Total male progeny        | 79.2 ± 7.0     | 160.6 ± 13.3   |   |
| Total female progeny      | 78.2 ± 8.4     |                |   |
| Total progeny             | 157.4 ± 10.0   | 160.6 ± 13.3   |   |

Symbols: \*= p<.05, \*\*= p<.01, @= not comparable

### L. heterotoma

Table 49 compares the mean length of life and mean number of total progeny produced per female in each cohort of L. heterotoma. Unfertilized females lived significantly longer than their fertilized sibs ( $p < .05$ ). However, although the unfertilized cohort produced more total progeny on the average, the difference is not statistically significant.

The interpretation: a model based upon differential larval mortality

As mentioned earlier, relatively few investigators have delved into the problem of comparative reproductive success of fertilized and unfertilized haplodiploid organisms. Chabora (unpublished) investigated this problem in a new strain of L. heterotoma exposed to D. melanogaster hosts daily at 21 °C. His sample size was small, but upon analyzing the data (Wilcoxon Rank Sum Test) I found no significant difference between the productivity of the two cohorts.

In order to assess the effects of host species on the outcome of the experiments with L. boulandi, one other experiment was conducted with sympatric populations of L. boulandi and D. melanogaster (Ha77 and WO strains, respectively). The same experimental procedures utilized earlier were followed, although the sample size was smaller (6 and 7 females per experimental group). The mean number of total progeny per female was compared between cohorts by

the Wilcoxon Rank Sum Test, and is significantly higher in the unfertilized cohort (table 75 in the appendix).

The evidence for significantly higher productivity by unfertilized L. boulandi females is striking. The question remains, why? One can hypothesize that this phenomenon is an example of the Fisherian concept of differential costs in producing each sex as manifested in differential developmental mortality between the sexes? Flanders (1946) in his discussion of sex ratios in arrhenotokous parasitoids concludes that among the extrinsic factors that determine the sex ratio, the effect of host density on differential developmental mortality; on the interval between mating and emergence; and on oviposition response, are most important. The hypothesis that differential mortality between the sexes is occurring in L. boulandi under these conditions is modelled below.

Recall that L. boulandi is proovigenic. Let us assume, as we have done previously, that a female of any particular strain has a characteristic maximum number of eggs available to her for oviposition. Further, let us assume that throughout her life span a female will oviposit her entire egg complement singly into available hosts. Then, the mean number of male progeny produced by a population of unfertilized females should give us an estimate of the average developmental mortality of male eggs deposited in a particular host species or strain, under particular environmental conditions.

The Ha75 strain of L. boulandi has an average egg compliment of  $349.3 \pm 10.5$  eggs at hatching. Unfertilized females produced  $239.45 \pm 7.15$  male progeny, on the average. Therefore,  $349.3$  minus  $239.45$ , or  $109.85$  male eggs can be assumed to have died during development. This equates to 31.4% developmental mortality.

Let us now return to the simultaneous fertilized cohort. On the average,  $89.95 \pm 6.7$  successful male progeny were produced. We can utilize our estimate of male developmental mortality to calculate the total number of unfertilized eggs available to the females of that cohort in the following manner:

Let the number of male eggs =  $N_{me}$  ;

let the number of male progeny =  $N_m$ ;

and let the developmental mortality for males =  $M_m$ .

Then,  $N_m = (1 - M_m) (N_{me})$  and  $N_{me} = (N_m) / (1 - M_m) = 131.215$ .

Further, let the number of female eggs =  $N_{fe}$ ;

the number of female progeny =  $N_f$ ;

and let the developmental mortality for females =  $M_f$ .

Also, let the total number of eggs available =  $T_e$ .

Then,  $N_{fe} = (T_e) - (N_{me}) = 218.085$ ; and since  $N_{fe} = (N_f) / (1 - M_f)$ , by rearranging the equation and substituting



98.95 for  $N_f$ , we can calculate  $1-M_f$ , which equals 0.454. Therefore, the developmental mortality for female is 54.6%.

In order to test these values consider all the available information on the reproductive capacity of *L. boulandi* under the same experimental conditions. Five cohorts apply and are given in table 50. The overall number of male and female progeny per female (mean and standard error) are  $87.74 \pm 9.1$ , and  $102.7 \pm 12.5$ , respectively. The overall number of total progeny per female is  $190.5 \pm 11.8$ .

If male mortality is 31.4%, then  $N_{me}$ , on the average, equals 127.90, and  $N_{fe}$  equals 221.40. For this population of five cohorts, then,  $(1-M_f) = (N_f)/(N_{fe}) = 102.660/221.40 = 0.46$ , and  $M_f = 0.54$ . That is, the overall developmental mortality for female progeny is 54%. It is evident, therefore, that the calculations of developmental mortality rates, based upon this experiment may be generalized to the larger case of *L. boulandi* developing in *D. simulans* under high host density conditions. Under these conditions female developmental mortality is 1.5 times as high as that of males.

This phenomenon of differential larval mortality has been observed in other parasitoid systems. Wilkes (1963) in his study of the environmental causes of changes in the sex ratio of *Dahlbominus fuliginosus*, showed that under unfavorable conditions differential survival selectively favored males. *D. fuliginosus* is a gregarious parasitoid

TABLE 50. Composite data for the five cohorts continuously exposed to Drosophila simulans.

| Cohort                     | Number of progeny per female (mean $\pm$ SE) |                  |                  |
|----------------------------|----------------------------------------------|------------------|------------------|
|                            | Male                                         | Female           | Total            |
| Ha75/Ha                    | 90.9 $\pm$ 5.0                               | 93.5 $\pm$ 5.0   | 184.4 $\pm$ 5.2  |
| Series I                   | 116.5 $\pm$ 7.5                              | 66.0 $\pm$ 7.2   | 182.1 $\pm$ 6.4  |
| Series IV                  | 65.4 $\pm$ 6.5                               | 124.2 $\pm$ 7.0  | 189.7 $\pm$ 6.6  |
| Series V                   | 71.6 $\pm$ 8.0                               | 92.9 $\pm$ 8.7   | 164.5 $\pm$ 9.3  |
| Oviposition<br>rate exp't. | 95.2 $\pm$ 6.3                               | 136.7 $\pm$ 6.5  | 231.9 $\pm$ 6.8  |
| Mean                       | 87.7 $\pm$ 9.1                               | 102.7 $\pm$ 12.5 | 190.5 $\pm$ 11.8 |

and when hosts are unlimited, females selectively fertilize ova and oviposit female eggs into larger hosts than male eggs. This is a relatively common occurrence in gregarious parasitoids (Flanders, 1939; Doutt, 1959). However, when oviposition sites are limited for D. fuliginosus, Wilkes (1963) found that crowding within hosts led to increased mortality and a lower percentage of females in all but his high male producing stocks. Rotary and Gerling (1973) have shown that in Bracon hebetor reared on Angasta kuehniella, "female progeny is subjected to higher mortality during development."

There are many other explanations for this phenomenon. One could argue that courtship, mating, and the subsequent storage and use of sperm is energy draining and reduces the energy available to fertilized females for successful oviposition. The energetics involved here would be hard to quantify. However, the data for females from earlier life table experiments that were "poorly" inseminated (353 males and 3 females; 297 males and 10 females) seems to indicate that the energetics involved in mating does not affect the number of eggs laid.

One could conceive of the production of significantly more male progeny by an unfertilized female as a strategy selected for increasing her probability of contributing to the gene pools of subsequent generations. Unlike the case in diplodiploid organisms where an unfertilized female is

sterile, unfertilized haplodiploid females can still produce male progeny. The reproductive success (s.l.) of a female, whether fertilized or not, is thereby assured depending solely upon her ability to successfully find and oviposit in suitable hosts and the successful development of her progeny. Therefore, a fertilized female is not only assured of contributing her genes to the next generation via her sons and daughters, but is also assured of contributing genes to the following generation via her daughter's progeny. However, the success of an unfertilized female in contributing her genes to subsequent generations is solely dependent upon her sons' abilities to find and mate with appropriate females and the abilities of those females, in turn, to find suitable hosts. Unfertilized females that produce more sons will increase the probability that their genes will be incorporated into the next generation and hence be selected for in comparison to unfertilized females that produce as many, or fewer, progeny than fertilized females. Therefore, assuming that the number of successful progeny produced by unfertilized females is a heritable trait, selection should act to favor the production of more total progeny by a female when unfertilized.

While this scenario is intuitively pleasing the question remains as to the actual source of the increase in successful progeny production in unfertilized females. Since it is clear from the data presented previously

concerning the effects of host species, parasitoid strain, host availability, and oviposition rate that (1) females produce, on the average, fewer adult progeny than the number of eggs available; and (2) that females exhaust their entire egg compliment, the most parsimonious explanation supported by the data, is that in L. boulandi, sexual differences in developmental mortality is that source. Although arguments for the effects of the energetic drain of courtship, mating, and sperm storage on the reproductive output of a female can not be disproven, that investigation remains to be conducted.

L. boulandi and L. heterotoma: A Comparison of  
Reproductive Tactics

Let us now compare the reproductive tactics of fertilized cohorts of both species when exposed to continuously available D. simulans larvae.

Survivorship

Table 74 (in the appendix) presents the results of a one way analysis of variance for mean length of life. Although the L. boulandi cohort is longer lived, the difference is not significant.

Male progeny production schedule

The ANOVA for the mean number of days of ovipositing successful male eggs (DOMP) is presented in table 74. The L. heterotoma cohort spent more time in male progeny production, but again, the difference was not significant.

### Female progeny production schedule

The L. heterotoma cohort spent significantly more exposure periods in ovipositing successful fertilized eggs than did the L. boulandi cohort. In fact, female progeny were produced by L. heterotoma females during every successful exposure period. In L. boulandi, on the other hand, female progeny production ceased 3 days prior to the cessation of total progeny production. Moreover, the distribution of successful female progeny through time differs between the cohorts. In the L. heterotoma cohort the peak value for daily female progeny production occurs on the third day of exposure, gradually increasing from the first day. The subsequent decline in female production is also quite gradual in comparison to the L. boulandi cohort. The typical "L. boulandi pattern" of high productivity during the first two days of exposure followed by significant drop in productivity, is not evident in L. heterotoma. This may in part be due to the need for L. heterotoma females to learn to oviposit correctly (van Lenteren, 1976), or in part due to the fact that D. simulans is not a preferred host species, and as such, the female parasitoids may have withheld oviposition. Differences between daily fertility distributions were tested statistically by applying a test for association following Sokal and Rohlf (1969). The data was treated such that corresponding values per day of exposure could be compared.

For each cohort, the data was grouped for days 3,4,and 5, and days 6 through 16, so that no observed or expected frequencies would be less than 5. Table 51 presents the observed values and expected values under the hypothesis of association, and the Chi Square value. The distributions are highly significantly different ( $p < .01$ ).

#### Numbers of progeny produced

L. boulandi, the species sympatric with the host population, faired more successfully in producing progeny than did L. heterotoma. When considered separately the average number of total male progeny or total female progeny produced per female in each cohort did not differ significantly between the species. However, when the total number of progeny (TM+TF) are considered, the difference is significant ( $p < .05$ ). Generally, we would expect that an indigenous host-parasitoid complex would differ significantly in success in comparison to a novel combination of host and parasitoid, although the direction of this difference normally can not be predicted. One further reason for lower productivity in L. heterotoma is the fact that it is an old strain, cultured for many years, and as such may have become less viable. Preliminary experiments with newer strains yield much higher reproductive capacities (500-600 eggs per female at eclosion), and higher net reproductive rates (Chabora and Kopelman, unpublished).

TABLE 51. Test of independence for the age specific fertility distributions between cohorts of L. boulandi and L. heterotoma.

| Days          | 0-1                       | 2-4   | 5-15  | Totals |
|---------------|---------------------------|-------|-------|--------|
| Cohort        | Female progeny per female |       |       |        |
| L. boulandi   | 78.45                     | 9.70  | 10.80 | 98.95  |
| L. heterotoma | 16.47                     | 53.06 | 8.31  | 77.88  |
| Totals        | 94.92                     | 62.76 | 19.11 | 176.79 |

G = 74.33 with 2 degrees of freedom

Probability of exceeding G is < .01



## Summary

An experiment was conducted to compare the survivorship and overall reproductive success of fertilized and unfertilized cohorts of L. boucardi and L. heterotoma when exposed to either D. simulans or D. melanogaster. Further, hypotheses concerning differential "costs" in the production of each sex were examined.

Regardless of host species, unfertilized L. boucardi females were found to live an average of 1.5 days longer than their fertilized sisters, but this difference is not significant. More importantly, unfertilized females produced significantly more progeny per female than fertilized ones.

In L. heterotoma, although unfertilized females lived significantly longer, no significant differences could be found between the mean number of progeny produced per female in either cohort.

Several hypothesis are offered to explain the observed differences in productivity in the L. boucardi cohorts. These include differential developmental mortality between the sexes and effects of the energetic drain of copulation and sperm storage on productivity. A model based upon differential mortality is formulated and tested. It is also proposed that the strategy of producing significantly more progeny when unfertilized, may have been selected for.

The reproductive tactics and progeny production schedules of both parasitoid species are compared. The L. heterotoma cohort did not follow the typical "early explosive" pattern of progeny production exhibited by L. boulardi. Rather, the progeny production schedule of L. heterotoma was distributed through significantly more exposure periods. L. boulardi produced significantly more progeny per female. This is attributed to the sympatric nature of the host and parasitoid populations and to the possible decrease in viability of L. heterotoma after many years in culture.

## CHAPTER 4

### THEORETICAL CONSIDERATIONS AND INTERPRETATION OF THE LIFE-HISTORY TACTICS OF LEPTOPILINA BOULARDI

Classically, the development of life-history theory has been based upon two schools of thought: the stochastic school (Cohen, 1966; Holgate, 1967; Murphy, 1968; Schaffer, 1974; and others), and the deterministic school (Cole, 1954; Lewontin, 1965; MacArthur & Wilson, 1967; Gadgil & Bossert, 1970; Pianka, 1970, 1972; Roughgarden, 1971; Gadgil & Solbrig, 1972; ; Cole, 1954; Lewontin, 1965; and others). The deterministic view deals with models in which the survivorship and fecundity distributions of populations do not fluctuate, while the stochastic view tries to incorporate these variations into their models (Stearns, 1976). Both schools have attempted to predict which tactics, or combinations of life-history traits would evolve in organisms living under specified conditions.

The deterministic school predicts that in environments that favor rapid population growth selection would favor: (a) early age at first reproduction; (b) semelparity; (c) short generation time; (d) large clutch size; (e) little or no parental care; (f) large reproductive effort, and (g)

numerous small offspring. In saturated environments, they contend that selection would favor: (a) delayed reproduction; (b) iteroparity; (c) small clutch sizes; (d) smaller reproductive effort; (e) parental care, and (f) a few large offspring.

The stochastic school predicts that in fluctuating environments in which juvenile mortality is variable, selection would favor: (a) late maturity; (b) iteroparity; (c) small reproductive effort; (d) longer life; (e) fewer broods per young and, (f) more broods (Stearns, 1976). They also predict that if juvenile mortality is variable in a stable environment, or if adult mortality is variable in an unstable environment, selection would favor: (a) increased reproductive effort; (b) early maturity; (c) iteroparity; (d) shorter life, and (e) fewer but larger clutches.

This dichotomy in the theoretical approaches to the evolution of life-history tactics has led, as is often the case in the biological community, to theoretical myopia on the parts of both schools. Based partly upon the lack of empirical data and partly upon oversimplified assessments of the cause and effect relationships at work in the evolution of life-history tactics, theoreticians sternly adhere to their predicted suites of traits as being immutable. Stearns (1976) warns that "...we should remain open to the possibility that the assemblage of traits, the tactics, predicted by  $r$  and  $K$  selection or by bet hedging, or their

descendants, are not iron clad entities permitting no exceptions. In nature organisms may respond with some traits to maximizing  $r$ , with others to bet-hedging. Both causal systems operate at once, with different outcomes, on balance for different traits."

This is exactly what has evolved in L. boulardi, a set of life-history tactics that combine adaptations to maximizing 'r' and bet-hedging. When hosts are available in high density patches, L. boulardi can utilize these patches efficiently and explosively. However, to hedge its bets against the probability of not finding suitable host patches, L. boulardi has opted for a strategy of longevity, regardless of reproductive state, to assure the probability of finding adequate host patches. Thus when hosts are patchily distributed in time, females can live long enough to withstand periods of limited or no host availability and maintain reproductive success.

In order to more clearly understand the adaptive nature of this highly plastic reproductive strategy, one must consider it on at least two levels : (1) its evolution in terms of the availability and stability of host patches in nature, and (2) the constraints of experimental design on the searching efficiency and behavior of the female parasitoids.

(i) Life history tactics, larval mortality and environmental severity.

Price (1973) in his discussion of the egg production strategies of the ichneumonid parasitoids of Neodiprion, argued that due to predation pressure, dessication, and other causes, early host larval stages and hence their parasitoids have a much lower probability of survival than do later host larval and pupal stages, and their parasitoids. Therefore, he continued, in order to insure successful replacement, parasitoids of early larval stages should produce significantly more eggs than parasitoids of later developmental stages. This trend was found in the Ichneumonidae and Tachinidae (Price 1973, 1975), but awaits further study in other groups. Although we can make no definitive statement concerning the relative numbers of eggs in a suite of Eucoilids parasitizing different larval and pupal stages, we can readily accept the premise that early larval parasitoids are exposed to high juvenile mortality. It follows then that the high number of readily available eggs in newly hatched females of L. boulandi and L. heterotoma should be interpreted in this context.

Gotto (1962) described a similar schema for parasitic and commensal copepods. In stable calm water environments where readily available hosts are abundant, he suggested that a few large eggs would be favored. Larger eggs, it was argued, would produce larger, competitively superior larvae

better able to find appropriate hosts in a saturated environment. Where the hosts were patchily distributed, highly vagile, or in an unstable environment, then many smaller eggs would be favored in order to spread the risk of total reproductive failure.

Evans and Smith (1952) argued that the magnitude of the net reproductive rate measured under optimal conditions in the laboratory, should indicate the severity, or "rigorousness of the natural environment in terms of individual replacement." Since under optimal conditions for replacement, a population need only exhibit a net reproductive rate of unity, any departure from unity should reflect the difference between the natural environment and optimal conditions for replacement. The high net reproductive rate exhibited by L. boulandi under all experimental conditions should be taken as further evidence of the low probability of successful progeny survival in nature.

We may also interpret L. boulandi's repeated reproduction as an adaptation to the same problem. As theoreticians from both schools agree, repeated reproduction should evolve in populations living in fluctuating environments, in order to spread the risk of reproductive failure. We can interpret L. boulandi's high reproductive effort and schedule of repeated reproduction, as adaptations to environmental fluctuations in response to the instability and ephemeral

nature of host patches and the consequent low probability of progeny survival.

(ii) Life history tactics and the distribution of hosts in time and space.

In nature, suitable hosts are not continuously available in high density patches for the duration of a female's life, nor are females confined to a particular host patch. Parasitoid females must spend time and energy in searching for suitable host patches, and have therefore evolved elaborate mechanisms to insure efficient host searching and discrimination (see Vinson, 1975, 1976a,b, for reviews). The evolution and maintenance of these mechanisms should be taken as proof that the parasitoid's environment is indeed patchy with respect to host availability in time and space.

The traits described above, i.e., high reproductive capacity and repeated reproduction, are not only adaptations to overcoming low progeny survival, but also to patchy host distribution and the low probability of finding suitable host patches at any particular point in time. Keeping in mind that the distribution of successful reproduction throughout life is dependent upon the distribution of available hosts, it follows that the longevity shown by L. bouhardi has evolved to offset the low probability of finding suitable host patches at any particular point in time.



One further facet of L. boulandi's life history tactics, shown by Chabora et al., 1979, and in experiments to be discussed later, is its variable emergence strategy. Masaki (1980), Giesel (1976) and Stearns (1976, 1977) consider polymodal emergence patterns as a bet-hedging strategy against the risk of reproductive failure due to a fluctuating environment, and to maximize the chance that offspring will hatch in an environment suitable for their own reproduction. By spreading emergence through time, the probability of an entire brood hatching during a period of unfavorable environmental conditions is decreased or eliminated.

One final aspect to consider is the productivity of unfertilized females. As stated earlier, one could conceive of the production of significantly more progeny by an unfertilized female as a strategy selected for increasing her probability of contributing to the gene pools of later generations. Since an unfertilized female is not sterile, her success in contributing her genes to subsequent generations is solely dependent upon her sons' abilities to find and mate with appropriate females and the abilities of those females, in turn, to find suitable hosts. Unfertilized females that produce more sons will increase the probability that their genes will be incorporated into the next generation and hence be selected for in comparison to unfertilized females that produce as many, or fewer,

progeny than fertilized females. Therefore, assuming that the number of successful progeny produced by unfertilized females is a heritable trait, selection should act to favor the production of more total progeny by a female when unfertilized. Again we see a strategy that will both optimize 'r' and hedge bets against reproductive failure.

Giesel (1976) stated that the reproductive strategy of iteroparous organisms is based on a three-level phenomenon.

"Certain patterns of age-specific reproduction, selected for by patterns of environmental heterogeneity characterize a population or species.....These seem to have evolved in response to the environmental conditions historically faced by the population and are generally as predicted by theory. However, we also find genetic polymorphism for development time and shapes of fecundity distribution within populations. These add adaptive variability to the population's demographic structure, and give it response plasticity not otherwise available. Finally, individuals are able to regulate their reproductive efforts and allocations of available energy in response to variations in nutrient level and other environmental conditions. Such phenotypic plasticity of reproductive pattern sometimes constitutes the major part of reproductive strategy."

L. boulandi's life-history tactics as described above, seem to fit Giesel's statement closely. We can characterize it as the life-history of an ultimate opportunist, adapted to utilize hosts that we speculate are patchily distributed in time and space. It is adapted to maximizing 'r', and bet-hedging and can exploit host patches efficiently under a continuous range of host distribution patterns.

## APPENDIX

TABLE 52. Analysis of variance table for comparison of reproductive variables between the D. melanogaster reared cohort and the D. simulans reared cohort.

TABLE 52, (continued)

## Variable : Length of life

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 16.25          | 1  | 16.25       | 1.11    |
| Within  | 1342.74        | 92 | 14.60       |         |
| Total   | 1358.98        | 93 |             |         |

## Variable : Days of male production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 1.11           | 1  | 1.11        | 0.25    |
| Within  | 400.05         | 92 | 4.35        |         |
| Total   | 401.16         | 93 |             |         |

## Variable : Days of female production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 5.62           | 1  | 5.62        | 1.03    |
| Within  | 499.37         | 92 | 5.43        |         |
| Total   | 504.99         | 93 |             |         |

## Variable : Total male production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 124593.38      | 1  | 124593.38   | 43.16   |
| Within  | 265707.13      | 92 | 2887.03     | **      |
| Total   | 390200.50      | 93 |             |         |

TABLE 52, (continued)

## Variable : Total female production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 30587.24       | 1  | 30587.24    | 11.26   |
| Within  | 249968.00      | 92 | 2717.04     | **      |
| Total   | 280555.19      | 93 |             |         |

## Variable : Total progeny production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 278645.88      | 1  | 278645.88   | 95.58   |
| Within  | 268221.13      | 92 | 2915.45     | **      |
| Total   | 546867.00      | 93 |             |         |

## Variable : Total post-reproductive period

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 8.98           | 1  | 8.98        | 1.20    |
| Within  | 684.89         | 92 | 7.44        |         |
| Total   | 693.87         | 93 |             |         |

## Variable : Post-reproductive period for female progeny

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 42.82          | 1  | 42.82       | 2.43    |
| Within  | 1619.31        | 92 | 17.60       |         |
| Total   | 1662.13        | 93 |             |         |

TABLE 53. Analysis of variance table for comparison of reproductive variables between the Series I and Series II cohorts exposed to D. simulans.

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| Variable : Length of life |                |    |             |         |
|---------------------------|----------------|----|-------------|---------|
|                           | Sum of squares | df | Mean square | F ratio |
| <hr/>                     |                |    |             |         |
| Between                   | 6.02           | 1  | 6.02        | 0.62    |
| Within                    | 447.96         | 46 | 9.74        |         |
| Total                     | 453.98         | 47 |             |         |

| Variable : Total male production |                |    |             |         |
|----------------------------------|----------------|----|-------------|---------|
|                                  | Sum of squares | df | Mean square | F ratio |
| <hr/>                            |                |    |             |         |
| Between                          | 55012.91       | 1  | 55012.91    | 37.39   |
| Within                           | 67687.38       | 46 | 1471.47     | **      |
| Total                            | 122700.25      | 47 |             |         |

| Variable : Total female production |                |    |             |         |
|------------------------------------|----------------|----|-------------|---------|
|                                    | Sum of squares | df | Mean square | F ratio |
| <hr/>                              |                |    |             |         |
| Between                            | 315.19         | 1  | 315.19      | 0.29    |
| Within                             | 49454.71       | 46 | 1075.10     |         |
| Total                              | 49769.89       | 47 |             |         |

TABLE 53, (continued)

| Variable : Total progeny production |                |    |             |         |
|-------------------------------------|----------------|----|-------------|---------|
|                                     | Sum of squares | df | Mean square | F ratio |
| Between                             | 63656.30       | 1  | 63656.30    | 42.36   |
| Within                              | 69121.44       | 46 | 1502.64     | **      |
| Total                               | 132777.74      | 47 |             |         |

| Variable : Total post-reproductive period |                |    |             |         |
|-------------------------------------------|----------------|----|-------------|---------|
|                                           | Sum of squares | df | Mean square | F ratio |
| Between                                   | 30.08          | 1  | 30.08       | 13.59   |
| Within                                    | 101.83         | 46 | 2.21        | **      |
| Total                                     | 131.92         | 47 |             |         |

| Variable : Post-reproductive period for female progeny |                |    |             |         |
|--------------------------------------------------------|----------------|----|-------------|---------|
|                                                        | Sum of squares | df | Mean square | F ratio |
| Between                                                | 408.33         | 1  | 408.33      | 58.41   |
| Within                                                 | 321.58         | 46 | 6.99        | **      |
| Total                                                  | 729.92         | 47 |             |         |



TABLE 54. Nonparametric analysis (Wilcoxon rank sum test)  
of reproductive variables between the Series I and Series  
III cohorts exposed to D. simulans.

TABLE 54, (continued)

## Wilcoxon Scores (Rank Sums)

Variable : Length of life

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series I   | 24 | 433.50           | 408.00               | 24.74               | 18.06         |
| Series III | 9  | 127.50           | 153.00               | 24.74               | 14.17         |

Wilcoxon 2-sample test (normal approximation)

s= 127.50      z=-1.01      prob &gt; |z| 0.31

t-test approximate significance = 0.32

## Wilcoxon Scores (Rank Sums)

Variable : Male progeny

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series I   | 24 | 493.50           | 408.00               | 24.74               | 20.56         |
| Series III | 9  | 67.50            | 153.00               | 24.74               | 7.50          |

Wilcoxon 2-sample test (normal approximation)

s= 67.50      z=-3.44      prob &gt; |z| 0.0006

t-test approximate significance = 0.0017

TABLE 54, (continued)

## Wilcoxon Scores (Rank Sums)

Variable : Female progeny

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series I   | 24 | 448.50           | 408.00               | 24.74               | 18.69         |
| Series III | 9  | 112.50           | 153.00               | 24.74               | 12.50         |

Wilcoxon 2-sample test (normal approximation)

s= 112.50      z=-1.62      prob &gt; |z| 0.11

t-test approximate significance = 0.12

## Wilcoxon Scores (Rank Sums)

Variable : Total progeny

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series I   | 24 | 511.00           | 408.00               | 24.74               | 21.29         |
| Series III | 9  | 50.00            | 153.00               | 24.74               | 5.56          |

Wilcoxon 2-sample test (normal approximation)

s= 50.00      z=-4.14      prob &gt; |z| 0.0000

t-test approximate significance = 0.0002

TABLE 54, (continued)

## Wilcoxon Scores (Rank Sums)

Variable : Total post-reproductive period

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series I   | 24 | 459.50           | 408.00               | 24.74               | 19.15         |
| Series III | 9  | 101.50           | 153.00               | 24.74               | 11.28         |

Wilcoxon 2-sample test (normal approximation)

s= 101.50      z=-2.06      prob &gt; |z| 0.04

t-test approximate significance = 0.05

## Wilcoxon Scores (Rank Sums)

Variable : Post-reproductive period for female progeny

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series I   | 24 | 496.00           | 408.00               | 24.74               | 20.67         |
| Series III | 9  | 65.00            | 153.00               | 24.74               | 7.22          |

Wilcoxon 2-sample test (normal approximation)

s= 65.00      z=-3.54      prob &gt; |z| 0.0004

t-test approximate significance = 0.001

TABLE 55. Analysis of variance table for comparison of reproductive variables between the Series I and Series IV cohorts exposed to D. simulans.

Variable : Length of life

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 0.22           | 1  | 0.22        | 0.03    |
| Within  | 359.06         | 45 | 7.98        |         |
| Total   | 359.28         | 46 |             |         |

Variable : Days of male production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 0.30           | 1  | 0.30        | 0.15    |
| Within  | 91.57          | 45 | 2.03        |         |
| Total   | 91.87          | 46 |             |         |

Variable : Days of female production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 169.33         | 1  | 169.33      | 48.25   |
| Within  | 157.94         | 45 | 3.51        | **      |
| Total   | 327.28         | 46 |             |         |

Variable : Total male production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 30128.36       | 1  | 30128.36    | 25.87   |
| Within  | 52409.41       | 45 | 1164.65     | **      |
| Total   | 82537.75       | 46 |             |         |

TABLE 55, (continued)

## Variable : Total female production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 39748.82       | 1  | 39748.82    | 33.60   |
| Within  | 53232.77       | 45 | 1182.95     | **      |
| Total   | 92981.56       | 46 |             |         |

## Variable : Total progeny production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 669.43         | 1  | 669.43      | 0.67    |
| Within  | 44509.86       | 45 | 989.11      |         |
| Total   | 45175.29       | 46 |             |         |

## Variable : Total post-reproductive period

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 1.57           | 1  | 1.57        | 0.42    |
| Within  | 167.75         | 45 | 3.73        |         |
| Total   | 169.32         | 46 |             |         |

## Variable : Post-reproductive period for female progeny

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 162.77         | 1  | 162.77      | 16.54   |
| Within  | 442.84         | 45 | 9.84        | **      |
| Total   | 605.62         | 46 |             |         |

TABLE 56. Analysis of variance table for comparison of reproductive variables between the Series I and Series V cohorts exposed to D. simulans.



TABLE 56, (continued)

## Variable : Length of life

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 39.89          | 1  | 39.89       | 2.49    |
| Within  | 754.06         | 47 | 16.04       |         |
| Total   | 793.96         | 48 |             |         |

## Variable : Days of male production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 5.20           | 1  | 5.20        | 1.22    |
| Within  | 200.72         | 47 | 4.27        |         |
| Total   | 205.92         | 48 |             |         |

## Variable : Days of female production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 29.29          | 1  | 29.29       | 6.09    |
| Within  | 225.97         | 47 | 4.81        | *       |
| Total   | 255.26         | 48 |             |         |

## Variable : Total male production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 24229.79       | 1  | 24229.79    | 16.36   |
| Within  | 69613.69       | 47 | 1481.14     | **      |
| Total   | 93843.44       | 48 |             |         |

TABLE 56, (continued)

## Variable : Total female production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 8819.95        | 1  | 8819.95     | 5.62    |
| Within  | 73757.44       | 47 | 1569.31     | *       |
| Total   | 82577.38       | 48 |             |         |

## Variable : Total progeny production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 3812.40        | 1  | 3812.40     | 2.40    |
| Within  | 74716.84       | 47 | 1589.72     |         |
| Total   | 78529.24       | 48 |             |         |

## Variable : Total post-reproductive period

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 58.01          | 1  | 58.01       | 7.92    |
| Within  | 344.39         | 47 | 7.33        | **      |
| Total   | 402.41         | 48 |             |         |

## Variable : Post-reproductive period for female progeny

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 2.21           | 1  | 2.21        | 0.12    |
| Within  | 859.62         | 47 | 18.29       |         |
| Total   | 861.84         | 48 |             |         |

TABLE 57. Nonparametric analysis (Wilcoxon rank sum test)  
of reproductive variables between the Series II and Series  
III cohorts exposed to D. simulans.

TABLE 57, (continued)

## Wilcoxon Scores (Rank Sums)

Variable : Length of life

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series I   | 24 | 442.00           | 408.00               | 24.74               | 18.42         |
| Series III | 9  | 119.00           | 153.00               | 24.74               | 13.32         |

Wilcoxon 2-sample test (normal approximation)

s= 119.00      z=-1.35      prob &gt; |z| 0.18

t-test approximate significance = 0.19

## Wilcoxon Scores (Rank Sums)

Variable : Male progeny

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series I   | 24 | 372.00           | 408.00               | 24.74               | 15.50         |
| Series III | 9  | 189.00           | 153.00               | 24.74               | 21.00         |

Wilcoxon 2-sample test (normal approximation)

s= 189.00      z= 1.48      prob &gt; |z| 0.14

t-test approximate significance = 0.15

TABLE 57, (continued)

## Wilcoxon Scores (Rank Sums)

Variable : Female progeny

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series I   | 24 | 442.50           | 408.00               | 24.74               | 18.44         |
| Series III | 9  | 118.50           | 153.00               | 24.74               | 13.17         |

Wilcoxon 2-sample test (normal approximation)

s= 118.50      z=-1.37      prob &gt; |z| 0.17

t-test approximate significance = 0.18

## Wilcoxon Scores (Rank Sums)

Variable : Total progeny

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series I   | 24 | 417.00           | 408.00               | 24.74               | 17.38         |
| Series III | 9  | 144.00           | 153.00               | 24.74               | 16.00         |

Wilcoxon 2-sample test (normal approximation)

s= 144.00      z=-0.34      prob &gt; |z| 0.73

t-test approximate significance = 0.73

TABLE 57, (continued)

## Wilcoxon Scores (Rank Sums)

Variable : Total post-reproductive period

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series I   | 24 | 384.00           | 408.00               | 24.74               | 16.00         |
| Series III | 9  | 177.00           | 153.00               | 24.74               | 19.67         |

Wilcoxon 2-sample test (normal approximation)

s= 177.00      z= 0.99      prob &gt; |z| 0.32

t-test approximate significance = 0.33

## Wilcoxon Scores (Rank Sums)

Variable : Post-reproductive period for female progeny

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series I   | 24 | 354.00           | 408.00               | 24.74               | 14.75         |
| Series III | 9  | 207.00           | 153.00               | 24.74               | 23.00         |

Wilcoxon 2-sample test (normal approximation)

s= 207.00      z= 2.20      prob &gt; |z| 0.03

t-test approximate significance = 0.03

TABLE 58. Analysis of variance table for comparison of reproductive variables between the Series II and Series IV cohorts exposed to D. simulans.

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Variable : Length of life

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 3.85           | 1  | 3.85        | 0.46    |
| Within  | 377.77         | 45 | 8.39        |         |
| Total   | 381.62         | 46 |             |         |

Variable : Total male production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 3418.11        | 1  | 3418.11     | 2.66    |
| Within  | 57833.25       | 45 | 1285.18     |         |
| Total   | 61251.36       | 46 |             |         |

Variable : Total female production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 47060.63       | 1  | 47060.63    | 45.84   |
| Within  | 46197.68       | 45 | 1026.62     | **      |
| Total   | 93258.25       | 46 |             |         |

TABLE 58, (continued)

## Variable : Total progeny production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 75844.90       | 1  | 75844.90    | 49.69   |
| Within  | 68682.15       | 45 | 1526.27     | **      |
| Total   | 144527.05      | 46 |             |         |

## Variable : Total post-reproductive period

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 17.41          | 1  | 17.41       | 11.88   |
| Within  | 65.91          | 45 | 1.46        | **      |
| Total   | 83.32          | 46 |             |         |

## Variable : Post-reproductive period for female progeny

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 52.31          | 1  | 52.31       | 14.61   |
| Within  | 161.18         | 45 | 3.58        | **      |
| Total   | 213.49         | 46 |             |         |



TABLE 59. Analysis of variance table for comparison of reproductive variables between the Series II and Series V cohorts exposed to D. simulans.

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| Variable : Length of life |                |    |             |         |
|---------------------------|----------------|----|-------------|---------|
|                           | Sum of squares | df | Mean square | F ratio |
| <hr/>                     |                |    |             |         |
| Between                   | 77.35          | 1  | 77.35       | 4.70    |
| Within                    | 772.77         | 47 | 16.44       | *       |
| Total                     | 850.12         | 48 |             |         |

| Variable : Total male production |                |    |             |         |
|----------------------------------|----------------|----|-------------|---------|
|                                  | Sum of squares | df | Mean square | F ratio |
| <hr/>                            |                |    |             |         |
| Between                          | 6604.89        | 1  | 6604.89     | 4.14    |
| Within                           | 75037.56       | 47 | 1596.54     | *       |
| Total                            | 81642.44       | 48 |             |         |

| Variable : Total female production |                |    |             |         |
|------------------------------------|----------------|----|-------------|---------|
|                                    | Sum of squares | df | Mean square | F ratio |
| <hr/>                              |                |    |             |         |
| Between                            | 12510.04       | 1  | 12510.04    | 8.81    |
| Within                             | 66722.38       | 47 | 1419.63     | **      |
| Total                              | 79232.38       | 48 |             |         |

TABLE 59, (continued)

## Variable : Total progeny production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 37294.90       | 1  | 37294.90    | 17.73   |
| Within  | 98889.41       | 47 | 2104.03     | **      |
| Total   | 136814.31      | 48 |             |         |

## Variable : Total post-reproductive period

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 173.11         | 1  | 173.11      | 33.54   |
| Within  | 242.56         | 47 | 5.16        | **      |
| Total   | 415.67         | 48 |             |         |

## Variable : Post-reproductive period for female progeny

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 479.59         | 1  | 479.59      | 39.00   |
| Within  | 577.96         | 47 | 12.30       | **      |
| Total   | 1057.55        | 48 |             |         |

TABLE 60. Nonparametric analysis (Wilcoxon rank sum test)  
of reproductive variables between the Series IV and Series  
III cohorts exposed to D. simulans.

TABLE 60, (continued)

## Wilcoxon Scores (Rank Sums)

Variable : Length of life

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series IV  | 23 | 419.50           | 379.50               | 23.86               | 18.24         |
| Series III | 9  | 108.50           | 148.50               | 23.86               | 12.06         |

Wilcoxon 2-sample test (normal approximation)

s= 108.50      z=-1.66      prob &gt; |z| 0.10

t-test approximate significance = 0.11

## Wilcoxon Scores (Rank Sums)

Variable : Male progeny

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series IV  | 23 | 411.50           | 379.50               | 23.86               | 17.89         |
| Series III | 9  | 116.50           | 148.50               | 23.86               | 12.94         |

Wilcoxon 2-sample test (normal approximation)

s= 116.50      z=-1.32      prob &gt; |z| 0.19

t-test approximate significance = 0.20

TABLE 60, (continued)

## Wilcoxon Scores (Rank Sums)

Variable : Female progeny

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series IV  | 23 | 472.00           | 379.50               | 23.86               | 20.52         |
| Series III | 9  | 56.00            | 148.50               | 23.86               | 6.22          |

Wilcoxon 2-sample test (normal approximation)

s= 56.00      z=-3.86      prob &gt; |z| 0.0001

t-test approximate significance = 0.0005

## Wilcoxon Scores (Rank Sums)

Variable : Total progeny

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series IV  | 23 | 481.00           | 379.50               | 23.86               | 20.91         |
| Series III | 9  | 47.00            | 148.50               | 23.86               | 5.22          |

Wilcoxon 2-sample test (normal approximation)

s= 47.00      z=-4.23      prob &gt; |z| 0.0000

t-test approximate significance = 0.0002

TABLE 60, (continued)

## Wilcoxon Scores (Rank Sums)

Variable : Total post-reproductive period

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series IV  | 23 | 429.00           | 379.50               | 23.86               | 18.65         |
| Series III | 9  | 99.00            | 148.50               | 23.86               | 11.00         |

Wilcoxon 2-sample test (normal approximation)

s= 99.00      z=-2.05      prob &gt; |z| 0.04

t-test approximate significance = 0.05

## Wilcoxon Scores (Rank Sums)

Variable : Post-reproductive period for female progeny

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series IV  | 23 | 401.50           | 379.50               | 23.86               | 17.46         |
| Series III | 9  | 126.50           | 148.50               | 23.86               | 14.06         |

Wilcoxon 2-sample test (normal approximation)

s= 126.50      z=-0.90      prob &gt; |z| 0.37

t-test approximate significance = 0.37

TABLE 61. Nonparametric analysis (Wilcoxon rank sum test)  
of reproductive variables between the Series V and Series  
III cohorts exposed to D. simulans.

TABLE 61, (continued)

## Wilcoxon Scores (Rank Sums)

Variable : Length of life

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series V   | 25 | 495.00           | 437.50               | 25.62               | 19.80         |
| Series III | 9  | 100.00           | 157.50               | 25.62               | 11.11         |

Wilcoxon 2-sample test (normal approximation)

s= 100.00      z=-2.23      prob &gt; |z| 0.03

t-test approximate significance = 0.03

## Wilcoxon Scores (Rank Sums)

Variable : Male progeny

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series V   | 25 | 466.00           | 437.50               | 25.62               | 18.64         |
| Series III | 9  | 129.00           | 157.50               | 25.62               | 14.33         |

Wilcoxon 2-sample test (normal approximation)

s= 129.00      z=-1.09      prob &gt; |z| 0.27

t-test approximate significance = 0.28



TABLE 61, (continued)

## Wilcoxon Scores (Rank Sums)

Variable : Female progeny

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series V   | 25 | 504.00           | 437.50               | 25.62               | 20.16         |
| Series III | 9  | 91.00            | 157.50               | 25.62               | 10.11         |

Wilcoxon 2-sample test (normal approximation)

s= 91.00      z=-2.58      prob &gt; |z| 0.01

t-test approximate significance = 0.01

## Wilcoxon Scores (Rank Sums)

Variable : Total progeny

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series V   | 25 | 524.50           | 437.50               | 25.62               | 20.98         |
| Series III | 9  | 70.50            | 157.50               | 25.62               | 7.83          |

Wilcoxon 2-sample test (normal approximation)

s= 70.50      z=-3.38      prob &gt; |z| 0.0007

t-test approximate significance = 0.02

TABLE 61, (continued)

## Wilcoxon Scores (Rank Sums)

Variable : Total post-reproductive period

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series V   | 25 | 528.50           | 437.50               | 25.62               | 21.14         |
| Series III | 9  | 66.50            | 157.50               | 25.62               | 7.39          |

Wilcoxon 2-sample test (normal approximation)

s= 66.50      z=-3.53      prob &gt; |z| 0.0004

t-test approximate significance = 0.001

## Wilcoxon Scores (Rank Sums)

Variable : Post-reproductive period for female progeny

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Series V   | 25 | 509.50           | 437.50               | 25.62               | 20.38         |
| Series III | 9  | 85.50            | 157.50               | 25.62               | 9.50          |

Wilcoxon 2-sample test (normal approximation)

s= 85.50      z=-2.79      prob &gt; |z| 0.005

t-test approximate significance = 0.09

TABLE 62. Analysis of variance table for comparison of reproductive variables between the Series IV and Series V cohorts exposed to D. simulans.

TABLE 62, (continued)

## Variable : Length of life

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 45.13          | 1  | 45.13       | 3.04    |
| Within  | 683.88         | 46 | 14.87       |         |
| Total   | 729.00         | 47 |             |         |

## Variable : Days of male production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 2.88           | 1  | 2.88        | 0.88    |
| Within  | 150.37         | 46 | 3.27        |         |
| Total   | 153.25         | 47 |             |         |

## Variable : Days of female production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 60.67          | 1  | 60.67       | 9.02    |
| Within  | 309.25         | 46 | 6.72        | **      |
| Total   | 369.92         | 47 |             |         |

## Variable : Total male production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 455.33         | 1  | 455.33      | 0.35    |
| Within  | 59759.57       | 46 | 1299.12     |         |
| Total   | 60214.90       | 47 |             |         |

TABLE 62, (continued)

## Variable : Total female production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 11763.94       | 1  | 11763.94    | 7.68    |
| Within  | 70500.44       | 46 | 1532.62     | **      |
| Total   | 82264.38       | 47 |             |         |

## Variable : Total progeny production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 7590.46        | 1  | 7590.46     | 4.70    |
| Within  | 74277.58       | 46 | 1614.73     | *       |
| Total   | 81787.04       | 47 |             |         |

## Variable : Total post-reproductive period

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 77.44          | 1  | 77.44       | 11.55   |
| Within  | 308.47         | 46 | 6.71        | **      |
| Total   | 385.92         | 47 |             |         |

## Variable : Post-reproductive period for female progeny

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 206.10         | 1  | 206.10      | 13.56   |
| Within  | 699.22         | 46 | 15.20       | **      |
| Total   | 905.31         | 47 |             |         |

TABLE 63. Analysis of variance table for comparison of reproductive variables between the fifty replicate 1 hour limited and the fifty replicate continuous cohorts, exposed to D. simulans.

TABLE 63, (continued)

## Variable : Length of life

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 108.11         | 1  | 108.11      | 16.96   |
| Within  | 599.37         | 94 | 6.38        | **      |
| Total   | 707.49         | 95 |             |         |

## Variable : Days of male production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 4.08           | 1  | 4.08        | 1.17    |
| Within  | 328.88         | 94 | 3.50        |         |
| Total   | 332.96         | 95 |             |         |

## Variable : Days of female production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 566.97         | 1  | 566.97      | 119.62  |
| Within  | 445.53         | 94 | 4.74        | **      |
| Total   | 1012.50        | 95 |             |         |

## Variable : Total male production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 49650.63       | 1  | 49650.63    | 62.28   |
| Within  | 74943.63       | 94 | 797.28      | **      |
| Total   | 124594.65      | 95 |             |         |

TABLE 63, (continued)

## Variable : Total female production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 30759.88       | 1  | 30759.88    | 26.79   |
| Within  | 107927.88      | 94 | 1148.17     | **      |
| Total   | 138687.75      | 95 |             |         |

## Variable : Total progeny production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 2250.48        | 1  | 2250.48     | 1.57    |
| Within  | 134573.00      | 94 | 1431.63     |         |
| Total   | 136823.44      | 95 |             |         |

## Variable : Total post-reproductive period

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 216.16         | 1  | 216.16      | 46.84   |
| Within  | 433.83         | 94 | 4.62        | **      |
| Total   | 649.99         | 95 |             |         |

## Variable : Post-reproductive period for female progeny

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 1197.76        | 1  | 1197.76     | 121.43  |
| Within  | 927.22         | 94 | 9.86        | **      |
| Total   | 2124.98        | 95 |             |         |



TABLE 64. Analysis of variance table for comparison of reproductive variables between the continuous and delayed cohorts, exposed to D. melanogaster (WO strain), April, 1979.

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| Variable : Length of life |                |    |             |         |
|---------------------------|----------------|----|-------------|---------|
|                           | Sum of squares | df | Mean square | F ratio |
| <hr/>                     |                |    |             |         |
| Between                   | 19.01          | 1  | 19.01       | 4.75    |
| Within                    | 144.25         | 36 | 4.01        | *       |
| Total                     | 163.26         | 37 |             |         |

| Variable : Total male production |                |    |             |         |
|----------------------------------|----------------|----|-------------|---------|
|                                  | Sum of squares | df | Mean square | F ratio |
| <hr/>                            |                |    |             |         |
| Between                          | 13161.02       | 1  | 13161.02    | 6.39    |
| Within                           | 74226.44       | 36 | 2061.85     | *       |
| Total                            | 87387.44       | 37 |             |         |

| Variable : Total female production |                |    |             |         |
|------------------------------------|----------------|----|-------------|---------|
|                                    | Sum of squares | df | Mean square | F ratio |
| <hr/>                              |                |    |             |         |
| Between                            | 33689.71       | 1  | 33689.71    | 32.46   |
| Within                             | 37370.14       | 36 | 1038.06     | **      |
| Total                              | 71059.81       | 37 |             |         |

TABLE 64, (continued)

## Variable : Total progeny production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 88964.31       | 1  | 88964.31    | 38.05   |
| Within  | 84173.69       | 36 | 2338.15     | **      |
| Total   | 173137.69      | 37 |             |         |

## Variable : Total post-reproductive period

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 241.60         | 1  | 241.60      | 65.18   |
| Within  | 133.45         | 36 | 3.71        | **      |
| Total   | 375.05         | 37 |             |         |

## Variable : Post-reproductive period for female progeny

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 342.32         | 1  | 342.32      | 33.89   |
| Within  | 363.57         | 36 | 10.10       | **      |
| Total   | 705.89         | 37 |             |         |

TABLE 65. Analysis of variance table for comparison of reproductive variables between the continuous and intermittent cohorts, exposed to D. melanogaster (W0 strain), April, 1979.

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| Variable : Length of life |                |    |             |         |
|---------------------------|----------------|----|-------------|---------|
|                           | Sum of squares | df | Mean square | F ratio |
| <hr/>                     |                |    |             |         |
| Between                   | 119.29         | 1  | 119.29      | 14.32   |
| Within                    | 291.63         | 35 | 8.33        | **      |
| Total                     | 410.92         | 36 |             |         |

| Variable : Total male production |                |    |             |         |
|----------------------------------|----------------|----|-------------|---------|
|                                  | Sum of squares | df | Mean square | F ratio |
| <hr/>                            |                |    |             |         |
| Between                          | 4267.47        | 1  | 4267.47     | 1.79    |
| Within                           | 83560.88       | 35 | 2387.45     |         |
| Total                            | 87828.31       | 36 |             |         |

| Variable : Total female production |                |    |             |         |
|------------------------------------|----------------|----|-------------|---------|
|                                    | Sum of squares | df | Mean square | F ratio |
| <hr/>                              |                |    |             |         |
| Between                            | 3.24           | 1  | 3.24        | 0.00    |
| Within                             | 56757.67       | 35 | 1621.65     |         |
| Total                              | 56760.91       | 36 |             |         |

TABLE 65, (continued)

## Variable : Total progeny production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 4506.13        | 1  | 4506.13     | 2.07    |
| Within  | 76176.00       | 35 | 2176.46     |         |
| Total   | 80682.00       | 36 |             |         |

## Variable : Total post-reproductive period

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 515.68         | 1  | 515.68      | 231.72  |
| Within  | 77.89          | 35 | 2.23        | **      |
| Total   | 593.57         | 36 |             |         |

## Variable : Post-reproductive period for female progeny

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 922.16         | 1  | 922.16      | 158.55  |
| Within  | 203.56         | 35 | 5.81        | **      |
| Total   | 1125.73        | 36 |             |         |

TABLE 66. Analysis of variance table for comparison of reproductive variables between the continuous and 1 hour limited cohorts, exposed to D.\_\_\_\_melanogaster (WO strain), April, 1979.

TABLE 66, (continued)

## Variable : Length of life

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 577.20         | 1  | 577.20      | 133.03  |
| Within  | 156.19         | 36 | 4.34        | **      |
| Total   | 733.39         | 37 |             |         |

## Variable : Days of male production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 0.001          | 1  | 0.001       | 0.004   |
| Within  | 107.08         | 36 | 2.97        |         |
| Total   | 107.08         | 37 |             |         |

## Variable : Days of female production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 8.65           | 1  | 8.65        | 1.03    |
| Within  | 274.72         | 36 | 7.63        |         |
| Total   | 283.39         | 37 |             |         |

## Variable : Total male production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 1855.38        | 1  | 1855.38     | 0.62    |
| Within  | 97877.31       | 36 | 2718.81     |         |
| Total   | 99732.69       | 37 |             |         |

TABLE 66, (continued)

## Variable : Total female production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 1732.27        | 1  | 1732.27     | 0.99    |
| Within  | 62691.25       | 36 | 1741.42     |         |
| Total   | 64423.51       | 37 |             |         |

## Variable : Total progeny production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 7173.15        | 1  | 7173.15     | 3.47    |
| Within  | 74502.44       | 36 | 2069.51     |         |
| Total   | 81675.56       | 37 |             |         |

## Variable : Total post-reproductive period

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 548.00         | 1  | 548.00      | 167.34  |
| Within  | 117.89         | 36 | 3.28        | **      |
| Total   | 665.89         | 37 |             |         |

## Variable : Post-reproductive period for female progeny

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 574.74         | 1  | 574.74      | 39.37   |
| Within  | 525.58         | 36 | 14.60       | **      |
| Total   | 1100.31        | 37 |             |         |

TABLE 67. Analysis of variance table for comparison of reproductive variables between the continuous and 2 hour limited cohorts, exposed to D.\_\_\_\_melanogaster (WO strain), April, 1979.



TABLE 67, (continued)

## Variable : Length of life

|                     | Sum of squares | df | Mean square | F ratio |
|---------------------|----------------|----|-------------|---------|
| Between             | 72.28          | 1  | 72.28       | 10.43   |
| Within <sup>o</sup> | 256.49         | 37 | 6.93        | **      |
| Total               | 328.77         | 38 |             |         |

## Variable : Days of male production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 9.34           | 1  | 9.34        | 5.28    |
| Within  | 65.43          | 37 | 1.77        | *       |
| Total   | 74.77          | 38 |             |         |

## Variable : Days of female production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 62.45          | 1  | 62.45       | 14.07   |
| Within  | 164.22         | 37 | 4.44        | **      |
| Total   | 226.67         | 38 |             |         |

## Variable : Total male production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 3565.33        | 1  | 3565.33     | 1.93    |
| Within  | 68021.50       | 37 | 1838.42     |         |
| Total   | 71586.81       | 38 |             |         |

TABLE 67, (continued)

## Variable : Total female production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 8.46           | 1  | 8.46        | 0.01    |
| Within  | 40350.57       | 37 | 1090.56     |         |
| Total   | 40359.02       | 38 |             |         |

## Variable : Total progeny production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 3921.07        | 1  | 3921.07     | 1.99    |
| Within  | 73089.63       | 37 | 1975.40     |         |
| Total   | 77010.69       | 38 |             |         |

## Variable : Total post-reproductive period

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 137.79         | 1  | 137.79      | 19.60   |
| Within  | 260.10         | 37 | 7.03        | **      |
| Total   | 397.90         | 38 |             |         |

## Variable : Post-reproductive period for female progeny

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 249.26         | 1  | 249.26      | 22.59   |
| Within  | 408.33         | 37 | 11.04       | **      |
| Total   | 657.59         | 38 |             |         |

TABLE 68. Analysis of variance table for comparison of reproductive variables between the 1 hour limited and 2 hour limited cohorts, exposed to D. melanogaster (WO strain), April, 1979.

TABLE 68, (continued)

## Variable : Length of life

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 238.71         | 1  | 238.71      | 26.01   |
| Within  | 321.18         | 35 | 9.18        | **      |
| Total   | 559.89         | 36 |             |         |

## Variable : Days of male production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 8.66           | 1  | 8.66        | 3.19    |
| Within  | 94.91          | 35 | 2.71        |         |
| Total   | 103.57         | 36 |             |         |

## Variable : Days of female production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 22.96          | 1  | 22.96       | 3.60    |
| Within  | 223.37         | 35 | 6.38        |         |
| Total   | 246.32         | 36 |             |         |

## Variable : Total male production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 243.68         | 1  | 243.68      | 0.16    |
| Within  | 54689.03       | 35 | 1562.54     |         |
| Total   | 54932.71       | 36 |             |         |

TABLE 68, (continued)

## Variable : Total female production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 1465.27        | 1  | 1465.27     | 1.10    |
| Within  | 46821.48       | 35 | 1337.77     |         |
| Total   | 48286.75       | 36 |             |         |

## Variable : Total progeny production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 513.87         | 1  | 513.87      | 0.47    |
| Within  | 37907.10       | 35 | 1083.06     |         |
| Total   | 38420.97       | 36 |             |         |

## Variable : Total post-reproductive period

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 136.65         | 1  | 136.65      | 19.27   |
| Within  | 248.10         | 35 | 7.09        | **      |
| Total   | 384.76         | 36 |             |         |

## Variable : Post-reproductive period for female progeny

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 68.94          | 1  | 68.94       | 3.98    |
| Within  | 606.30         | 35 | 17.32       |         |
| Total   | 675.24         | 36 |             |         |

TABLE 69. Analysis of variance table for comparison of reproductive variables between the continuous and delayed cohorts exposed to D. melanogaster (WO strain), January, 1980.

---

| Variable : Length of life |                |    |             |         |
|---------------------------|----------------|----|-------------|---------|
|                           | Sum of squares | df | Mean square | F ratio |
| <hr/>                     |                |    |             |         |
| Between                   | 40.03          | 1  | 40.03       | 3.41    |
| Within                    | 423.05         | 36 | 11.75       |         |
| Total                     | 463.08         | 37 |             |         |

| Variable : Total male production |                |    |             |         |
|----------------------------------|----------------|----|-------------|---------|
|                                  | Sum of squares | df | Mean square | F ratio |
| <hr/>                            |                |    |             |         |
| Between                          | 45713.80       | 1  | 45713.80    | 20.08   |
| Within                           | 81964.80       | 36 | 2276.80     | **      |
| Total                            | 127678.60      | 37 |             |         |

| Variable : Total female production |                |    |             |         |
|------------------------------------|----------------|----|-------------|---------|
|                                    | Sum of squares | df | Mean square | F ratio |
| <hr/>                              |                |    |             |         |
| Between                            | 9664.11        | 1  | 9664.11     | 3.61    |
| Within                             | 96261.12       | 36 | 2673.92     |         |
| Total                              | 105925.22      | 37 |             |         |

TABLE 69, (continued)

## Wilcoxon Scores (Rank Sums)

## Variable : Total progeny

| Cohort     | N  | Sum of<br>Scores | Expected<br>Under H0 | Std dev<br>Under H0 | Mean<br>Score |
|------------|----|------------------|----------------------|---------------------|---------------|
| Continuous | 19 | 448.50           | 370.50               | 34.25               | 23.61         |
| Delayed    | 19 | 292.50           | 370.50               | 34.25               | 15.39         |

Wilcoxon 2-sample test (normal approximation)

s = 448.50      z = 2.27      prob &gt; |z| 0.024

t-test approximate significance = 0.03

## Variable : Total post-reproductive period

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 111.18         | 1  | 111.81      | 9.35    |
| Within  | 427.90         | 36 | 11.89       | **      |
| Total   | 539.08         | 37 |             |         |

## Variable : Post-reproductive period for female progeny

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 375.29         | 1  | 375.29      | 42.26   |
| Within  | 328.32         | 36 | 9.32        | **      |
| Total   | 713.61         | 38 |             |         |

TABLE 70. Analysis of variance table for comparison of reproductive variables between the continuous and intermittent cohorts, exposed to D. melanogaster (WO strain), January, 1980.

---

| Variable : Length of life |                |    |             |         |
|---------------------------|----------------|----|-------------|---------|
|                           | Sum of squares | df | Mean square | F ratio |
| <hr/>                     |                |    |             |         |
| Between                   | 2.13           | 1  | 2.13        | 0.20    |
| Within                    | 379.57         | 36 | 10.54       |         |
| Total                     | 381.71         | 37 |             |         |

| Variable : Total male production |                |    |             |         |
|----------------------------------|----------------|----|-------------|---------|
|                                  | Sum of squares | df | Mean square | F ratio |
| <hr/>                            |                |    |             |         |
| Between                          | 47535.09       | 1  | 47535.09    | 21.01   |
| Within                           | 81458.62       | 36 | 2262.74     | **      |
| Total                            | 128993.69      | 37 |             |         |

| Variable : Total female production |                |    |             |         |
|------------------------------------|----------------|----|-------------|---------|
|                                    | Sum of squares | df | Mean square | F ratio |
| <hr/>                              |                |    |             |         |
| Between                            | 13005.50       | 1  | 13005.50    | 5.65    |
| Within                             | 82909.50       | 36 | 2303.04     | *       |
| Total                              | 95915.00       | 37 |             |         |



TABLE 70, (continued)

## Variable : Total progeny production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 10812.66       | 1  | 10812.66    | 4.55    |
| Within  | 85646.33       | 36 | 2379.07     | *       |
| Total   | 96459.25       | 37 |             |         |

## Variable : Total post-reproductive period

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 354.10         | 1  | 354.10      | 70.12   |
| Within  | 181.79         | 36 | 5.05        | **      |
| Total   | 535.89         | 37 |             |         |

## Variable : Post-reproductive period for female progeny

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 920.23         | 1  | 920.23      | 168.48  |
| Within  | 196.63         | 36 | 5.46        | **      |
| Total   | 1116.87        | 37 |             |         |

TABLE 71. Analysis of variance table for comparison of reproductive variables between the continuous and 1 hour limited cohorts, exposed to D.\_\_\_\_melanogaster (WO strain), January, 1980.

TABLE 71, (continued)

## Variable : Length of life

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 49.31          | 1  | 49.31       | 3.59    |
| Within  | 480.41         | 35 | 13.73       |         |
| Total   | 539.73         | 36 |             |         |

## Variable : Days of male production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 29.79          | 1  | 29.79       | 11.11   |
| Within  | 93.88          | 35 | 2.68        | **      |
| Total   | 123.66         | 36 |             |         |

## Variable : Days of female production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 54.56          | 1  | 54.56       | 11.09   |
| Within  | 172.18         | 35 | 4.92        | **      |
| Total   | 226.76         | 36 |             |         |

## Variable : Total male production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 40099.56       | 1  | 40099.56    | 17.66   |
| Within  | 79489.00       | 35 | 2271.11     | **      |
| Total   | 119588.56      | 36 |             |         |

TABLE 71, (continued)

## Variable : Total female production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 0.28           | 1  | 0.28        | 0.00    |
| Within  | 98691.31       | 35 | 2819.75     |         |
| Total   | 98691.56       | 36 |             |         |

## Variable : Total progeny production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 40309.87       | 1  | 40309.87    | 11.10   |
| Within  | 127093.63      | 35 | 3631.25     | **      |
| Total   | 167403.44      | 36 |             |         |

## Variable : Total post-reproductive period

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 155.78         | 1  | 155.78      | 15.24   |
| Within  | 357.79         | 35 | 10.22       | **      |
| Total   | 513.57         | 36 |             |         |

## Variable : Post-reproductive period for female progeny

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 207.65         | 1  | 207.65      | 14.86   |
| Within  | 489.05         | 35 | 13.97       | **      |
| Total   | 696.70         | 36 |             |         |

TABLE 72. Analysis of variance table for comparison of reproductive variables between the unfertilized and fertilized cohorts of L. boulandi exposed to D. simulans.

| Variable : Length of life |                |    |             |         |
|---------------------------|----------------|----|-------------|---------|
|                           | Sum of squares | df | Mean square | F ratio |
| Between                   | 21.02          | 1  | 21.02       | 3.03    |
| Within                    | 263.35         | 38 | 6.93        |         |
| Total                     | 284.37         | 39 |             |         |

| Variable : Total progeny production |                |    |             |         |
|-------------------------------------|----------------|----|-------------|---------|
|                                     | Sum of squares | df | Mean square | F ratio |
| Between                             | 25553.05       | 1  | 25553.05    | 20.63   |
| Within                              | 47074.69       | 38 | 1238.81     |         |
| Total                               | 72627.69       | 39 |             | **      |

TABLE 73. Analysis of variance table for comparison of reproductive variables between the unfertilized and fertilized cohorts of L. heterotoma exposed to D. simulans.

---

| Variable : Length of life |                |    |             |         |
|---------------------------|----------------|----|-------------|---------|
|                           | Sum of squares | df | Mean square | F ratio |
| <hr/>                     |                |    |             |         |
| Between                   | 24.03          | 1  | 24.03       | 5.99    |
| Within                    | 148.33         | 37 | 4.01        | *       |
| Total                     | 172.36         | 38 |             |         |

| Variable : Total progeny production |                |    |             |         |
|-------------------------------------|----------------|----|-------------|---------|
|                                     | Sum of squares | df | Mean square | F ratio |
| <hr/>                               |                |    |             |         |
| Between                             | 97.74          | 1  | 97.74       | 0.03    |
| Within                              | 108469.00      | 37 | 2931.59     |         |
| Total                               | 108566.69      | 38 |             |         |

TABLE 74. Analysis of variance table for comparison of reproductive variables between the fertilized cohorts of L. heterotoma and L. boulardi, exposed to D. simulans.

TABLE 74, (continued)

## Variable : Length of life

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 12.47          | 1  | 12.47       | 2.37    |
| Within  | 183.86         | 35 | 5.25        |         |
| Total   | 196.32         | 36 |             |         |

## Variable : Days of male production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 3.54           | 1  | 3.54        | 1.33    |
| Within  | 92.75          | 35 | 2.65        |         |
| Total   | 96.29          | 36 |             |         |

## Variable : Days of female production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 58.93          | 1  | 58.93       | 7.98    |
| Within  | 258.31         | 35 | 7.38        | **      |
| Total   | 317.24         | 36 |             |         |

## Variable : Total male production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 1066.58        | 1  | 1066.58     | 1.22    |
| Within  | 30557.42       | 35 | 873.07      |         |
| Total   | 31624.00       | 36 |             |         |



TABLE 74, (continued)

## Variable : Total female production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 3965.50        | 1  | 3965.50     | 3.30    |
| Within  | 42003.50       | 35 | 1200.10     |         |
| Total   | 45969.00       | 36 |             |         |

## Variable : Total progeny production

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 9145.24        | 1  | 9145.24     | 5.85    |
| Within  | 54669.61       | 35 | 1561.99     | *       |
| Total   | 63814.85       | 36 |             |         |

## Variable : Total post-reproductive period

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 22.08          | 1  | 22.08       | 3.03    |
| Within  | 255.15         | 35 | 7.29        |         |
| Total   | 277.23         | 36 |             |         |

## Variable : Post-reproductive period for female progeny

|         | Sum of squares | df | Mean square | F ratio |
|---------|----------------|----|-------------|---------|
| Between | 155.62         | 1  | 155.62      | 11.64   |
| Within  | 347.55         | 35 | 9.93        | **      |
| Total   | 463.17         | 36 |             |         |

TABLE 75. Nonparametric analysis (Wilcoxon rank sum test) of total progeny production between the unfertilized and fertilized cohorts of L.\_\_\_\_boulardi exposed to D. melanogaster.

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| Cohort | Mean |
|--------|------|
|--------|------|

---

|              |        |
|--------------|--------|
| Unfertilized | 273.50 |
|--------------|--------|

|            |        |
|------------|--------|
| Fertilized | 148.29 |
|------------|--------|

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Wilcoxon Scores (Rank Sums)

| Cohort       | N | Sum of Scores | Expected Under H0 | Std dev Under H0 | Mean Score |
|--------------|---|---------------|-------------------|------------------|------------|
| Unfertilized | 6 | 57.00         | 42.00             | 7.00             | 9.50       |
| Fertilized   | 7 | 34.00         | 49.00             | 7.00             | 4.86       |

Wilcoxon 2-sample test (normal approximation)

s= 57.00      z= 2.21      prob > |z| 0.03

t-test approximate significance = 0.04

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