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A study of productivity in *Drosophila immigrans*

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A STUDY OF PRODUCTIVITY
IN DROSOPHILA IMMIGRANS

A Thesis
Presented to
The Faculty of the
Department of Biological Sciences
University of the Pacific

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

by
Lalita Helen Shenoy Waterman
December 1971

This thesis, written and submitted by

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INTRODUCTION AND HISTORICAL BACKGROUND

Sexual reproduction is a universal characteristic of higher organisms. It is affected by several factors, some of which are food supply, temperature, humidity, light intensity, space, the presence or absence of other animals, and the availability of suitable mates.

Internal fertilization occurs in all the major groups of terrestrial animals, including insects, reptiles, birds, and mammals. In wild and domestic⁷ mammals the presence of the male can have important effects in stimulating the female at the onset of the breeding season, and can synchronize her heats with those of adjacent females (Sadlier, 1969). The necessary prerequisite for fertile conception is the presence and interaction of both a male and a female of the same species. Thus, the male himself acts as an environmental factor in the reproduction of the female, and can be very important in his effects on the productivity of the female population.

In insects, even when the intimate confrontation of a pair of individuals has occurred, mating is postponed until after a courtship ritual is performed. Some insects copulate only once and lay their eggs in a single batch; others lay batches of eggs at intervals, and may copulate repeatedly; a few others lay single eggs at fairly regular intervals. In all cases, however, fecundity of the female and fertility of the male are influenced by many factors.

There has been considerable confusion in the use of terms describing reproductive activity. Following the usage of Pearl (1927) and Alpatov (1932), I will use the term "fecundity" when speaking of the number of eggs laid by a female, whether or not the eggs are viable. The number of adult offspring produced by a female will be referred to as the "productivity".

Environmental influences may limit the productivity of a female not only by their effects on longevity but also by restricting egg production and oviposition in other ways. Nutrition has a powerful effect on the rate of development, organ size, life span, fecundity, and productivity of the female (Clark and Rockstein, 1964). Metabolism is a function of the ambient temperature in insects, since they are poikilothermic animals. Within a range of temperature that permits survival, if that range does not destroy some part of the reproductive system, egg production can be expected to increase with temperature (Patton, 1963).

Insects differ in the extent to which copulation affects egg production. Some insects produce a normal number of eggs without being mated; but in most non-parthenogenetic species, virgin females either do not form mature eggs or when they do, such infertile eggs are rarely laid (Gerber, 1967). In many insects, the development of eggs is deficient in the absence of males. When males are present, egg maturation or oviposition is "activated". Thus, no eggs develop until after copulation in the tsetse fly, Glossina palpalis (Mellanby, 1937) and several Anopheles species (Roy, 1940). In the roach genus, Periplaneta, mating accelerates egg maturation (Roth and Willis, 1956). Mating enhances egg production in the large milkweed bug, Oncopeltus fasciatus (Gorden and Lohr, 1968). Unmated Musca domestica produce notably fewer eggs than mated females (Glaser, 1923). In the curculionid beetle, Sitona cylindricollis, frequent or continuous contact with males is necessary for sustained production of oocytes and eggs by females (Garthe, 1970).

Not only may copulation provide the initial stimulus for oogenesis, but also the deposition of eggs is in some cases directly dependent on copulation. Thus, in the firebrat, Thermobia domestica (Sweetman, 1938), the

bean weevil, Acanthoscelides obtectus (Bushnell and Boughton, 1940), and the Mediterranean flour moth, Ephestia (Brandt, 1947), oviposition is retarded until after copulation. The same applies to many acridiids. In the desert locust, Schistocerca gregaria, copulation hastens sexual maturity and fecundity of the female, but it is not necessary for her sexual maturation (Husain and Mathur, 1945). In the hog louse, Haematopinus, however, copulation seems to have no effect; egg laying commences three days after the final moult with or without the presence of the male (Florence, 1921).

In general, the literature indicates that older females, when mated, lay smaller numbers of eggs with a lower viability than those from younger mothers. Woke, Ally, and Rosenberger (1956) reported that the age of the mosquito, Aedes aegypti, at the time of the blood meal was a significant factor in the number of eggs laid. Thus, at five days of age they obtained a mean value of 89 eggs per female. However, four-week-old females produced a mean of only 56. Richards and Kolderic (1957) observed a decline in egg production in older Oncopeltus fasciatus, and reported that the few eggs laid late in the fecund period weighed less, took longer to develop, and had a lower hatching percentage. Greenberg (1955) observed a reduction in egg production with advancing parental age for paired Musca domestica maintained at 25° C. Callahan (1962) demonstrated a similar decline in reproductive capacity with increasing maternal age for two strains of the same species. Moreover, the eggs laid by older flies were less viable than those laid by young parents.

The mechanisms of "activation" of ovulation and/or oviposition have remained relatively unexplored, and the few species that have been investigated seem to demonstrate quite a bit of variability with regard to "acti-

4

vating" mechanisms. In the locust, either precopulatory contact with normal males or copulation with castrate males will induce production of fertile eggs (Norris, 1954). However, in the bed bug, Cimex lectularius, only the presence of sperm in the female oviduct causes egg maturation and subsequent production of fertile eggs (Davis, 1965). Egg development in this species never occurs until the female has been fertilized (Mellanby, 1939). After fertilization, egg development is apparently controlled by a hormone produced by the corpora allata.

Narain (1962), showed that egg production in the fruit fly, Drosophila melanogaster, increases rapidly within the first few days of life, attaining a maximum on the fourth day of egg laying. Thereafter, egg production decreases till the fortieth day of egg laying. Hanson and Ferris (1929) demonstrated that mated females lay 1.63 to 2.00 times the number of eggs that virgins lay, and that females mated to sterile males produce about the same number of eggs as those mated to fertile males. Mating in this same species causes an immediate and considerable acceleration in egg production (Laurinat, 1930). Merle and David (1967) subjected D. melanogaster females to an exclusively glucide diet and found that virgin females lay fewer eggs than females that are fertilized. The addition of males to isolated females stimulates egg laying. In another publication, Merle (1970) stated that virgin, sugar-fed females mature significantly fewer eggs than mated sugar-fed females. However, the principal difference between the two kinds of females lies in the rate of egg deposition. The latter lay their eggs very quickly during their first week of life. The former retain the mature eggs in the ovarioles; egg deposition is very low and begins only after a week of life. Cook (1970) reported that young virgin D. melanogaster females lay almost no

eggs, while mated individuals of the same age exhibit a high fecundity. Even mating with sterile males results in a marked increase in egg laying by the females. By 72 hours post-mating, however, the level drops to that of virgin females.

Butz and Hayden (1962) showed that the number of D. melanogaster adults emerging from eggs laid by parents 35 days old is considerably lower than that from parents 24 hours old. Moreover, a series of experiments involving parents of (1) the same age, (2) young males and old females, and (3) young females and old males showed that the viability of the emerging adults is negatively correlated with the age of the maternal parent. O'Brian (1961) also observed that, at 25° C., offspring from older D. melanogaster parents produce fewer viable eggs and for a shorter period of time than offspring from younger parents, which continue to lay eggs over a 46-day period.

Regardless of whether one is looking at various aspects of insect reproduction from the point of view of being able to control certain insect populations when necessary or whether one is looking at them merely as basic research, much more information regarding reproduction in insects is needed.

Within the genus Drosophila, no generalizations can be made about the effects of delayed mating on the fecundity and the productivity of females, as all the work has been confined to one species, D. melanogaster. Because this work should be extended to other species within the genus I have chosen to work with the widely distributed species, Drosophila immigrans Sturtevant, 1921. In the present experiments, I have examined the effects of delayed mating on the fecundity and productivity of a sample of these females.

MATERIALS AND METHODS

The original stock of Drosophila immigrans used in this study was collected beside a stream in Jackson, Calaveras County, California. These flies were grown for several generations in a Forma Scientific Model 12 incubator at $25 \pm 1^{\circ}$ C. They were exposed to light daily from 7 a.m. to 7 p.m., and kept in the dark for 12 hours. This was accomplished by placing a Tensor lamp connected to an automatic timer in the incubator. The flies were cultured in 500 ml. jars with plastic foam stoppers on Carolina Instant Drosophila medium #67-5002 (Carolina Biological Supply Company) seeded with live Fleischmann's baker's yeast.

Preliminary experiments with varying quantities of food were performed in order to determine the optimum amount for production of large flies. The reason for this was that Tantawy and Vetokhiv (1959) showed that in Drosophila pseudoobscura there is a positive correlation between the size of the female and her lifetime egg production. In the present work, control and experimental vials contained 4 grams instant medium and 30 ml. water, and in all the following experiments large, undamaged flies were used. The parents of all the flies used in this work were less than seven days post-eclosion at the time of oviposition.

A pilot set of experiments was conducted in order to get an approximation of the fecundity of D. immigrans. One randomly chosen, newly-hatched, virgin female and two newly-hatched males were placed in an 80 ml. vial. All three were transferred to a fresh vial every 24 hours, and an egg count of the used vial was made using a dissection microscope. The same procedure was repeated with females kept virgin for 10 days. Both sets of experiments were repeated 60 times.

In the definitive experiments to be reported here, the controls were established by placing three newly-hatched, virgin females (collected within four hours of hatching) and three newly-hatched males in a vial containing medium. The flies were transferred to freshly prepared vials every 48 hours. New males of a similar age were given in case of death or escape of males. The used vials were kept in the incubator under the experimental conditions for the eggs to develop. When the pupae started to hatch, the young flies were counted every 24 hours, and the mean number of offspring per female was recorded.

The treatments were set up in the same manner except that the virgin females were first isolated for certain lengths of time e.g. 2, 4, 6, ...24 days before being placed in the presence of newly-hatched males. During their period of isolation they were kept in groups of three in separate vials, and were transferred to fresh vials every 48 hours. Offspring counts were made in exactly the same manner as the control experiments. A total of 20 replicates of the controls and each treatment was made, and 780 flies of each sex were used in all. These data were then analyzed by means of the Student's t-test.

RESULTS

Table 1 shows the mean fecundity of 60 females mated soon after eclosion, and 60 females mated 10 days later. The mean fecundity per control female reaches a peak on the sixth day of life. Females kept virgin for 10 days lay fewer eggs, and these are laid over a longer period of time.

The results of the definitive experiments are presented in Table 2. Each datum is a mean of the number of offspring produced per female in each of the 20 vials over the two-day period indicated. There were three females per vial until they began to die in the period of 34 to 50 days. Several conclusions can be drawn from these data.

First, it can be seen in Table 2 as well as in the pilot experiments that females do not lay fertile eggs before three to four days after eclosion. Also, oviposition of viable eggs continues until 34 to 42 days of adult life when the females are kept in groups of three. However, in the pilot experiments shown in Table 1, it can be seen that egg laying ceases between 16 to 22 days following hatching when the females are kept single with only males present.

Secondly, the mean productivity per control female reaches a peak on the fifth or sixth day following eclosion. The females kept virgin, however, all have peak productivity on the third or fourth day after being placed with males.

Thirdly, there is a striking difference between the peak productivities of females kept virgin for six or more days and that of the controls. Control females and those kept virgin for only two or four days produce significantly more offspring during their "peak" interval than do those kept virgin for six or more days (Figure 1).

Finally, the total productivity declines with increased length of virginity, as seen in Table 3. For example, the mean total productivity of females kept virgin for six days is 233 (S. D. = 61) and that of the controls is 431 (S. D. = 53). The difference between these means is significant at the 0.5% level.

It must be mentioned, at this point, that egg counts in the pilot experiments are only estimates owing to the limited facilities available for counting eggs accurately. Also, since egg counts were made only once every 24 hours, quite a few of the eggs had hatched into larvae, which had burrowed into the media, and hence could not be seen.

As the period of isolation increases the number of virgin females starts dwindling. None of them live past 24 days of virginity. On the other hand, Table 4 shows that there is no significant difference between the longevities of the mated females in the definitive work, regardless of their lengths of virginity. However, the longevities of the single females in the pilot experiments are lower than those of the grouped females in the definitive work.

TABLE 1

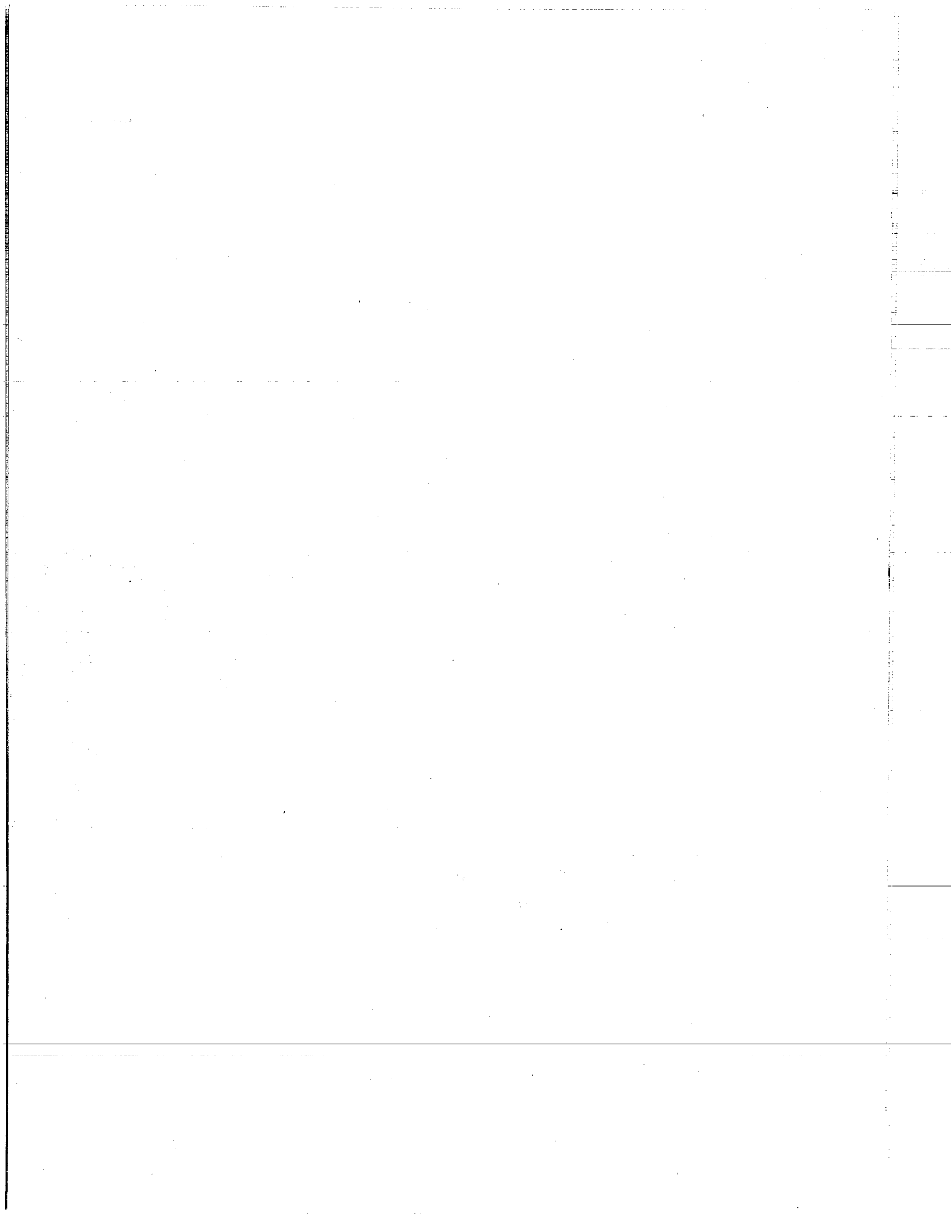
MEAN NUMBER OF EGGS COUNTED PER FEMALE PER DAY IN SIXTY
DROSOPHILA IMMIGRANS

Days	0-day virgins	10-day virgins
1	0	0
2	0	0
3	1	0
4	3	1
5	9	0
6	16	2
7	14	2
8	7	4
9	4	4
10	2	3
11	1	2
12	0	8
13	4	4
14	1	5
15	0	6
16	1	3
17	0	2
18	0	5
19	0	1
20	0	3
21	0	0
22	0	1
23	0	0
24	0	0
25		0

TABLE 2

MEAN PRODUCTIVITY PER DROSOPHILA IMMIGRANS FEMALE PER TWO-DAY INTERVAL

Days	Length of Virginity												
	0	2	4	6	8	10	12	14	16	18	20	22	24
2	0	0	0	0	0	0	0	0	0	0	0	0	0
4	21	1	0	0	0	0	0	0	0	0	0	0	0
6	82	19	2	0	0	0	0	0	0	0	0	0	0
8	58	75	70	12	0	0	0	0	0	0	0	0	0
10	46	54	56	36	13	0	0	0	0	0	0	0	0
12	40	39	43	30	23	9	0	0	0	0	0	0	0
14	31	30	35	26	21	13	10	0	0	0	0	0	0
16	28	28	30	24	18	20	13	7	0	0	0	0	0
18	24	26	27	20	17	13	12	8	2	0	0	0	0
20	23	23	23	23	18	13	12	10	12	3	0	0	0
22	21	21	21	19	14	13	10	10	12	8	2	0	0
24	18	18	18	15	12	11	10	5	10	8	8	1	0
26	14	13	14	12	9	7	8	4	10	9	9	6	1
28	11	9	9	9	6	2	5	3	4	8	7	6	2
30	8	6	4	4	4	0	7	4	2	4	5	8	5
32	4	6	3	2	2	1	4	4	2	3	4	6	3
34	4	4	2	1	2	0	2	3	0	1	3	3	2
36	3	3	1	0	2	0	2	4	2	0	2	2	2
38	2	2	0	0	3	0	1	4	0	1	3	2	1
40	2	2	0	0	2	1	0	1	0	0	2	0	1
42	1	2	0	0	3	1	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0	0
46	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0	0



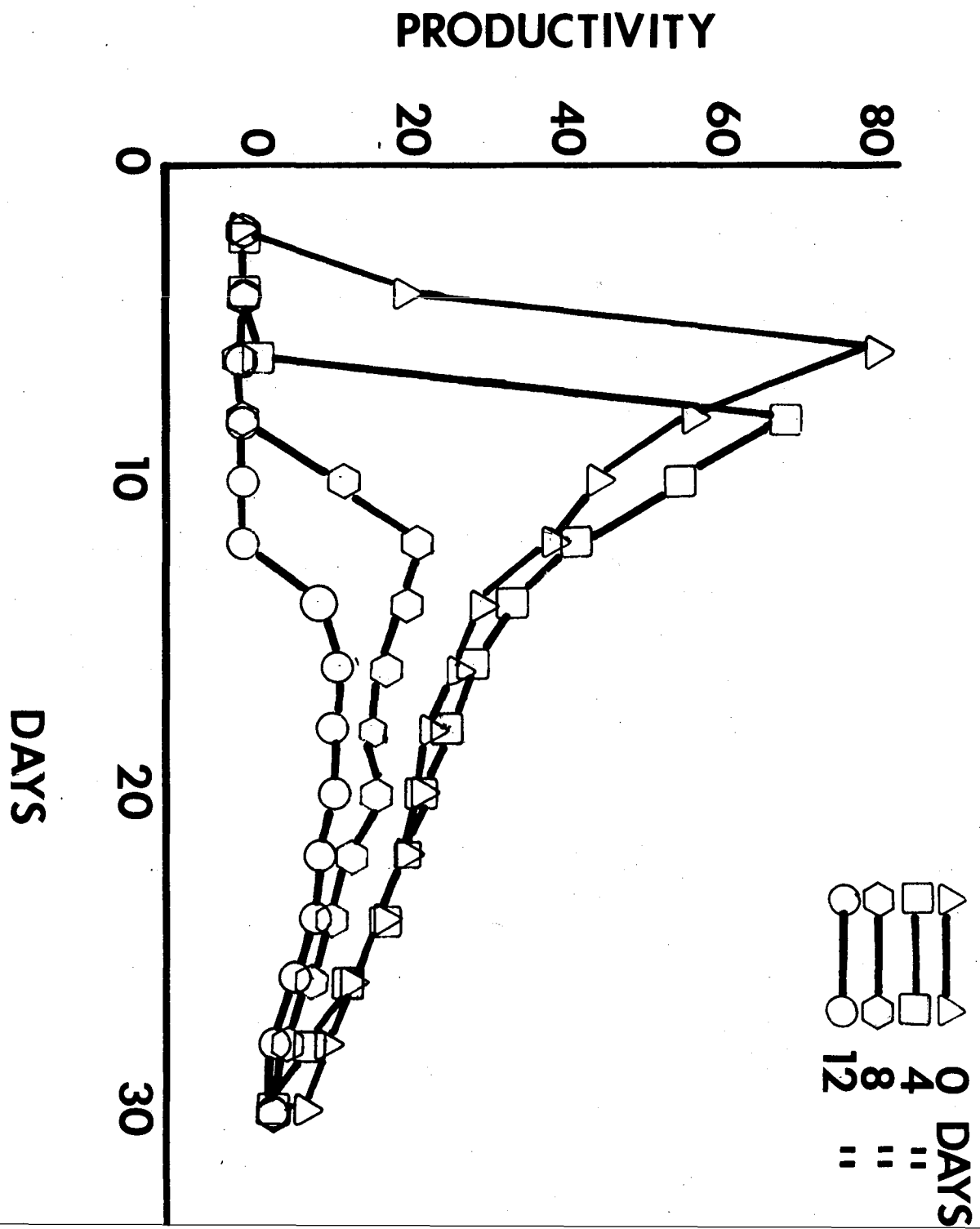


TABLE 3

MEAN TOTAL PRODUCTIVITY OF 60 DROSOPHILA IMMIGRANS FEMALES

Days of Virginity	Mean	S. D.
0	431	53
2	371	43
4	360	26
6	233	61
8	149	30
10	100	42
12	87	39
14	58	42
16	56	28
18	41	23
20	33	22
22	28	24
24	12	13

TABLE 4

MEAN LIFE SPAN (IN DAYS) FOLLOWING ECLOSION OF 60 D. IMMIGRANS FEMALES

	Days of Virginity	Mean Life Span
Pilot Exp.	0	19
	10	20
Definitive Exp.	0	38
	2	36
	4	35
	6	35
	8	36
	10	35
	12	35
	14	37
	16	35
	18	33
	20	34
	22	36
	24	35

DISCUSSION

The pilot experiments indicate that no eggs are laid by control D. immigrans females until the third day of life. This is also indicated by the first appearance of offspring in the three to four day vials of the control experiments in the definitive work. This is slightly different from that reported for other species. For example, no eggs are laid by D. melanogaster females during the first 24 hours of life (Hanson and Ferris, 1929), while on the average, Drosophila busckii females do not reach sexual maturity until two days after eclosion (Wolfsberg, 1958).

Production of offspring in D. melanogaster may begin on the second day of life, increasing rapidly to a maximum on the fourth and fifth days, and then declining gradually until shortly before death (Hanson and Ferris, 1929). These authors concluded that the slowing up is one feature of age, and that there is generally one day or more of non-production before death. Narain (1962), also, found that daily egg production in this species shows a rapid increase during the first few days reaching a peak on the fourth day of egg laying. Thereafter, egg production gradually decreases. Unfortunately, he does not mention any correlation between days following mating and days of egg laying. On the other hand, David and Clavel (1967) observed a peak on the third day following mating in this same species. The apparent discrepancy between these results may be due to differences in nutritional media and/or experimental design. D. busckii does not exhibit any egg laying rhythm. The mean number of eggs per female per day ranges from 32 to 44 (Wolfsberg, 1958). Shima, Kaneko, and Momma (1962) noted that Drosophila virilis females lay the largest number of eggs on the fifth day post-mating. My experiments have shown that productivity

in D. immigrans reaches a peak about the sixth day following mating, and then tapers off gradually.

The mean productivity observed in the experiments reported here for D. immigrans control females at the time of peak production is 41 offspring per female per day, which is less than the 74.0 and 95.1 noted by Narain (1962) and David and Clavel (1967) respectively in D. melanogaster. This is within the range observed by Gregg and Day (1965) in Drosophila hydei. These authors obtained "optimum" values of 40 to 60 eggs per female per day. It must not be forgotten that all these authors studied fecundity whereas my experiments have examined productivity.

Hanson and Ferris (1929), Merle and David (1967), and Cook (1970) observed that D. melanogaster females mated soon after eclosion produce a far greater number of offspring than those females mated at a later date. My experiments with D. immigrans have demonstrated similar results. Merle and David, however, pointed out that fecundity in D. melanogaster is not affected if copulation occurs within the first five days post-eclosion. Later mating results in a decrease in productivity. My experiments, however, show that isolation of D. immigrans females for even four days results in a striking difference in productivity (Table 3). This difference may be attributed to species and/or dietary differences.

My experiments, together with those previously mentioned, raise the interesting problem of how the male stimulates oviposition in the female. That he plays a very important role in stimulating reproduction in the female is apparent from Tables 1 and 2.

In some insects, egg laying commences only after copulation. The act of copulation constitutes a physical (mechanical) stimulus to egg lay-

ing in Drosophila melanophila (= D. melanogaster) (Guyénot, 1912). Here, it seems that the effect is merely on oviposition: the eggs are formed but are not laid unless mating has occurred. Guyénot believed that, in addition to the act of mating, the presence of sperm in the seminal receptacles of the female acts as a stimulant to oviposition. Yet, Hanson and Ferris (1929) demonstrated that mating with a sterile male (in which spermatophores or accessory gland secretion are produced) stimulates oviposition in females of the same species.

In other species, it is the development of eggs that is deficient in the absence of the male. In Schistocerca, the rate of oogenesis is increased when females are exposed to the effect of male pheromone (Highnam and Lusi, 1962). The presence of mature males brings about the release of neurosecretory substance, and consequently stimulates egg formation. In many insects the deposition of yolk in oocytes is dependent on the presence of a hormone secreted by the corpus allatum (Scharrer, 1948). This was observed in the bed bug, Rhodnius (Wigglesworth, 1936), the grasshopper, Melanoplus (Pfeiffer, 1939), the beetle, Leptinotarsa (Wilde, 1954), and the earwig, Anisolabis (Ozeki, 1958). Impregnation, however, seems to be a prerequisite for the corpus allatum to exert its action (Mellanby, 1939). Thus, in the roach Diploptera punctata, the stimulus connected with mating appears to activate the corpus allatum, and it is thought to be nervous (Engelmann, 1958).

Which of these theories is the correct one for D. immigrans cannot be stated at this time. It seems quite possible, however, that mating in the female can provide an important stimulus by way of the ventral nerve cord, brain, and corpus allatum, to induce the subsequent production of off-

spring. Whether it is the development of eggs that is stimulated by mating or whether it is the deposition of eggs that is stimulated is not clear at present.

Del Solar and Palomino (1966) observed that D. melanogaster females prefer to oviposit near the places where eggs have already been laid by other females. This may be part of the reason why Shima, Kaneko, and Momma (1962) observed only 29.5 eggs per single female at the time of peak production in D. virilis. My work seems to be in agreement with the foregoing in that a comparison of the emerged flies shows that the average productivity per female is higher in the definitive experiments where the flies were kept in groups of three. On the other hand, Drosophila pseudoobscura females tend to lay more eggs in clean vials than in those previously occupied (Del Solar, 1970).

Every insect species has a characteristic life span under defined conditions. Hanson and Ferris (1929) obtained a mean life span of 20.13 days for D. melanogaster females reared at 25° C. Howard (1939) reviewed the life spans for certain orders of insects and showed that adult mayflies live for one day, some Lepidoptera about 60 days, certain beetles more than 10 years, and some termites more than 25 years. Differences in life span, due to genetic constitution can be seen in the work of Gonzalez (1939) and Maynard Smith (1959). Gonzalez obtained a mean value of 40.1 days for the life span of adult D. melanogaster females. Maynard Smith, on the other hand, obtained mean values of 36.4 days for inbred lines of Drosophila subobscura, and 60.0 days for outbred populations. Inasmuch as the longevity of insect populations may be readily modified by intrinsic and extrinsic factors, the adult life spans presented in Table 4 are, therefore, defin-

able for D. immigrans only within the limitations of our laboratory conditions.

It is generally accepted that males have a shorter duration of life than females (Rockstein, 1964). Male Musca domestica (Rockstein and Lieberman, 1959), and male Tribolium madens and Tribolium confusum (Park, 1945) have a shorter life span than comparable females. Throughout my experiments, the D. immigrans males seemed to die earlier than comparable females.

The activities which lead up to reproduction are very important in the life cycle of the insect. The production of eggs, however small, is always a drain on the female's reserves of strength, and there seems to be an inverse correlation between longevity and fecundity. The life span of D. subobscura females can be prolonged when the rate of egg laying is reduced (Maynard Smith, 1959). Thus, ovariless females (no egg production) and virgin females (low egg production) live longer than mated females (with a high egg production). Similarly, a greater longevity of virgin females over mated females in D. melanogaster has also been shown by Bilewicz (Comfort, 1956). However, within the limits of these experiments, there appear to be no significant differences in longevity between experimental and control D. immigrans females.

At 25° C., the developmental period from egg to adult in D. busckii is 12 days (Wolfsberg, 1958). My experiments have demonstrated similar results for D. immigrans. The minimum time taken by the eggs to develop into flies was 11 to 12 days. The developmental period was slightly longer in more crowded vials, and then approached 25 to 30 days.

~~The major conclusion of importance is that the male plays a very~~
important role in stimulating the production of offspring in the female D.

immigrans. Both the sperm and the paragonial fluid which the female receives at mating are possible sources of a stimulant for oviposition. Brieger and Butterworth (1970) found a lipid present exclusively in the ejaculatory bulb of adult D. melanogaster which they feel may be involved in some aspect of reproduction since it is transferred to the female during mating. Leahy (1966) showed significant evidence that the paragonial substance is the most important influence in stimulating oviposition whilst Merle (1970) demonstrated that it is the presence of viable spermatozoa in the female genital tract that is the most important in the same species. She suggested that a nervous mechanism is involved. It may be possible to test the latter theory by blocking nerve pathways between the reproductive tract and the brain of the female and then studying the effects of mating. If the oviposition stimulant is indeed a chemical substance secreted by the male, it will have to be more specifically identified. In either case, it is quite clear that further experiments need to be carried out in order to make any definite statements regarding an "activating" mechanism for reproduction in D. immigrans.

SUMMARY

In this study it has been demonstrated that Drosophila immigrans females begin laying fertile eggs on the third or fourth day following eclosion, with productivity reaching a peak between the fifth and sixth days of adult life. A delay in mating of even four days decreases the rate as well as the volume of productivity. Based on the evidence in the literature, it is suggested that the stimulus to oviposition may be mechanical or chemical on the corpora allata via the ventral nerve cord.

The longevity of D. immigrans females in groups is approximately 20 days, whereas that of single females is approximately 35 days. It is not altered by the length of virginity prior to mating or the volume of productivity after it. However, no females live past 24 days of virginity.

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