

PARTHENOGENETIC REPRODUCTION IN THE REPLETA SPECIES
GROUP OF THE GENUS DROSOPHILA

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PREFACE

This study is an investigation of parthenogenesis in the repleta species group of the genus Drosophila. The major objectives are to determine the ability of F_1 and F_2 virgin females to reproduce parthenogenetically and to establish parthenogenetic strains from impaternal females.

I wish to express my sincere gratitude to my thesis adviser, Dr. L. Herbert Bruneau, for his advice and constructive criticism. My appreciation is also expressed to the chairman of my committee, Dr. Kenneth Wiggins, for his continuous support and guidance. I am also indebted to Dr. Glenn Todd and Dr. Lloyd Wiggins for assistance in the preparation of this manuscript.

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CHAPTER I

INTRODUCTION

Parthenogenesis is a fairly common phenomenon in insects. Suomalainen (1962) in his review pointed out that thelytokous parthenogenesis, or the development of females from unfertilized eggs, is widespread but sporadic, that is, occurring in single species or races rather than being characteristic of larger groups. This suggests that many of the known cases of thelytoky are probably of recent origin, and that its successful development from bisexual forms, and the consequent loss of males, must have occurred many times.

The origin of parthenogenesis is, so far, obscure in its details. However, investigation on the flies of the family Drosophilidae reports the observation of parthenogenesis in the genus Drosophila. Stalker (1951, 1954) discovered a low rate of parthenogenesis in 23 species in a survey of 28 members of the genus Drosophila. Of these surveyed, three species; D. parthenogenetica, D. polymorpha and D. affinis produced adult progeny; and the other twenty species, impatenate individuals died in embryonic or larval stages. Carson (1961, 1962a) found a similar phenomenon in impatenate adults in two species. Further, Carson, Wheeler and Heed (1957), Murdy and Carson (1959) and Carson (1962b) found in Drosophila mangebeirae a wholly thelytokous species that is very widespread geographically and in which 60% of the eggs hatch; of these approximately 80% survive to the adult stage.

The studies of Stalker (1954, 1956) indicate that continued selection for parthenogenesis results, at least in the case of D. parthenogenetica, and probably many other species of Drosophila, in gradual increase in the rate of parthenogenesis over many generations. The condition, therefore, is probably based on a polygenic system. Also, the very low rates of parthenogenesis observed are of some potential value to the species in supplying the first step toward thelytoky. Its eventual development depends on the right combination of ecological and genetical factors at the right time. Carson (1967) directly demonstrated that low level facultative parthenogenesis can be built into major mode of reproduction by selection. Following discovery of a low rate (not above 1%) of facultative diploid thelytoky in several wild strains of Drosophila mercatorum, Carson was able to increase the rate artificially about 60-fold, or approximately 6%. The study tends to support the idea that the condition is based on a polygenic system. Stalker (1954) suggests that ultimately, isolated parthenogenetic strains might arise with a rather complete sort of reproductive isolation in which thelytokous females might refuse to mate with fertile males, or might become structurally or physiologically unable to use the sperm they receive in such matings. Also, Carson (1961) regards the existence of a low rate of genetically based parthenogenesis, such as found in D. parthenogenetica, D. polymorpha and D. robusta, as possibly representing an evolutionary stage through which the obligatory parthenogenetic species D. mangabeirae may have passed during the evolution of its parthenogenesis.

In a study of a parthenogenetic strain of D. mercatorum, Henslee (1966) found natural sexual isolation arose in the absence of any selection for isolation. Further, sexual isolation was enhanced in one

strain by artificial selection. Ikeda and Carson (1973) were successful in increasing the reluctance to mate on the part of parthenogenetically produced females of D. mercatorum. They found significant differences between an original parthenogenetic unselected strain and a selected one after the first cycle of selection, and further reluctance to mate increased with the second selection cycle. These facts give strength to the views of Stalker (1954) and Carson (1961, 1967) that wholly parthenogenetic strain of flies may develop when a male shortage or some form of sexual isolation exists.

The early views of Darlington (1937), White (1948) and Suomalainen (1950) suggests that parthenogenesis in the animal kingdom is an "evolutionary dead end" and the fate of parthenogenetic groups is extinction. Traditionally it is thought the parthenogenetic systems lead an organism into obligatory, and uniform homozygosity, rigidly fixed heterozygosity, or some other evolutionary dead end. Recent studies by Carson (1967, 1973), Carson, Wei and Niederkorn (1967), Carson and Snyder (1972) and Asher (1970) present contrasting views in which parthenogenetic reproducing animals may retain genetic plasticity. Further studies by White (1970), Smith (1971) and Suomalainen and Saura (1973) concludes that the evolutionary possibilities of parthenogenetic animals have been underestimated -- the relative rarity of parthenogenesis has been explained away too easily by theorizing that it is a blind alley of evolution because parthenogenetic animals cannot respond to a changing environment.

Since the discovery of facultative parthenogenesis and the theoretical importance of this subject by Stalker (1951, 1954), Carson (1961, 1962a, 1967, 1973), Carson, Wheeler and Heed (1957), little attention

has been given to how widespread the ability of natural populations to reproduce parthenogenetically really exists. The present investigation presents data bearing on the question in selected members of the repleta group of Drosophila species.

Statement of the Problem

Parthenogenesis in Drosophila was first discovered in a strain of D. parthenogenetica by Stalker (1951). One of the questions arising from the study, and the problem of this study, is whether parthenogenetic reproduction is widespread in the genus Drosophila. Even in genetically well-investigated species rare parthenogenetic development might be over-looked, especially if terminated with death in embryonic or early larval life. The purpose of this study was two-fold. The first objective was to determine the ability of F_1 and F_2 virgin females of natural populations, of the repleta group of the genus Drosophila to reproduce parthenogenetically. The second objective was to establish parthenogenetic strains from this group if they do reproduce parthenogenetically.

The recent studies of Asher (1970) and Carson (1973) appear to contradict the general opinion that parthenogenetic species represent a dead end because of their inability to maintain genetic plasticity. Their studies indicate that automictic parthenogenetic reproduction can sustain varying degrees of genetic plasticity, provided selection favors the heterozygote, and they emphasize parthenogenetic reproduction as an important evolutionary means. The amount of parthenogenetic reproduction, if present in the repleta species group would give an indication of how widespread the phenomenon is and the possible importance in the evolution within the genus Drosophila.

CHAPTER II

MATERIALS AND METHODS

The flies used in this investigation were limited to certain species in the repleta species group of the subgenus Drosophila Fallen.

Collection of Flies

The repleta species group is the largest of any group of Drosophila. Patterson and Stone (1952) placed fifty-two different forms in this species group, including three pairs of subspecies. Fifteen species are endemic to the Neartic region and fifteen to the Neotropical, thirteen are common to both regions, and six are cosmopolitan. All but two of the forty-nine species are represented in the Neartic and Neotropical regions, indicating, as a group this complex of species was originally native to and evolved in the new world. Further cytotaxonomic studies by Wasserman (1954, 1960, 1962, 1963) have demonstrated phylogenetic relationships among 46 species with 68 species placed in the repleta group. The distribution maps of Patterson and Wagner (1943); Patterson and Mainland (1944) and Patterson and Stone (1952) illustrates the concentration of the repleta group in and around the transition tract between the Neartic and Neotropical regions in Mexico. Several collected species are also recorded in various semi-tropical areas of Florida and California.

The geographical range and types of habitats of the repleta group are very diverse and contains both "wild" and "domestic" species. Dobzhansky (1965) describes "domestic" species as "those occurring near human habitations, gardens, orchards, places of storage of food products, and garbage dumps and are not found in habitats reasonably remote from such places". The highly successful pathenogenetic strains of D. mercatorum, reported by Carson (1962a, 1967, 1973), belong to the repleta group and are found as a "domestic" species in the United States and as a "wild" species in Mexico, Central America and South America.

Collections were made in widely diverse areas of Mexico and the lower Rio Grande Valley in Texas. The geographic origins are shown in Figure 1. The flies used in this study are limited mainly to the areas of highest concentration and are mainly "domestic" species from those areas.

Drosophila collections were made by sweeping with an insect net. Collection sites were refuse containers alongside the highways, garbage containers and fruits in produce markets, and yeasted banana baits placed at various locations around camping areas of state parks. Collections were made regularly from the banana baits early in the morning and the late afternoon when collection numbers are usually highest for Drosophila. All flies collected were etherized lightly, sexed and tentatively classified under a dissecting microscope. Final identification was completed in the laboratory using keys in Patterson (1943), Patterson and Wagner (1943), Patterson and Mainland (1944) and Wheeler (1954).

The natural population-caught females were put on Instant Drosophila Medium (Carolina Biological Supply) while in the field and transferred

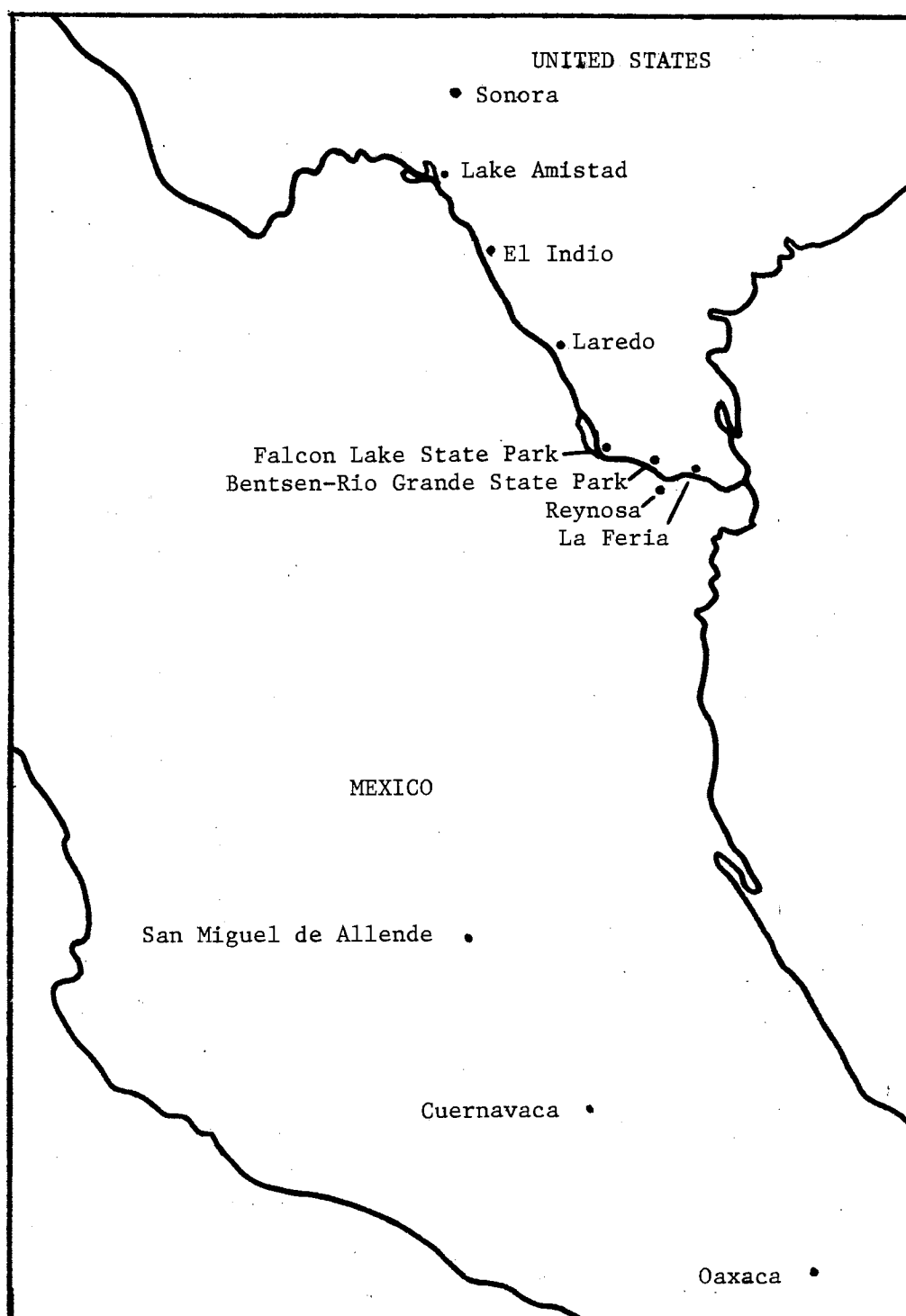


Figure 1. Drosophila Collection Areas

to well-yeasted cornmeal-molasses-agar medium when returning to the laboratory. The natural population-caught males were discarded or kept in separate containers so none of the natural population-caught females mated after collecting in the laboratory.

A total of nine species and nineteen strains of the repleta group of Drosophila were collected and tested for parthenogenetic development. The species, geographic origin of the strain and the collection site are given in Tables I - IX. They will be hereafter referred to by the letter designation shown in the tables.

TABLE I
STRAINS OF DROSOPHILA ALDRICHI USED IN THE STUDY

Geographic Origin of Strain	Symbol Used in This Paper	Collection Site
La Feria, Texas	LF	Garbage Can
Laredo, Texas	L	Baits
Reynosa, Tamaulipas, Mexico	R	Garbage Can

TABLE II
STRAINS OF DROSOPHILA HAMATOFILA USED IN THE STUDY

Geographic Origin of Strain	Symbol Used in This Paper	Collection Site
Lake Amistad, Texas	A	Baits
El Indio, Texas	Y	Yucca Blossoms
Sonora, Texas	S	Baits

TABLE III
STRAINS OF DROSOPHILA HYDEI USED IN THE STUDY

Geographic Origin of Strain	Symbol Used in This Paper	Collection Site
Cuernavaca, Morelos, Mexico	C	Garbage Can
La Feria, Texas	LF	Produce Market
Oaxaca, Oaxaca, Mexico	O	Baits

TABLE IV
STRAINS OF DROSOPHILA HYDEOIDES USED IN THE STUDY

Geographic Origin of Strain	Symbol Used in This Paper	Collection Site
Bentsen-Rio Grande State Park, Texas	B	Baits

TABLE V
STRAINS OF DROSOPHILA LONGICORNIS USED IN THE STUDY

Geographic Origin of Strain	Symbol Used in This Paper	Collection Site
San Miguel de Allende, Guanajuato, Mexico	SMA	Baits
Bentsen-Rio Grande State Park, Texas	B	Baits

TABLE VI
STRAINS OF DROSOPHILA MERIDIANA USED IN THE STUDY

Geographic Origin of Strain	Symbol Used in This Paper	Collection Site
San Miguel de Allende, Guanajuato, Mexico	SMA	Baits
La Feria, Texas	LF	Produce Market

TABLE VII
STRAINS OF DROSOPHILA MULLERI USED IN THE STUDY

Geographic Origin of Strain	Symbol Used in This Paper	Collection Site
Bentsen-Rio Grande State Park, Texas	B	Baits
La Feria, Texas	LF	Produce Market
Falcon Lake State Park, Texas	F	Baits

TABLE VIII
STRAINS OF DROSOPHILA MERIDIANA RIOENSIS USED IN THE STUDY

Geographic Origin of Strain	Symbol Used in This Paper	Collection Site
Falcon Lake State Park, Texas	F	Baits

TABLE IX
STRAINS OF DROSOPHILA SPENCERI USED IN THE STUDY

Geographic Origin of Strain	Symbol Used in This Paper	Collection Site
Laredo, Texas	L	Baits

Origin of Experimental Stocks

The observations and experiments were carried out on F_1 and F_2 stocks derived from the natural population stocks collected. The females of each species, or strain of a species collected, were cultured in half pint milk bottles containing a standard well-yeasted cornmeal-molasses-agar medium (see Strickberger, 1962). The flies were changed to fresh food three times per week. When the number of F_1 females was large enough they were used in parthenogenetic development tests. In those species that the total number of F_1 females was too small; all F_1 males and females were kept in a mass culture to produce an F_2 generation. Tests using F_1 and F_2 females were identical for the rest of the experiments reported.

Testing Schedule

Adult flies were collected from the culture bottles that had been cleared of adult flies within a twenty-four hour period prior to collecting time. Flies collected at this time were thus 0 to 24 hours old. The flies that were small in size or had obvious defects were discarded at that time. Fifteen newly emerged females were collected (etherized lightly and sexed under microscope). Only ten of these were tested; the others were discarded unless needed for replacement of losses or deaths.

All flies were reared and tested at $25 \pm 2^\circ$ C. Flies were aged seven days from the time of emergence on well-yeasted cornmeal-agar medium with no paper in the vials. Aging flies were put on fresh food on the fourth day. At testing, females were no less than seven, no more than eight days old when they went into the first egg-laying vial. On

the seventh day, groups of ten virgin females were placed in single 95mm x 25mm, well-yeasted food vials containing no paper. Flies were changed to fresh food and allowed to oviposit every 48 hours for a period of ten changes. The empty vials, containing the eggs laid by these virgins, were kept for a period of not less than 30 days to determine if any of the eggs developed into an impaternate adult. The time for development from egg to adult for most species is less than 16-18 days at 25° C.

Ten tests, of groups of 10 females, were run for a total of 100 females of each species or strain tested. The vials from which the females had been transferred were examined daily under a dissecting microscope up to and including the fourth day after oviposition. The presence of dead embryos, pupae and living impaternate adults were observed and recorded daily. The dead embryos were detected by the mottled-looking brownish-black discoloration associated with their decomposition. This method of detecting early embryonic development would of course result in the missing of those cases in which embryonic development was terminated very early, or in which no discoloration occurred, and should thus give an underestimate rather than an overestimation of the frequency of embryonic development.

Vials were examined several times a week for the emergence of adult flies. When such a fly was found, the following procedure was carried out. The fly was isolated, etherized and examined for any morphological peculiarities. If it was reasonably freshly emerged, this fact could be noted because it takes several days for a specimen of the species that produced impaternate flies to attain the body color characteristic of the adult. The food was systematically searched until the empty pupa case from which the fly emerged was found. All

information obtained on each impaternate fly was recorded (See Appendix A).

Estimates of Parthenogenetic Rate

Estimates of rates of parthenogenetic reproduction were made by isolating a sample of five virgin females of species or strain to be tested. The females were collected and aged to seven days using the same procedures as used with the regular tested virgin females. Each female to be tested was provided with a vial of food with a small lump of yeast for 24 hours. The eggs laid during this period were counted under a dissecting microscope. The procedure was repeated for 20 such periods. The total eggs laid for the 20 periods were tabulated for each of the five virgin females tested. A mean number of eggs laid per female for 20 periods was computed from the five females tested (See Appendix B). The total number of eggs screened for all females of each species or strain was estimated by (a) multiplying the mean number of eggs laid per female per 20 periods by (b) the number of females tested. The rate of parthenogenesis is then expressed in percent unfertilized eggs giving rise in impaternate offspring or in terms of offspring per million eggs.

Establishment of Parthenogenetic Strains

Each impaternate adult female fly was used in an attempt to establish a wholly parthenogenetic strain of flies. Isolated females were put in vials containing well-yeasted food. Flies were changed to a fresh vial of food after a 48 hour period. The procedure was repeated for ten changes as the fly was challenged to produce a unisexual strain of flies.

Observations for embryos, pupa or impaternate flies were maintained and recorded the same as with the bisexual strains (See Appendix A). After the tests for parthenogenetic development, the impaternate females were placed in vials with males of the same strain to determine fertility levels.

CHAPTER III

RESULTS AND DISCUSSION

Results

The data resulting from all of the tests for parthenogenetic development are summarized in Tables X-XVIII. The number of unfertilized eggs examined are estimated from the fecundity tests given to individual females (See Appendix B).

Parthenogenetic Development in *Drosophila* *aldrichi*

The data in Table X indicate no parthenogenetic development in *D. aldrichi*. None of the virgin females of the three strains of *D. aldrichi* would lay eggs. No eggs were observed in any of the tests using groups of ten virgin females or the fecundity rate tests using single virgin females in vials.

Parthenogenetic Development in *Drosophila* *hamatofila*

The three strains of *Drosophila hamatofila* collected and tested have the results summarized in Table XI. Both the F_1 and F_2 generations of virgin females were capable of producing offspring that developed to the larval stage, but none lived to the adult stage.

TABLE X
RATES OF PARTHENOGENETIC DEVELOPMENT
IN DROSOPHILA ALDRICHI

Strain	Generation	Total Unfertilized Eggs Examined	Dead Embryos	Total Dead Larvae	Total Adults
LF	F ₂	0			
L	F ₂	0			
R	F ₂	0			

TABLE XI
RATES OF PARTHENOGENETIC DEVELOPMENT
IN DROSOPHILA HAMATOFILA

Strain	Generation	Total Unfertilized Eggs Examined	Dead Embryos	Total Dead Larvae	Total Adults
A	F ₁	35,560	+	0	0
Y	F ₂	53,960	+	2	0
S	F ₁	55,700	+	1	0

(+) Indicates observed

(-) Indicates not observed

Parthenogenetic Development in *Drosophila hydei*

The parthenogenetic development tests of the three strains of *Drosophila hydei* are summarized in Table XII. All three strains were capable of producing offspring that developed to the larval stage, one of the larvae developed to the pupa stage before death, and one strain produced two viable adults. The characteristics of those adults are reported elsewhere in this paper.

TABLE XII
RATES OF PARTHENOGENETIC DEVELOPMENT
IN *DROSOPHILA HYDEI*

Strain	Generation	Total Unfertilized Eggs Examined	Dead Embryos	Total Dead Larvae	Total Adults
C	F ₁	55,260	+	5	2
LF	F ₂	86,660	+	2	0
O	F ₂	72,720	+	1	0

(+) Indicates observed

(-) Indicates not observed

Parthenogenetic Development in *Drosophila*
hydeoides

Only one strain of *Drosophila hydeoides* was collected and tested for parthenogenetic development. The summarized results are given in

Table XIII. Development in this strain progressed to the larval stage before dying.

TABLE XIII
RATES OF PARTHENOGENETIC DEVELOPMENT
IN DROSOPHILA HYDEOIDES

Strain	Generation	Total Unfertilized Eggs Examined	Dead Embryos	Total Dead Larvae	Total Adults
B	F ₂	15,520	+	1	0

(+) Indicates observed

(-) Indicates not observed

Parthenogenetic Development in Drosophila

longicornis

Drosophila longicornis parthenogenetic development data are summarized in Table XIV. Only the F₂ generations were tested because of small numbers collected, in one strain, and the low fecundity rate of the other strain. Only one strain was capable of any parthenogenetic development.

Parthenogenetic Development in Drosophila

meridiana

The summarized data in Table XV indicate that both Drosophila meridiana strains tested had eggs start parthenogenetic development,

but none of the eggs developed to the larval stage.

TABLE XIV
RATES OF PARTHENOGENETIC DEVELOPMENT
IN DROSOPHILA LONGICORNIS

Strain	Generation	Total Unfertilized Eggs Examined	Dead Embryos	Total Dead Larvae	Total Adults
SMA	F ₂	23,980	+	0	0
B	F ₂	9,080	-	0	0

(+) Indicates observed
(-) Indicates not observed

TABLE XV
RATES OF PARTHENOGENETIC DEVELOPMENT
IN DROSOPHILA MERIDIANA

Strain	Generation	Total Unfertilized Eggs Examined	Dead Embryos	Total Dead Larvae	Total Adults
SMA	F ₂	11,700	+	0	0
LF	F ₂	25,880	+	0	0

(+) Indicates observed
(-) Indicates not observed

Parthenogenetic Development in Drosophila

mulleri

The summarized data in Table XVI indicate that Drosophila mulleri has a high fecundity rate and parthenogenetic development, to the larval stage, existed in all three strains tested. Data are presented elsewhere in this paper concerning the impaternal female of the B strain.

TABLE XVI
RATES OF PARTHENOGENETIC DEVELOPMENT
IN DROSOPHILA MULLERI

Strain	Generation	Total Unfertilized Eggs Examined	Dead Embryos	Total Dead Larvae	Total Adults
B	F ₂	42,740	+	2	1
LF	F ₁	21,440	+	1	0
F	F ₂	24,960	+	1	0

(+) Indicates observed

(-) Indicates not observed

Parthenogenetic Development in Drosophila

meridiana rioensis

The results of the one strain of Drosophila meridiana rioensis tested for parthenogenetic development are presented in Table XVII. The data indicate a low fecundity rate but larval stage of development

was observed. The fecundity rate may be underestimated as the flies appeared to oviposit more eggs when in groups of ten than when only one fly was in a vial for egg counts.

TABLE XVII
RATES OF PARTHENOGENETIC DEVELOPMENT
DROSOPHILA MERIDIANA RIOENSIS

Strain	Generation	Total Unfertilized Eggs Examined	Dead Embryos	Total Dead Larvae	Total Adults
F	F ₂	8,620	+	1	0

(+) Indicates observed
(-) Indicates not observed

Parthenogenetic Development in Drosophila
spenceri

The summarized data in Table XVIII indicates a low level of fecundity and parthenogenetic development to the embryo stage in the one strain of Drosophila spenceri collected and tested.

TABLE XVIII
RATES OF PARTHENOGENETIC DEVELOPMENT
IN DROSOPHILA SPENCERI

Strain	Generation	Total Unfertilized Eggs Examined	Dead Embryos	Total Dead Larvae	Total Adults
L	F ₂	12,400	+	0	0

(+) Indicates observed
(-) Indicates not observed

Impaternate Drosophila

From one of the three strains of Drosophila hydei (Table XII), two impaternate females were obtained from approximately 55,260 eggs, a rate of approximately 36.19 per million eggs. One of the two flies appears to have been fully fertile, and the other, completely sterile. The reproductive system of the sterile female was dissected out in saline solution and examined. The ovaries apparently had not developed and no eggs were present. Notes on the characteristics and fertility level of these females will be found in Table XIX.

One of the three strains of Drosophila mulleri (Table XVI) produced one impaternate female from approximately 42,740 eggs for a rate of 23.39 flies per million eggs. The fly, when mated, produced many offspring of both sexes but produced no parthenogenetic offspring. Notes on the characteristics are summarized in Table XIX. All of the three impaternate females were apparently diploid. Carson (personal communication) found

TABLE XIX

FERTILITY AND OTHER CHARACTERISTICS OF IMPATERNATE DROSOPHILA

Strain-Species	Fertility	Morphological Abnormalities	Remarks
C- <u>hydei</u> #1	Sterile	Ovaries not developed	
C- <u>hydei</u> #2	Fertile; produced many offspring of both sexes when mated	None	Laid eggs as virgin, none developed
B- <u>mulleri</u>	Fertile; produced many offspring of both sexes when mated	None	Laid eggs as virgin; one larva developed

that diploid females are readily distinguished by the spacing and size of the hairs on the wing blade. Since each hair is derived from a single cell, a count of the number of hairs per unit space gives the cell size and hence indicates whether diploidy or polyploidy is present.

Discussion

The results of the study indicate that F_1 or F_2 generations, of two of the nine species, of the natural population-caught flies, of the repleta species group, possessed the capability to reproduce parthenogenetically, and three of the other species had strains that developed to the larval stage. Eight of the nine species had some parthenogenetic embryonic development. The adult impaternate females, of the two species that reproduced parthenogenetically; failed to reproduce any offspring parthenogenetically, however; both species reproduced bisexually when mated.

It is especially interesting that F_1 virgin females of natural population-caught flies are capable of reproducing parthenogenetically. This is particularly important because if the virgin females had developed in a natural habitat and no males were present; they may have reproduced parthenogenetically in natural surroundings. The fertility of the impaternate females suggests the likelihood that they arose through automictic fusion of meiotic nuclei in the cytoplasm of the unfertilized egg (See Stalker, 1954, 1956; Carson, Wheeler and Heed, 1957; Murdy and Carson, 1959; Metz, 1959; Sprackling, 1960). It is not possible to say definitely whether the impaternate flies were diploid or not, however, the genetic state accompanying parthenogenesis appears to be a stable one, this is manifested by the fertility of two of the females. Also,

the wing size would indicate a diploid state (Carson, personal communication).

The C strain of D. hydei developed two impaternate females and all three strains tested produced parthenogenetic development to the larval stage. The strains were from widely separated geographical locations so such a finding does not preclude the possibility of the existence of strains with greater parthenogenetical potential, but nevertheless it would appear that the finding is not due to a single, locally peculiar situation. The findings appear to be consistent with the results of Stalker (1954) as he reported parthenogenetic development to the larval stage in a strain of D. hydei from the St. Louis, Missouri area.

The three strains of Drosophila mulleri were all from the lower Rio Grande Valley in Texas and were not widely separated geographically as were the D. hydei strains. The results were consistent as expected as all three strains had parthenogenetic development to the larval stage and the B strain developed a viable impaternate adult female.

Laboratory experiments on parthenogenetic development in small populations can, of course, only be indicative and not demonstrative of events in nature. They can, however, show what might happen, rather than what had happened, in wild populations. The investigator can only estimate the rate of parthenogenetic development potential as may occur in a natural population. Natural parthenogenetic reproduction exists in the F_1 or F_2 generation of natural population-caught females in two species of the repleta group, and parthenogenetic development to the larval stage was present in three of the nine species tested. All but one of the tested species exhibited embryonic development. These facts indicate that the probability of low rates of parthenogenetic

reproductive behavior might occur in several species of the repleta group of the genus Drosophila. They also strengthen the view of Stalker (1954) that they are of some potential value in supplying the first step toward thelytoky, its eventual development depends on the right combination of ecological and genetical factors at the right time.

CHAPTER IV

SUMMARY

1. Studies were made to determine if virgin F_1 or F_2 females of natural population-caught flies, of the repleta group of the genus Drosophila, would reproduce parthenogenetically and if impaternate females would reproduce parthenogenetically.
2. Experiments using 10 groups of 10 virgin females, of 19 strains, of nine species of the repleta group, were tested for parthenogenetic development.
3. Of the nine species tested for parthenogenetic development, eight species exhibited embryonic development, five species developed to the larval stage and two species produced impaternate females.
4. None of the impaternate females reproduced any impaternate offspring but two of the three reproduced viable offspring bisexually when mated.
5. From one of the three strains of D. hydei, two impaternate females were obtained from 55,260 eggs; a rate of approximately 36.19 per million unfertilized eggs laid. One female was fertile and one was sterile.
6. One impaternate fertile female developed from approximately 42,740 unfertilized eggs laid by virgin D. mulleri females. The rate of parthenogenetic reproduction in the strain was 23.39 flies per million eggs.

7. All three adult impaternate flies were diploid.

8. The evidence indicates the probability that low rates of parthenogenetic reproductive behavior might occur in several species of the repleta group of the genus Drosophila.

9. The present study gives strength to the views of Stalker that the observed low rates of parthenogenetic reproduction has potential value in supplying the first step toward thelytoky.

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APPENDIX A
FORM USED IN RECORDING PARTHENOGENETIC
DEVELOPMENT

PARTHENOGENETIC DEVELOPMENT

SPECIES: _____

STRAIN: _____

CYCLE: day 0 : clear
day 1 : collect
day 4 : change
days 8-27 : test days
day 27 : discard

Test Number: _____

Date of Collection:

Date of Test Starting:

Date of Test Ending:

Number of Adult Females: _____

Number of Adult Males: _____

Number of Larvae: _____

Embryonic Development: _____

Notes:

APPENDIX B
ESTIMATES OF FECUNDITY RATES IN
VIRGIN DROSOPHILA

TABLE XX

FECUNDITY RATE IN VIRGIN LF STRAIN
DROSOPHILA ALDRICHI

Date of Collection: 6/6

Date of Test Starting: 6/13

Date of Test Ending: 7/3

Eggs/Vial

Day	Female No. 1	Female No. 2	Female No. 3	Female No. 4	Female No. 5
1	0	0	0	0	0
2	0	0	0	0	0
3	0	0	0	0	0
4	0	0	0	0	0
5	0	0	0	0	0
6	0	0	0	0	0
7	0	0	0	0	0
8	0	0	0	0	0
9	0	0	0	0	0
10	0	0	0	0	0
11	0	0	0	0	0
12	0	0	0	0	0
13	0	0	0	0	0
14	0	0	0	0	0
15	0	0	0	0	0
16	0	0	0	0	0
17	0	0	0	0	0
18	0	0	0	0	0
19	0	0	0	0	0
20	0	0	0	0	0
Totals:	0	0	0	0	0

Grand Total: 0

Mean Number Eggs/Female/20 days: 0

Mean Number Eggs/Female/Day: 0

Estimated Number Eggs/100 Females/20 Days: 0

TABLE XXI

FECUNDITY RATE IN VIRGIN L STRAIN
DROSOPHILA ALDRICHI

Date of Collection: 6/7

Date of Test Starting: 6/14

Date of Test Ending: 7/4

Eggs/Vial

Day	Female No. 1	Female No. 2	Female No. 3	Female No. 4	Female No. 5
1	0	0	0	0	0
2	0	0	0	0	0
3	0	0	0	0	0
4	0	0	0	0	0
5	0	0	0	0	0
6	0	0	0	0	0
7	0	0	0	0	0
8	0	0	0	0	0
9	0	0	0	0	0
10	0	0	0	0	0
11	0	0	0	0	0
12	0	0	0	0	0
13	0	0	0	0	0
14	0	0	0	0	0
15	0	0	0	0	0
16	0	0	0	0	0
17	0	0	0	0	0
18	0	0	0	0	0
19	0	0	0	0	0
20	0	0	0	0	0
Totals:	0	0	0	0	0

Grand Total: 0

Mean Number Eggs/Female/20 Days: 0

Mean Number Eggs/Female/Day: 0

Estimated Number Eggs/100 Females/20 Days: 0

TABLE XXII

FECUNDITY RATE IN VIRGIN R STRAIN
DROSOPHILA ALDRICHI

Date of Collection: 6/6

Date of Test Starting: 6/13

Date of nest Ending: 7/3

Eggs/Vial

Day	Female No. 1	Female No. 2	Female No. 3	Female No. 4	Female No. 5
1	0	0	0	0	0
2	0	0	0	0	0
3	0	0	0	0	0
4	0	0	0	0	0
5	0	0	0	0	0
6	0	0	0	0	0
7	0	0	0	0	0
8	0	0	0	0	0
9	0	0	0	0	0
10	0	0	0	0	0
11	0	0	0	0	0
12	0	0	0	0	0
13	0	0	0	0	0
14	0	0	0	0	0
15	0	0	0	0	0
16	0	0	0	0	0
17	0	0	0	0	0
18	0	0	0	0	0
19	0	0	0	0	0
20	0	0	0	0	0
Totals:	0	0	0	0	0

Grand Total: 0

Mean Number Eggs/Female/20 Days: 0

Mean Number Eggs/Female/Day: 0

Estimated Number Eggs/100 Females/20 Days: 0

TABLE XXIII
FECUNDITY RATE IN VIRGIN A STRAIN
DROSOPHILA HAMATOFILA

Date of Collection: 6/7

Date of Test Starting: 6/14

Date of Test Ending: 7/4

Eggs/Vial

Day	Female No. 1	Female No. 2	Female No. 3	Female No. 4	Female No. 5
1	0	0	0	0	29
2	0	0	0	0	20
3	0	0	12	0	39
4	33	0	23	0	0
5	34	0	2	39	32
6	0	0	0	0	0
7	0	0	20	61	0
8	0	0	25	70	0
9	0	0	9	0	0
10	48	0	50	63	29
11	19	0	18	13	20
12	38	49	41	57	0
13	31	0	27	69	0
14	50	0	45	60	13
15	51	0	50	58	31
16	69	55	21	65	0
17	0	0	0	0	27
18	0	0	0	0	0
19	13	0	31	36	0
20	15	0	27	32	9

Totals:	401	104	401	623	249
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Grand Total: 1,778

Mean Number Eggs/Female/20 Days: 355.6

Mean Number Eggs/Female/Day: 17.78

Estimated Number Eggs/100 Females/20 Days: 35,560

TABLE XXIV
FECUNDITY RATE IN VIRGIN Y STRAIN
DROSOPHILA HAMATOFILA

Date of Collection: 6/6

Date of Test Starting: 6/13

Date of Test Ending: 7/3

Eggs/Vial

Day	Female No. 1	Female No. 2	Female No. 3	Female No. 4	Female No. 5
1	0	0	0	0	0
2	0	0	0	0	0
3	0	0	0	0	33
4	0	0	18	0	31
5	0	0	27	24	28
6	0	0	18	0	30
7	0	0	18	32	55
8	31	14	51	43	43
9	22	0	20	19	47
10	0	21	53	79	65
11	34	0	69	24	62
12	25	0	49	19	41
13	51	0	30	49	80
14	51	60	40	65	76
15	66	68	36	72	68
16	52	28	45	92	51
17	0	25	11	36	54
18	44	0	5	35	42
19	48	0	0	65	25
20	0	0	4	29	50
Totals:	424	216	494	683	881

Grand Total: 2,698

Mean Number Eggs/Female/20 Days: 539.6

Mean Number Eggs/Female/Day: 26.98

Estimated Number Eggs/100 Females/20 Days: 53,960

TABLE XXV
FECUNDITY RATE IN VIRGIN S STRAIN
DROSOPHILA HAMATOFILA

Date of Collection: 6/6

Date of Test Starting: 6/13

Date of Test Ending: 7/3

Eggs/Vial

Day	Female No. 1	Female No. 2	Female No. 3	Female No. 4	Female No. 5
1	0	0	0	0	0
2	0	0	0	0	0
3	46	0	0	42	0
4	52	0	0	51	29
5	44	0	0	37	0
6	50	0	19	56	0
7	71	0	17	50	54
8	0	40	0	51	68
9	59	9	0	12	0
10	74	39	0	3	4
11	0	0	40	2	0
12	52	53	66	78	72
13	48	39	61	40	52
14	60	75	71	71	45
15	75	60	50	0	0
16	15	0	71	50	0
17	64	76	49	0	0
18	77	42	48	0	0
19	0	53	1	27	17
20	0	28	32	44	4
Totals:	787	514	525	614	345

Grand Total: 2,785

Mean Number Eggs/Female/20 Days: 557.0

Mean Number Eggs/Female/Day: 27.85

Estimated Number Eggs/100 Females/20 Days: 55,700

TABLE XXVI
FECUNDITY RATE IN VIRGIN C STRAIN
DROSOPHILA HYDEI

Date of Collection: 3/20

Date of Test Starting: 3/27

Date of Test Ending: 4/16

Eggs/Vial

Day	Female No. 1	Female No. 2	Female No. 3	Female No. 4	Female No. 5
1	46	43	66	54	62
2	19	52	18	0	32
3	40	45	12	46	33
4	5	20	45	5	0
5	30	73	37	39	0
6	0	39	18	7	0
7	18	43	1	21	54
8	0	66	82	19	0
9	20	25	30	0	0
10	22	34	0	9	0
11	23	28	41	0	45
12	0	0	29	0	32
13	67	22	56	0	37
14	17	30	21	0	3
15	34	18	46	0	74
16	61	19	21	42	70
17	47	18	33	0	1
18	38	11	29	0	81
19	50	37	42	0	36
20	26	37	28	27	55

Totals:	563	661	655	269	615
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Grand Total: 2,763

Mean Number Eggs/Female/20 Days: 552.6

Mean Number Eggs/Female/Day: 27.63

Estimated Number Eggs/100 Females/20 Days: 55,260

TABLE XXVII

FECUNDITY RATE IN VIRGIN LF STRAIN
DROSOPHILA HYDEI

Date of Collection: 6/6

Date of Test Starting: 6/13

Date of Test Ending: 7/3

Eggs/Vial

Day	Female No. 1	Female No. 2	Female No. 3	Female No. 4	Female No. 5
1	46	0	0	7	7
2	68	68	13	88	138
3	70	53	19	6	13
4	0	72	48	65	91
5	96	16	67	70	43
6	27	76	0	0	40
7	0	23	0	0	0
8	135	105	0	19	51
9	125	105	0	67	90
10	0	0	0	51	91
11	8	16	0	0	34
12	0	74	0	70	65
13	84	38	0	0	38
14	54	57	4	66	81
15	69	22	0	40	45
16	54	44	3	26	76
17	62	51	17	74	88
18	79	46	29	66	111
19	58	89	0	23	20
20	51	63	72	0	97
Totals:	1086	1018	272	738	1219

Grand Total: 4,333

Mean Number Eggs/Female/20 Days: 866.6

Mean Number Eggs/Female/Day: 43.33

Estimated Number Eggs/100 Females/20 Days: 86,660

TABLE XXVIII
FECUNDITY RATE IN VIRGIN O STRAIN
DROSOPHILA HYDEI

Date of Collection: 6/6

Date of Test Starting: 6/13

Date of Test Ending: 7/3

Eggs/Vial

Day	Female No. 1	Female No. 2	Female No. 3	Female No. 4	Female No. 5
1	0	85	13	0	0
2	35	57	66	19	52
3	19	91	39	71	9
4	39	47	27	3	25
5	47	66	73	28	22
6	17	40	53	13	34
7	51	69	59	3	40
8	22	70	0	0	0
9	14	55	34	31	23
10	0	53	0	18	21
11	0	41	18	0	0
12	0	65	44	0	0
13	22	45	55	33	0
14	14	74	51	38	39
15	19	54	64	23	52
16	14	60	42	26	4
17	45	77	80	0	25
18	42	78	49	51	20
19	27	29	23	1	32
20	96	135	112	88	75
Totals:	524	1291	902	446	473

Grand Total: 3,636

Mean Number Eggs/Female/20 Days: 727.2

Mean Number Eggs/Female/Day: 36.36

Estimated Number Eggs/100 Females/20 Days: 72,720

TABLE XXIX
FECUNDITY RATE IN VIRGIN B STRAIN
DROSOPHILA HYDEOIDES

Date of Collection: 6/7

Date of Test Starting: 6/14

Date of Test Ending: 7/4

Eggs/Vial

Day	Female No. 1	Female No. 2	Female No. 3	Female No. 4	Female No. 5
1	0	0	0	0	0
2	8	0	12	3	2
3	8	0	6	3	9
4	8	13	2	5	9
5	0	0	11	9	4
6	0	19	10	10	23
7	10	12	9	10	17
8	10	0	11	8	2
9	11	14	12	8	25
10	9	7	9	9	6
11	3	16	26	9	2
12	2	0	0	0	4
13	8	9	4	5	8
14	17	19	20	12	6
15	7	7	9	10	0
16	15	16	0	9	13
17	6	2	23	0	9
18	17	12	6	6	7
19	2	6	4	13	5
20	12	0	9	1	7
Totals:	153	152	183	130	158

Grand Total: 776

Mean Number Eggs/Female/20 Days: 155.2

Mean Number Eggs/Female/Day: 7.76

Estimated Number Eggs/100 Females/20 Days: 15,520

TABLE XXX
FECUNDITY RATE IN VIRGIN SMA STRAIN
DROSOPHILA LONGICORNIS

Date of Collection: 6/6

Date of Test Starting: 6/13

Date of Test Ending: 7/3

Eggs/Vial

Day	Female No. 1	Female No. 2	Female No. 3	Female No. 4	Female No. 5
1	0	0	0	0	0
2	0	0	0	0	0
3	0	9	0	39	0
4	8	6	0	0	13
5	0	13	6	6	6
6	0	0	5	2	7
7	12	10	12	8	0
8	9	0	0	3	37
9	39	26	0	3	26
10	0	4	0	5	12
11	0	0	0	0	27
12	26	6	11	0	6
13	34	56	19	51	29
14	18	40	16	46	34
15	19	0	7	0	12
16	0	39	30	0	0
17	42	21	12	47	25
18	3	0	8	46	20
19	7	0	8	0	19
20	26	2	17	13	31
Totals:	243	232	151	269	304

Grand Total: 1,199

Mean Number Eggs/Female/20 Days: 239.8

Mean Number Eggs/Female/Day: 11.99

Estimated Number Eggs/100 Females/20 Days: 23,980

TABLE XXXI

FECUNDITY RATE IN VIRGIN B STRAIN
DROSOPHILA LONGICORNIS

Date of Collection: 6/7

Date of Test Starting: 6/14

Date of Test Ending: 7/4

Eggs/Vial

Day	Female No. 1	Female No. 2	Female No. 3	Female No. 4	Female No. 5
1	0	4	0	3	8
2	5	4	4	3	0
3	3	0	4	7	0
4	7	5	4	7	0
5	7	3	0	0	3
6	0	3	13	13	3
7	12	7	3	1	0
8	0	0	3	1	5
9	7	0	9	0	8
10	8	12	10	16	4
11	0	3	0	2	3
12	8	10	0	3	5
13	8	6	16	4	0
14	2	0	0	0	0
15	8	12	17	1	0
16	7	0	6	20	4
17	4	6	0	9	1
18	3	2	0	1	3
19	5	10	16	8	5
20	3	2	5	5	2
Totals:	97	89	110	104	54

Grand Total: 454

Mean Number Eggs/Female/20 Days: 90.8

Mean Number Eggs/Female/Day: 4.54

Estimated Number Eggs/100 Females/20 Days: 9,080

TABLE XXXII
FECUNDITY RATE IN VIRGIN SMA STRAIN
DROSOPHILA MERIDIANA

Date of Collection: 6/7

Date of Test Starting: 6/14

Date of Test Ending: 7/4

Eggs/Vial

Day	Female No. 1	Female No. 2	Female No. 3	Female No. 4	Female No. 5
1	0	0	8	0	0
2	6	1	8	0	3
3	9	4	3	3	3
4	21	4	12	12	8
5	0	17	12	9	2
6	0	3	14	8	6
7	5	0	0	0	0
8	22	20	31	19	11
9	12	19	40	0	9
10	13	0	0	23	10
11	2	1	0	0	0
12	8	0	13	0	0
13	0	0	12	0	0
14	7	10	5	9	0
15	3	0	6	5	3
16	0	3	4	4	3
17	0	12	3	6	4
18	6	2	0	0	1
19	6	0	9	4	3
20	0	0	11	3	7
Totals:	120	96	191	105	73

Grand Total: 585

Mean Number Eggs/Female/20 Days: 117

Mean Number Eggs/Female/Day: 5.85

Estimated Number Eggs/100 Females/20 Days: 11,700

TABLE XXXIII
FECUNDITY RATE IN VIRGIN LF STRAIN
DROSOPHILA MERIDIANA

Date of Collection: 6/6

Date of Test Starting: 6/13

Date of Test Ending: 7/3

Eggs/Vial

Day	Female No. 1	Female No. 2	Female No. 3	Female No. 4	Female No. 5
1	0	0	2	6	0
2	13	9	31	32	7
3	9	26	32	12	13
4	0	31	3	26	2
5	27	14	9	26	23
6	19	19	26	23	11
7	10	20	9	9	13
8	10	7	7	21	17
9	4	0	19	17	9
10	0	20	3	0	0
11	23	19	31	21	9
12	6	30	26	12	5
13	9	6	7	12	10
14	22	36	9	18	34
15	22	0	32	9	23
16	12	19	6	31	4
17	6	6	13	12	0
18	7	6	9	8	6
19	8	6	3	0	4
20	2	6	21	14	7
Totals:	209	282	297	309	197

Grand Total: 1,294

Mean Number Eggs/Female/20 Days: 258.8

Mean Number Eggs/Female/Day: 12.94

Estimated Number Eggs/100 Females/20 Days: 25,880

TABLE XXXIV
FECUNDITY RATE IN VIRGIN B STRAIN
DROSOPHILA MULLERI

Date of Collection: 6/9

Date of Test Starting: 6/16

Date of Test Ending: 7/6

Eggs/Vial

Day	Female No. 1	Female No. 2	Female No. 3	Female No. 4	Female No. 5
1	0	0	0	0	27
2	0	0	0	0	22
3	26	0	19	0	41
4	38	0	10	63	0
5	0	37	0	33	16
6	20	16	0	12	27
7	0	0	22	0	0
8	8	0	0	19	18
9	48	0	50	52	37
10	17	0	0	19	51
11	0	12	0	0	0
12	46	23	10	65	7
13	18	17	46	60	7
14	27	12	38	69	0
15	45	10	19	57	0
16	50	8	109	51	52
17	21	0	0	13	43
18	0	27	61	32	40
19	31	13	12	36	37
20	27	19	39	61	19
Totals:	422	194	435	642	444

Grand Total: 2,137

Mean Number Eggs/Female/20 Days: 427.4

Mean Number Eggs/Female/Day: 21.37

Estimated Number Eggs/100 Females/20 Days: 42,740

TABLE XXXV

FECUNDITY RATE IN VIRGIN LF STRAIN
DROSOPHILA MULLERI

Date of Collection: 6/6

Date of Test Starting: 6/13

Date of Test Ending: 7/3

Eggs/Vial

Day	Female No. 1	Female No. 2	Female No. 3	Female No. 4	Female No. 5
1	9	13	12	10	5
2	5	6	3	11	10
3	5	9	0	6	0
4	4	9	1	5	10
5	9	12	7	6	11
6	9	9	17	3	3
7	3	2	0	7	5
8	17	19	0	9	6
9	18	33	48	26	0
10	16	10	19	12	1
11	8	0	12	19	23
12	12	4	0	9	0
13	18	9	0	14	21
14	0	10	19	27	6
15	20	11	29	14	25
16	29	40	18	37	22
17	16	31	26	12	23
18	15	6	3	9	16
19	0	40	21	9	15
20	16	25	12	7	20
Totals:	229	298	247	252	222

Grand Total: 1,248

Mean Number Eggs/Female/20 Days: 249.6

Mean Number Eggs/Female/Day: 12.48

Estimated Number Eggs/100 Females/20 Days: 24,960

TABLE XXXVI

FECUNDITY RATE IN VIRGIN F STRAIN
DROSOPHILA MULLERI

Date of Collection: 6/7

Date of Test Starting: 6/14

Date of Test Ending: 7/4

Eggs/Vial

Day	Female No. 1	Female No. 2	Female No. 3	Female No. 4	Female No. 5
1	18	34	3	19	30
2	19	9	8	22	11
3	42	34	15	12	10
4	2	26	31	12	19
5	6	0	13	2	9
6	9	17	8	2	30
7	7	0	5	8	7
8	23	41	9	16	21
9	29	6	15	9	3
10	6	0	4	0	8
11	13	0	0	22	11
12	15	4	9	7	7
13	9	10	7	6	0
14	2	0	8	5	3
15	0	0	0	5	5
16	10	9	11	22	0
17	17	16	11	22	17
18	5	8	3	0	9
19	6	10	2	9	3
20	12	9	3	19	4
Totals:	250	233	165	217	207

Grand Total: 1,072

Mean Number Eggs/Female/20 Days: 214.4

Mean Number Eggs/Female/Day: 10.72

Estimated Number Eggs/100 Females/20 Days: 21,440

TABLE XXXVII

FECUNDITY RATE IN VIRGIN F STRAIN
DROSOPHILA MERIDIANA RIOENSIS

Date of Collection: 6/6

Date of Test Starting: 6/13

Date of Test Ending: 7/3

Eggs/Vial

Day	Female No. 1	Female No. 2	Female No. 3	Female No. 4	Female No. 5
1	0	3	0	12	0
2	4	8	5	0	14
3	5	9	7	11	0
4	8	0	2	1	7
5	3	5	0	0	0
6	3	5	9	1	0
7	10	10	8	12	0
8	0	12	0	0	0
9	9	9	19	11	23
10	0	0	0	0	0
11	2	0	3	0	0
12	11	11	0	0	0
13	2	4	0	1	0
14	7	8	9	17	8
15	4	3	0	0	9
16	5	8	0	2	7
17	0	0	0	13	7
18	3	3	0	0	2
19	1	0	0	3	2
20	9	2	5	12	3
Totals:	86	100	67	96	82

Grand Total: 431

Mean Number Eggs/Female/20 Days: 86.2

Mean Number Eggs/Female/Day: 4.31

Estimated Number Eggs/100 Females/20 Days: 8,620

TABLE XXXVIII
FECUNDITY RATE IN VIRGIN L STRAIN
DROSOPHILA SPENCERI

Date of Collection: 6/7

Date of Test Starting: 6/14

Date of Test Ending: 7/4

Eggs/Vial

Day	Female No. 1	Female No. 2	Female No. 3	Female No. 4	Female No. 5
1	6	0	0	13	14
2	0	17	0	10	6
3	9	21	0	0	0
4	12	9	0	0	18
5	0	20	6	5	9
6	0	0	2	5	3
7	8	12	4	9	2
8	9	4	10	16	2
9	3	4	9	1	0
10	13	21	3	7	4
11	0	0	4	12	9
12	4	9	2	3	9
13	11	6	9	8	4
14	9	9	6	5	3
15	0	9	4	4	13
16	0	0	0	18	9
17	5	0	2	11	0
18	5	0	2	13	3
19	7	6	6	9	14
20	9	9	8	6	0
Totals:	110	156	77	155	122

Grand Total: 620

Mean Number Eggs/Female/20 Days: 124

Mean Number Eggs/Female/Day: 6.2

Estimated Number Eggs/100 Females/20 Days: 12,400

VITA

Earl Dean Henslee

Candidate for the Degree of

Doctor of Education

Thesis: PARTHENOGENETIC REPRODUCTION IN THE REPLETA SPECIES GROUP OF
THE GENUS DROSOPHILA

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Personal Data: Born in Elk City, Oklahoma, June 12, 1927, the son
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Education: Graduated from Elk City High School, Elk City, Oklahoma
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ville High School, Collinsville, Illinois, 1960-65; Biology
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