1976

# The life cycle of seven species of Drosophila

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# THE LIFE CYCLE OF SEVEN SPECIES OF DROSOPHILA

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

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December 1976

This thesis, written and submitted by

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Dated December 6, 1976

In grateful memory to

Arthur J. Cullen D.M.L.

first Provost, Elbert Covell College

University of the Pacific 1961-1970

great scholar, beautiful human being, an outstanding model of interamericanism.
Dr. Cullen representa un modelo excepcional de interamericanismo digno de ser copiado por las neuvas generaciones. No solo vivió para el interamericanismo sino también para enseñarlo.

ACKNOWLEDGEMENTS

I would like to acknowledge gratefully the assistance and guidance of Dr. Alice S. Hunter during the research and writing of this paper. I would also like to thank Dr. Anne Funkhouser for helping me to solve problems during the planning of the experiment. Finally, I would like to thank my husband, Tony, and my parents, Maximiliano and Elvira; the former for his patience and understanding, and the latter for their encouragement, their faith, and for planting and nourishing the desire for knowledge.

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# INTRODUCTION AND REVIEW OF LITERATURE

Fertilization usually initiates a series of changes leading ultimately to the development of a new individual. When this new individual attains sexual maturity it is able to produce eggs or sperm for the initiation of another generation. This chain of events from fertilization to complete sexual maturity constitutes the life cycle of an individual. This term should be distinguished from ontogenesis which includes the development of the organism, maturity, senescence and death. The research to be reported in this paper concerns the life cycle of several species of Drosophila.

In insects there is a period of embryonic development inside of the egg, which after hatching (eclosion) is followed by the post-embryonic phase. The process of transformation of the post-embryonic insect into its adult form is called metamorphosis. In some insects this is a gradual process in which the nymph at each molt resembles more and more the adult form. This incomplete or hemimetabolic development lacks a pupal stage and is characteristic of grasshoppers and cockroaches. Other insects have a much more abrupt transformation from the larval to adult stage. This takes place in the pupa, and is the complete or holometabolous development characteristic of butterflies, beetles and flies.

The genus Drosophila in the family Drosophilidae of the order Diptera is characterized by complete metamorphosis. The stages of its development include the egg, 3 larval instars,

pupa and adult. The species D. melanogaster is so widely used in genetic and cytological studies that biologists tend to equate the genus Drosophila with this particular species. However, there are over 1,000 species in this genus and they occupy a broad range of habitats.

Drosophila are small flies from 2 to 5 mm in length with body color varying in different species from yellow through brown to black. This genus is characterized by an incomplete sub-costa and twice-broken costa of the wing. Typically there are 2-3 sternopleural bristles, but no mesopleural bristles. Drosophila are also characterized by convergent post-vertical bristles, well-developed oral vibrissae and plumose arista. There are 11 sub-genera which have been described on the basis of the number of filaments on the eggs, color and pattern of adults, and feeding habits.

Although the majority of Drosophila are attracted to bait of rotting fruit, this is not necessarily their normal diet. The location of the precise breeding and feeding sites is far from obvious for most of the species. Cosmopolitan species such as Drosophila melanogaster, D. hydei and D. immigrans do feed on the yeasts in fleshy fruits and lay eggs which develop within the fruits wherever these are available. However, many species live in regions where no fleshy fruits are available. In North America, D. pseudoobscura and D. persimilis have been found in rotting logs of aspen and other trees (Parson, 1973). Probably they are feeding on yeasts which grow in these places. Species

of the sub-genus Hirtodrosophila are known to be fungus feeders (e.g. D. flavopinicola, D. pinicola, D. sub-quinaria, and D. melanderi). Cosmopolitan species usually are able to feed and breed in a greater variety of sites while indigenous species have more specific niches (Parson, 1973). D. busckii of the sub-genus Dorsilopha feed and breed not only in fleshy fruits but also in many different rotting vegetables and flowers (Hunter, personal communication).

For some species, the breeding sites are extremely specific. In Central and South America there are Drosophila which require a specific species of plant (e.g. D. flavopilosa on Cestrum parqui) while others are poliphagous (e.g. D. florae, D. lutzii and D. ananassae). There are also Drosophila which breed on a specific animal (e.g. D. carcinophila which breeds in one species of crab (Carson, 1967). There are many other examples of niche specificity in the literature (reviewed in Parson, 1973) and probably many yet to be discovered. Feeding and breeding sites are not necessarily the same for larvae and adults, as demonstrated in studies of the yeast flora of the alimentary canal (Carson, Knapp and Phaff, 1956).

Since the species in this genus are found widely distributed with respect to climate as well as breeding site, it is to be expected that they may differ widely in the time of development of the various stages in the life cycle. Although D. melanogaster can complete its life cycle in only a few days, there are some species which probably normally

produce only one generation of offspring in a year. Reviewing the literature, one finds that many different species of Drosophila are used in research, but the time needed for development has not been uniformly reported. This basic information should be determined for species from different habitats and those which differ taxonomically to varying degrees in order to make comparisons and look for underlying principles. The relevant data are summarized on Table I.

Powsner (1935) reports that D. melanogaster requires 8 days plus 18 hours from egg-laying to the emergence of the adult at 25 C. According to Suzuki (1970) D. melanogaster requires 11-12 days at 22 C, 7-8 days at 29 C, 22 to 28 days at 17 C from laying of the eggs to fertile adults.

In another cosmopolitan species of a different subgenus, D. busckii, the developmental period from egg to adult takes 12 days. The females do not reach sexual maturity until 2 days after emerging from the pupae (Wolfsberg, 1958). Gregg and Day (1965) found that D. hydei requires 7 days after emerging from the pupae to reach sexual maturity. On the other hand, another cosmopolitan species D. immigrans requires only 11-12 days for development from egg to adult, and 3-4 days to lay fertile eggs (Waterman, 1971).

Some of the indigenous species have been reported to have extremely long life cycles. D. mesophragmatica requires 40 days from egg-laying to emerging of the adult when developing at its normal temperature of 15 C (Hunter, 1966).

The closely related D. paxani was reported to develop from egg to adult in 40 days at 16 C but required only 19 days at 25 C (Budnik, et. al., 1971). Spieth (1974) found that at 18 C D. pinicola and D. flavopinicola require from 12 to 15 days after emerging from the pupae to reach sexual maturity. The females start laying eggs about 3 days after mating, and each new generation requires 17-23 days for development from egg to adult. D. melanderi requires 30 days after emerging from the pupae to reach sexual maturity and each generation takes about 60 days for development from egg to adult (Spieth, 1974). Hunter (personal communication) found that at temperatures varying between 16-23 C, but staying at 20 C at least half the day, D. subquinaria required 17-19 days from egg to adult and D. suboccidentalis required 18-20 days from egg to adult. The adults required from 3-4 days after emerging from the pupae to reach sexual maturity.

In order to compare life cycles there are many environmental and physiological factors (humidity, temperature, age of the parents, diet, and crowding conditions) which must be considered.

Insects are ectothermic and their life cycles are affected by the temperature of their environment. Every insect species has a fairly well defined range of temperature within which it is able to survive. The extremes of this tolerance-range vary from species to species and also among individuals of the same species. In the case of D. melanogaster, males are more sensitive than females to abnormal

temperatures. When flies are kept at 32 C, 50% of the females and 96% of the males become sterile; the males are able to copulate but no sperm are produced, and the sperm in the male organ lose motility and subsequently degenerate (Young and Plough, 1926). The temperature limits between which reproduction can occur are often narrower than the range of temperature over which other activities of the same species remain normal. Females of D. subobscura which are exposed to 30.5 C during their early adult life show a greater reduction in the rate of oviposition during later life (Maynard-Smith, 1959). Another effect of temperature was shown with D. melanogaster. When reared as embryo, larva and pupa at 18 C the flies live longer than those reared throughout life at 28 C (Alpatov and Pearl, 1929). More recently it has been demonstrated that larvae of D. willistoni, D. equinoxialis, D. pseudoobscura and D. persimilis grown at lower temperature produce larger adults (Ray, 1960). Life span can be extended and at the same time 50% fertility is maintained when males and females of D. melanogaster are stored at 15 C for 89 days and later transferred to 25 C (Bos, 1974). Development can be extended up to a period of six months in D. pseudoobscura that have been kept at 5 C for 178 days and later transferred to 19 C for a period of 10 days (Druger, 1962). In general, within a range of temperature that permits survival, egg production can be expected to increase with increasing temperature (Patton, 1963).

Humidity effects are closely allied with temperature. The effect of humidity upon respiration is complicated by other factors, most important of which is water content of the insect. In alternating wet and dry exposures, imagos of D. melanogaster, have a higher respiration in saturated air (0.1472mm$^3$O$_2$/fly/hr.) than in dry air (0.129mm$^3$O$_2$/fly/hr.) (Thompson and Tennant, 1932). Temperature exerts a relatively greater effect under the extremes of moisture conditions and vice versa. Sotavalva (1941) observed that the wingbeat rose with increasing temperature to a plateau at about 28-32 C after which it declined until the thermal death point was reached at about 35 C. In a saturated atmosphere the wing-beat frequency increased steadily until death occurred at 39-40 C. The reaction to differences in relative humidity has been reported to be correlated with the age of the flies. Young males and females of D. melanogaster preferred drier environments when given a choice between 100 per cent and 77 per cent relative humidity. The intensity of this preference for drier environment decreased until flies were practically indifferent at 2 weeks of age (Perttunen and Ahonen, 1956). There is evidence that the rate of weight loss (i.e., water loss) in dry air increases with age (Kalmus, 1941; Perttunen and Salmi, 1956). Pittendrigh (1958) found that D. persimilis lost water by cuticular transpiration more rapidly than D. pseudoobscura, and that males lost water more rapidly than females.

A deficient diet may be expected to result in slowing down many physiological processes (decrease in growth, size, weight and fecundity). Since many of the reserves which go to form the eggs are laid down during the larval stage, egg production in the adult may be influenced by the nutrition of the larvae. Underfeeding of the larva of Drosophila will reduce the number of eggs laid by resultant adults (Alpatov, 1932). The fecundity and viability of the eggs of Drosophila females is influenced by the quantity and variety of yeasts in the diet. The different strains of yeasts probably vary in their vitamin content. Robertson and Sang (1944) and King and Wilson (1955) found that D. melanogaster during the height of egg production daily ingests yeast about equal to its own body weight and produces eggs approximately one third of its weight.

Sang (1956) found that 4-6 day old D. melanogaster females produce faster developing larvae than either younger (2-3 day old) or older (8-11 day old) females. O'Brian (1961) found that the age of the female parent affects the fecundity and longevity of her offspring, but not the rate of development. In D. melanogaster, Butz and Hayden (1962) showed that the number of adults resulting from eggs laid by parents 35 days old was considerably less than those from parents 24 hours of age. Moreover, the reduction in viability of the emerging adults was directly related to the age of the maternal parent. The older the mother the fewer the number of adult flies emerging.

Crowding of the offspring is an environmental factor that affects the rate of development of preadult flies. It has been shown in D. nasuta (Ranganath and Krishnamurthy, 1972) that only about 50% of the offspring emerged from crowded conditions.

The above review of the literature indicates that in a study of life cycle it will be necessary to control as closely as possible temperature, humidity, food and age of the parents.

The purpose of this work is to determine the life cycle of different species of Drosophila of different sub-genera and coming from different environments. The species studied are as follows:

Sub-genus Drosophila
(species)

| | | |
|---|---|---|
| D. virilis | (Sturtevant) | group virilis |
| D. immigrans | (Sturtevant) | group immigrans |
| D. viracochi | (Arncic and Koref-Santibañez) | group mesophragmatica |
| D. funebris | (Fabricius) | group funebris |

Sub-genus Sophophora

| | | |
|---|---|---|
| D. pseudoobscura | (Frolova) | group obscura |
| D. ananassae | (Doleschall) | group melanogaster |

Sub-genus Dorsilopha

| | |
|---|---|
| D. busckii | (Coquillett) |

TABLE I

LIFE CYCLE OF DIFFERENT SPECIES OF *DROSOPHILA*

| Species | Temp. | Time (days) | | References |
|---|---|---|---|---|
| | | Egg-laying to eclosion | Emergence to sexual maturity | |
| *D. melanogaster* | 25 C | 8 days + 18 hours | | Powsner, 1935 |
| *D. melanogaster* | 29 C | | 7-8 days | Suzuki, 1970 |
| *D. melanogaster* | 17 C | | 22-28 days | Suzuki, 1970 |
| *D. melanogaster* | 22 C | | 11-12 days | Suzuki, 1970 |
| *D. immigrans* | 25 C | 11-12 days | | Waterman, 1971 |
| *D. busckii* | 25 C | 12 days | 2 days | Wolfsberg, 1958 |
| *D. hydei* | 25 C | | 7 days | Gregg and Day, 1965 |
| *D. mesochracmatica* | 15 C | 40 days | | Hunter, 1966 |
| *D. pavani* | 16 C | 40 days | | Budnik, et. al., 1971 |
| *D. pavani* | 25 C | 19 days | | Budnik, et. al., 1971 |
| *D. pinicola* | 18 C | 17-23 days | 12-15 days | Spieth, 1974 |
| *D. flavopinicola* | 18 C | 17-23 days | 12-15 days | Spieth, 1974 |

TABLE I (cont.)

LIFE CYCLE OF DIFFERENT SPECIES OF *DROSOPHILA*

| Species | Temp. | Time (days) | | References |
|---|---|---|---|---|
| | | Egg-laying to eclosion | Emergence to Sexual maturity | |
| *D. melanderi* | 18 C | 60 days | 30 days | Spieth, 1974 |
| *D. sub-quinaria* | 16-23 C | 17-19 days | 3-4 days | Hunter, personal communication |
| *D. sub-occidentalis* | 16-23 C | 18-20 days | 3-4 days | Hunter, personal communication |

## METHODS AND MATERIALS

The original stocks of Drosophila virilis, D. immigrans, D. pseudoobscura, D. funebris and D. busckii from Stockton, California, D. viracochi from Bogotá, Colombia, and D. ananassae from Barquisimeto, Venezuela, were collected in nature by sweeping over bait. All flies except D. viracochi were raised for three generations in a Forma Scientific Model 12 incubator at 25±1 C. D. viracochi were grown at 20±1 C. All the flies were exposed to light daily from 8 a.m. to 8 p.m. The flies were cultured in 300 ml jars with plastic foam stoppers on Carolina Instant Drosophila medium (#67-5002, Carolina Biological Supply Company) to which 1 ml of a 10% autoclaved Fleischmann's bakers yeast solution was added.

In the present work, experimental vials contained 4 grams of medium, 30 ml of water and a few drops of 10% yeast suspension. Green food coloring was added to the medium so eggs could be seen easily with the aid of a dissecting microscope.

Three males and three females were isolated within two hours of hatching. They were maintained in isolation for 48 hours in separate 80 ml vials with food. The flies were never etherized and in order to sex them, they were isolated one by one in an empty vial and sexed with the aid of a dissecting microscope. Usually this was done during the morning from 8 a.m. to 10 a.m. or from 9 to 11 a.m. Three of the previously isolated males and three

females were then placed together in an empty vial and allowed to mate for 2 hours. After this time the females were separated from the males and placed in an 80 ml vial with food. The vials containing females were kept in the incubator and checked once each day with the dissecting microscope to determine the presence or absence of eggs, larva or pupa. The adult females were removed from the experimental vials when eggs were present. In cases where fertile eggs were not found after 48 hours the experiment was repeated using flies isolated for longer periods in units of 24 hours.

## RESULTS

As shown in Table II and Figure I, the life cycle of Drosophila at 25 C ranges from 21 days in D. virilis to 13 days plus 6 hours in D. ananassae. The other species fall within this range (16 days in D. busckii, 15 days in D. immigrans, 18 days in D. funebris and 18 days in D. pseudoobscura). D. viracochi requires 27 days, but was grown at 20 C, so is not directly comparable with the others.

The time required from emergence of the adult to sexual maturity represents the major portion of the life cycle in each species, ranging from 6 days in D. virilis to 1 day in D. immigrans with intermediate values of 3 days plus 6 hours for D. ananassae, and 2 days for D. funebris, D. pseudoobscura and D. busckii. Again, D. viracochi grown at 20 C requires 8 days and is outside of this range.

The time for egg-laying shows less variation. It is 3 days for D. pseudoobscura, D. busckii and D. immigrans and 2 days for D. virilis, D. funebris, D. ananassae and D. viracochi.

Eclosion time also showed slight variation from 4 days in D. virilis, 3 days in D. pseudoobscura, to 2 days in D. busckii, D. immigrans, D. funebris, D. ananassae and D. viracochi.

The pupal stage ranges from a high of 6 days in D. funebris to a low of 2 days in D. ananassae, with intermediate values of 4 days in D. pseudoobscura and D. immigrans and 3 days in D. virilis. Again, D. viracochi (7 days)

requires the longest time.

The time for emerging of the adult from the pupae varies from 6 days in D. pseudoobscura, D. virilis and D. funebris to 4 days in D. busckii, while D. immigrans and D. ananassae require 5 days, D. viracochi requires 8 days.

Table III shows the per cent of the life cycle which each stage occupies. In general, the pupal stage is the longest and the species differ most in the time to sexual maturity.

The multiple-range test was calculated for these data and the 95% confidence limits determined. It is concluded that the mean time for egg-laying is not significantly different for D. pseudoobscura, D. immigrans, D. busckii and D. funebris. However, there is a significant difference between the above values and those of D. virilis and D. ananassae; the latter 2 are not significantly different from each other.

There is not a significant difference between the means for the larval period of any of the species.

The mean time for the pupal stage is not significantly different for D. pseudoobscura, D. immigrans, D. busckii and D. funebris. However, there is a significant difference between the above values and those of D. virilis and D. ananassae, the latter 2 differ significantly from each other.

The mean time for the adult stage is not significantly different for D. pseudoobscura, D. virilis and D. funebris. However, there is a significant difference between the above

values and those of D. immigrans, D. buscki, and D. ananassae. There is no significant difference between D. immigrans and D. buscki. D. ananassae differs significantly from the latter two species.

TABLE II

LIFE CYCLE IN DAYS OF 7 SPECIES OF *DROSOPHILA*

| Species | Hatch to sexual maturity | Sexual maturity to laying-eggs | | Eggs to larvae | | larvae to pupae | | Pupae to adult | | Overall life cycle |
|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | Mean | Standard error | Mean | Standard error | Mean | Standard error | Mean | Standard error | |
| *D. pseudoobscura* | 2 | 3.00 | 0.19 | 2.50 | 0.17 | 4.00 | 0.20 | 6.00 | 0.21 | 17.5 |
| *D. virilis* | 6 | 1.80 | 0.17 | 3.60 | 0.18 | 3.30 | 0.26 | 6.10 | 0.12 | 20.8 |
| *D. busckii* | 2 | 3.10 | 0.10 | 2.00 | 0 | 5.00 | 0 | 4.30 | 0.15 | 16.4 |
| *D. immigrans* | 1 | 2.80 | 0.20 | 2.40 | 0.21 | 4.00 | 0.34 | 4.70 | 0.24 | 14.9 |
| *D. funebris* | 2 | 2.40 | 0.22 | 1.90 | 0.18 | 6.00 | 0.30 | 5.80 | 0.29 | 18.1 |
| *D. viracochi** | 8 | 2.00 | 0 | 2.30 | 0.15 | 7.00 | 0.34 | 8.00 | 0.37 | 27.0 |
| *D. ananassae* | 3 days + 6 hrs. | 1.70 | 0.17 | 2.10 | 0.07 | 2.10 | 0.18 | 3.60 | 0.14 | 12.5 + 6 hrs. |

*All species at 25 C except *D. viracochi* at 20 C

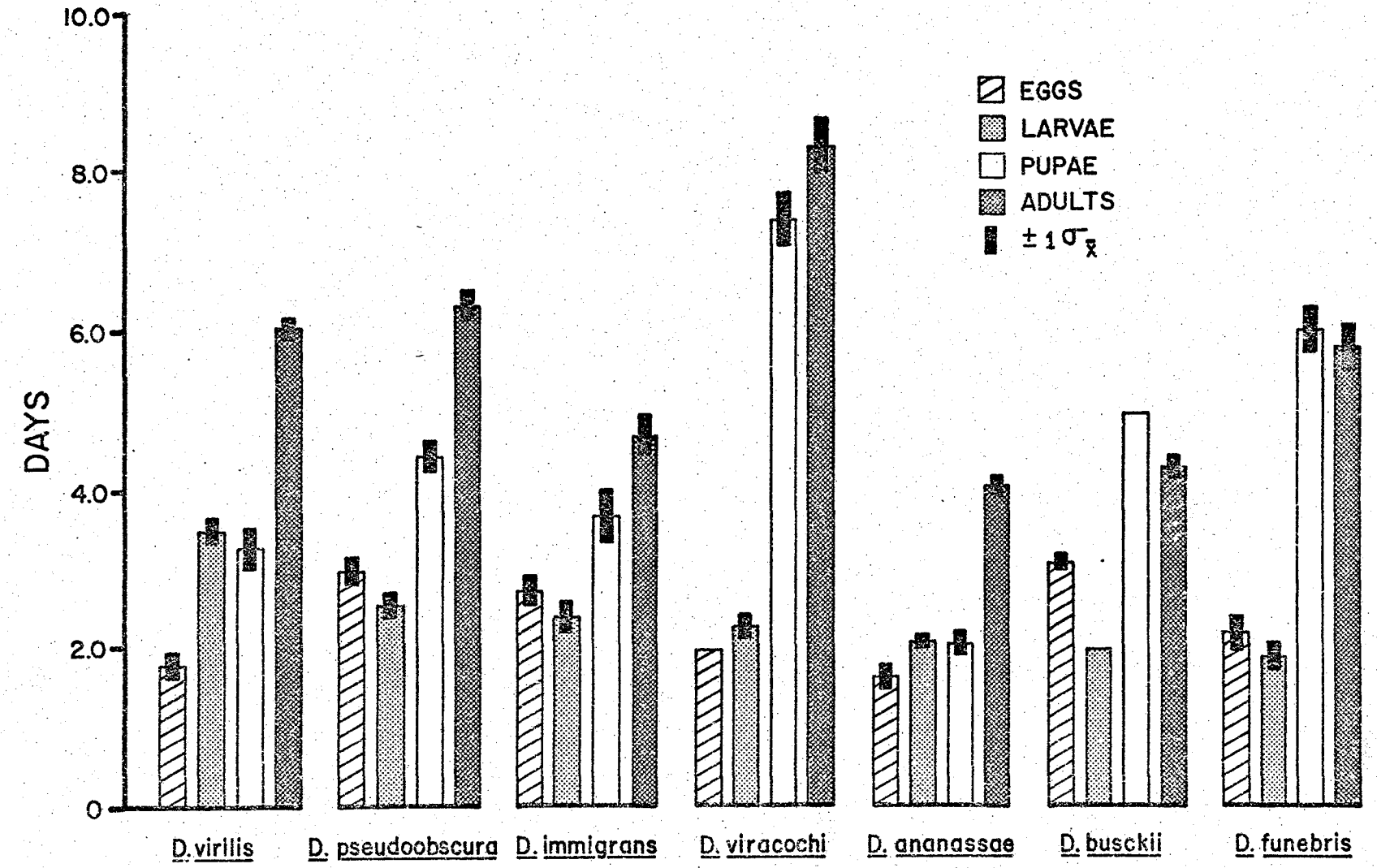
TABLE III

TIME REQUIRED IN EACH STAGE OF THE LIFE CYCLE

| Species | PERCENT OF DAYS | | | | NUMBER OF DAYS | |
|---|---|---|---|---|---|---|
| | ~~Hatch~~ emergence to sexual maturity | Sexual maturity to laying-eggs | Laying-eggs to larvae | Larvae to pupae | Pupae to adult | Overall life-cycle |
| D. pseudoobscura | 10 | 16 | 16 | 26 | 32 | 18 |
| D. virilis | 29 | 9 | 19 | 14 | 29 | 21 |
| D. buscki | 13 | 19 | 13 | 31 | 25 | 16 |
| D. immigrans | 7 | 20 | 13 | 27 | 33 | 15 |
| D. funebris | 11 | 11 | 11 | 33 | 33 | 18 |
| D. ananassae | 23 | 15 | 15 | 15 | 31 | 13 days + 6 hrs. |
| D. viracochi | 29 | 7 | 7 | 29 | 29 | (28) |

27 on Table II

FIGURE 1. Comparison of days required to complete each stage in the life cycle of D. virilis, D. pseudoobscura, D. immigrans, D. viracochi, D. ananassae, D. buzckii, and D. funebris. (All values are means, standard error shown.)


10.0
8.0
6.0
4.0
2.0
0
DAYS
EGGS
LARVAE
PUPAE
ADULTS
± 1 σ x̄
D. virilis
D. pseudoobscura
D. immigrans
D. viracochi
D. ananassae
D. busckii
D. funebris

## DISCUSSION

The data reported here show that the life cycle of *Drosophila* at 25 C ranges from a low of 13 days plus 6 hours in *D. ananassae* to 21 days in *D. virilis*. The other species studied fall within this range (16 days in *D. busckii*, 15 days in *D. immigrans*, 18 days in *D. funebris* and 18 days in *D. pseudoobscura*). *D. viracochi* requires 27 days, but this can not be compared with the above mentioned species since it was studied at 20 C. The time for emergence of the adult to sexual maturity is the major contribution to this time difference. *D. immigrans* requires only 1 day, *D. busckii*, *D. funebris*, and *D. pseudoobscura* require 2 days, *D. ananassae* requires 3 days plus 6 hours and *D. virilis* 6 days. Again, *D. viracochi* which requires 8 days is outside of this range since it was studied at 20 C. There is less difference in the time for the other stages of development. In general, it takes 2 to 3 days in order to lay fertile eggs after mating and 2 to 4 days in order to hatch as larvae, and from 2 to 8 days for the pupal stage. Comparison of these data with those previously reported in the literature is shown in Table IV.

The species reported here represent both cosmopolitan as well as indigenous forms from a variety of different environments as well as different taxonomic groups. The cosmopolitan species live in a broad geographic range of widely different temperatures and survive a wide seasonal difference in temperature. On the other hand *D. ananassae* is restricted

TABLE IV

COMPARISON OF LIFE CYCLES

| Species | Temp. | Time (days) | | | Reference |
|---|---|---|---|---|---|
| | | Egg-laying to eclosion | Sexual maturity | Egg-laying | |
| D. melanogaster | 25 C | 8 days+18 hours | | | Powsner, 1935 |
| D. immigrans | 25 C | 11-12 | | 3-4 | Waterman, 1971 |
| D. immigrans | 25 C | 11 | 1 | 3 | (This paper) |
| D. busckii | 25 C | 12 | 2 | | Wolfsberg, 1958 |
| D. busckii | 25 C | 11 | 2 | 3 | (This paper) |
| D. hydei | 25 C | | 7 | | Gregg and Day, 1965 |
| D. virilis | 25 C | 13 | 6 | | (This paper) |
| D. mesophragmatica | 15 C | 40 | | | Hunter, 1966 |
| D. pavani | 16 C | 40 | | | Budnik, et. al., 1971 |
| D. virgocchi | 20 C | 17 | 8 | | (This paper) |
| D. ananassae | 25 C | 8 | 3 days+6 hours | | (This paper) |
| D. pseudoobscura | 25 C | | | 3-5 | Wolfsberg, 1959 |
| D. pseudoobscura | 25 C | | 2 | 3 | (This paper) |
| D. funebris | 25 C | 14 | 2 | | (This paper) |

in distribution to warm climate while D. viracochi is limited to cool environments. The results reported here are quite consistent with those in the literature. D. melanogaster, for example, requires 8 days plus 18 hours from egg-laying to the emergence of the adult at 25 C (Powsner, 1935). Waterman (1971) reported that D. immigrans required from 3 to 4 days to lay fertile eggs and 11-12 days for development from egg to adult. We found this species to require only one day to reach sexual maturity, 3 more days for egg-laying, and 11 days from egg to adult. D. busckii (Wolfsberg, 1958) has been reported to require 12 days for development from egg to adult and 2 days to become sexually mature. We found that it requires 11 days for development from egg to adult, 2 days to become sexually mature and 3 more days for egg-laying. The species mentioned above are considered cosmopolitan species. They can be found wherever humans live. Some of them reach sexual maturity in a short time, but this is not always true for all the cosmopolitan species. D. hydei requires 7 days after emerging from the pupae to reach sexual maturity (Gregg and Day, 1965). We worked with D. virilis which is considered a cosmopolitan species, and we found that it takes 6 days in order to attain sexual maturity after emerging from the pupae and 13 days for development from egg to emergence of the adult.

Generally when flies are living at a low temperature development takes a longer period of time. This is true for D. mesophragmatica, which has been reported to require

40 days from egg-laying to emerging of the adult when developing at 15 C, which is the average temperature of its natural habitat (Hunter, 1966). The closely related D. pavani was reported to develop from egg to adult in 40 days at 16 C (Budnik, et. al., 1971). D. viracochi belongs to this group and at 20 C requires 8 days to attain sexual maturity and 17 days from egg-laying to emerging of the adult. It would be of interest to compare these closely related species at the same temperature.

When we consider a species such as D. ananassae that is restricted to a constant warm environment which is characterized by the lack of seasonal changes, we find that its life cycle is relatively short. D. ananassae requires 3 days plus 6 hours to attain sexual maturity and 8 days from egg-laying to emerging of the adult.

D. pseudoobscura is a species common to the mountains of California and consequently is subject to seasonal changes. According to Wolfsberg (1959) they lay eggs between the third and fifth day after emerging from the pupae and we have found that they reach sexual maturity 2 days after emerging from the pupae and require 3 more days until egg-laying at 25 C.

It is interesting to speculate on the biological advantage of the rapid attainment of sexual maturity. A short period, as for example 1 day for D. immigrans, might allow them a food supply which is of a short duration. Injured fruit supports yeast growth for only a limited time. A species which matures rapidly could lay eggs very soon after hatching, and utilize the same food in which it had developed.

A species which matures more slowly, such as D. virilis which requires 6 days may avoid competition with the rapidly reproducing species. Probably all cosmopolitan species are coexisting in similar environments and must be adapted in different ways in order to survive this competition. For example, Tantawy and El-Wakil (1970) found that although the lifetime egg production of D. funebris in isolation is significantly higher than that of D. virilis, the latter demonstrates a higher competitive ability. When D. virilis and D. funebris were reared together in population cages, D. funebris was eliminated by D. virilis within 90 days.

We found that D. funebris requires 14 days for development from egg to adult and 2 days to become sexually mature at 25 C. There is evidence that D. funebris withstands a great variety of different temperatures, probably due to the accumulation of appropriate temperature genes into their genome. Timofeeff-Ressovsky (1940), studying the relative viability of D. funebris from regions covering the major climatic zones of Europe, northern Africa and Russia, found that the northern populations were more resistant to low temperatures, and the southern populations more resistant to high temperatures. The eastern populations showed resistance to both high and low temperatures, which could be related to the type of 'continental' climate of these regions, characterized by low mean winter temperatures and a very high mean summer temperature.

Another advantage of differing lengths of life cycle might be related to the fact that Drosophila males will

court females of other species (Spieth, 1952). This waste of energy could be avoided if the species utilizing the same food supply were not sexually mature at the same time.

I would like to point out that the conditions under which this work has been conducted are extremely artificial and represent an oversimplification of the situation found in nature. Slight variation in any of those conditions might yield completely different results. Some of the differences between natural and artificial conditions are:

First: The amount of time allowed for mating was limited to 2 hours. All the species were treated the same experimentally without regard for possible differences in mating activity. It has been reported (Hunter, 1967) that D. mesophragmatica prefers the early morning for courting and copulation. Perhaps the specific morning hours used in this study are not the best hours for all the species.

Second: The temperature was maintained constant at 25 C. In nature the temperature fluctuates within a certain range through the day and night and the flies do not live at a constant temperature. Levins (1969) observed that D. willistoni, a species that usually lives in the tropics where there is no seasonal change and the temperature is more or less constant, can avoid heat stress by behavioral means. On the other hand, individuals that are subject to seasonal changes are able to use other biological mechanisms, one of which is hibernation. In D. persimilis, Mohn and Spiess (1963) found that the pupal and adult stage over-winter best, while in other species it is likely that over-wintering

may occur in the larval stage. Ives (1970) found evidence that larvae of D. melanogaster over-winter in rotten-apple piles in South Amherst, Massachusetts.

Third: The food supply was kept constant also. In nature there is not always food available and it has been shown that different species use different mechanisms of coping with the situation. For example, the development of ovarioles may be changed. Kambysellis and Heed (1971) have shown that the reproductive potential is decreased if the number of ovarioles per fly is low and only one egg can be found at any time in each sexually mature individual. If the conditions are suitable the number of ovarioles per fly can be increased and consequently increase the number of eggs laid. Eggs may be retained by the female, reach advanced stages of development and be laid when conditions are favorable. There is evidence that D. melanogaster retain their eggs when the media conditions for oviposition are unsuitable (David and Bouletreau-Merle, 1971). Genetic control of egg retention has been reported in D. melanogaster (King, 1963).

Fourth: The space available to the flies for all their activities of feeding, mating and egg-laying was limited in this experiment. They may not delay as long in laying eggs under more natural conditions. In nature for example, the sites for oviposition would be chosen by the flies depending upon their particular humidity preferences. Moore (1952) has shown that in competition experiments between the sibling species D. simulans and D. melanogaster, D. simulans is

better able to oviposit in the center of food cups and on food having dry surfaces; in other words, desiccation makes the medium less favorable for D. melanogaster as compared with D. simulans. Del Solar and Palomino (1966) reported that females of D. melanogaster prefer to lay eggs in sites previously used for oviposition by other females. Furthermore, Mainardi (1968) found that females of D. melanogaster preferred to lay eggs where males had previously been present. The fact that we passed the isolated females onto clean food may have also delayed the time for egg-laying because the female did not have the stimulus created by the presence of eggs laid by other females nor the stimulus of male pheromone present in the vial. On the other hand D. pseudoobscura females tend to lay more eggs in clean vials than in those previously occupied (Del Solar, 1970). Also it has been found (Ellis and Kessler, 1975) that males and females of D. melanogaster when housed in isolation after eclosion, showed higher mating frequencies and shorter latencies than group-housed flies.

Probably some of the species could become sexually mature before the time found in this work. For example some D. ananassae can become sexually mature after 72 hours. Some of the flies mate, but no eggs were laid. In all species some eggs never hatched. This might be due to lack of fertilization or perhaps to lethal genetic factors.

There is need for work to be done in this field where so little has been reported. It is necessary to learn more

about the ecology and distribution of these species. This basic information would make it easier for workers in other fields to use these different species.

In order to carry on these studies at a lower temperature, it is necessary to change the design of the experiment because at lower temperature the flies take a longer time to attain sexual maturity, and they are so inactive that 2 hours is insufficient for mating. It would be useful to have data at different temperatures because it would compare more closely with natural conditions.

SUMMARY

1. The duration of the life cycle (egg to sexual maturity) of 7 species of Drosophila grown under specific laboratory conditions is reported here at 25 C. It is 21 days for D. virilis, 16 days in D. busckii, 15 days in D. immigrans, 18 days in D. funebris, 18 days in D. pseudoobscura, in D. ananassae 13 days plus 6 hours and at 20 C it is 27 days for D. viracochi.

2. The time from hatching to sexual maturity is the major contribution to the time differences reported, e.g. 6 days for D. virilis compared to 1 day for D. immigrans.

3. Species indigenous to cool environment have a longer life cycle than those indigenous to a warm environment. Cosmopolitan species vary widely in the length of the life cycle but no phylogenetic patterns emerged.

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