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Population Growth of *Drosophila melanogaster* (Diptera: Drosophilidae) at Constant and Alternating Temperatures[1]

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ABSTRACT

Alternating temperatures resulted in higher values of the innate capacity for increase (r_m) of *Drosophila melanogaster* Meigen than mean constant temperatures within the range of temperature favorable for growth and reproduction. This difference resulted from slightly faster development and earlier attainment of maximum fecundity at alternating temperatures.

Preliminary mathematical models relating r_m to constant and alternating temperatures are derived. These models are:

$r_m = 0.587 - 0.0228(7.80e^{0.00012(30.3-t°C)^2})$ for constant temperatures, and

$r_m = 0.587 - 0.0228(9.96e^{0.0137(25.3-t°C)^2})$ for alternating temperatures. Average deviation between empirical and computed values is 2.3%. The efficacy of these models is restricted to temperatures favorable for reproduction.

In most natural environments, temperature undergoes usually regular diel variations with superimposed irregular fluctuations. A major inadequacy inherent in many laboratory studies on the effects of temperature on biological processes is that they are conducted at constant temperatures and therefore fail to approximate natural temperature conditions.

The literature concerning the relative effects of constant and fluctuating temperatures on rates of biological processes generally is extensive but inconsistent. Most such studies with insects have been concerned with effects on single life parameters such as development. Howe (1967) concluded that available evidence was insufficient to prove that variable temperature either stimulates or retards development of insect eggs.

Surprisingly few studies of the effects of varying temperatures on the growth of insect populations as a whole have been reported. Two recent exceptions are papers by Strong and Sheldahl (1970) and Phillip and Watson (1971), the former dealing with only the adult segment of the population.

The present paper is concerned with the effects of some constant and alternating temperatures on populations of a strain of *Drosophila melanogaster* Meigen and formulates preliminary predictive models of the effect of temperature on the intrinsic rate of population growth at temperatures within the favorable range.

MATERIALS AND METHODS

Experimental populations were observed in controlled environment cabinets at several constant and alternating temperature regimes shown in Table 1. Temperatures were controlled to ±0.5°C. Alternating temperatures cycled every 12 hr. Humidity in the cabinets was controlled usually to within ±5% of a value which gave about the same vapor pressure deficit at each temperature. Lighting was provided by a combination of fluorescent and incandescent lamps and a 16-hr photophase was maintained. The higher temperature of an alternating pair was programmed entirely within the light period; 4 hr of the lower temperature also occurred during the photophase.

A vestigial-winged strain of *D. melanogaster* obtained commercially and cultured at 25°C was used in the experiments. Stock cultures were reared in 850-ml bottles each containing 15 g of instant Drosophila medium (Carolina Biological Supply Company, Burlington, N. C.) and 4 g of yeast. Each culture was begun with 10 pairs of flies which were removed from the bottles after 4 or 5 days during which time sufficient eggs were laid. Yeast was added as needed. One such culture begun each week yielded a constant supply of experimental flies. Flies from these stock cultures were reared for one generation at each temperature regime and experimental flies for that particular regime were obtained from these cultures.

To determine age-specific survival and fecundity, 50 flies of each sex were collected within 12 hr of emergence and placed in a 425-ml mason jar. Four holes, 22 mm diam, cut in the sides of the jar and covered with organdy allowed circulation of air through the jar. Pearl 101 synthetic medium (Pearl et al. 1926) was used as an oviposition site. It was poured into a watchglass and allowed to set. A

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suspension of 0.1 g yeast in 2 ml distilled water was spread on the surface of the medium. The watchglass was placed over the mouth of the jar and attached with masking tape. The jar was inverted in a beaker and placed in the environmental chamber. Eggs laid were counted every 24 hr and the watchglass was replaced with a fresh one. Deaths of parent flies were also recorded daily. Temperature inside the jar was measured with a hypodermic thermistor and was identical with the chamber temperature.

Viability of eggs and developmental time of immature stages were determined for each temperature regime as follows. Between 200 and 300 newly emerged flies were transferred to an 850-ml bottle containing instant medium and yeast. The bottle was then placed at the appropriate experimental temperature. On the 5th day, the flies were transferred to a mason jar the mouth of which was closed with a watchglass containing Pearl's medium and yeast as before. Flies were allowed to oviposit for up to 4 hr. The watchglass was then removed, the eggs were counted, the watchglass was fastened over the mouth of another jar and replaced in the cabinet.

Previous pilot experiments at each temperature showed that all eggs hatched over a few hours and revealed the approximate time of hatch. On the basis of these results, all experiments were begun at an appropriate time so that hatch would occur during normal working hours. In this way, time of hatch of 50% of the eggs was accurately determined by frequent observation and larvae of known age were collected for future experiments.

One hundred larvae collected within 4 hr of hatch were placed in four 40-ml glass vials. Each vial contained 25 larvae, 3 g instant medium, 0.45 g yeast, and 15 ml water. Vials were plugged with sponge-rubber stoppers, placed in the temperature cabinet, and observed twice daily. Temperature inside the medium was measured with a hypodermic thermistor in several experiments and was usually within 0.5°C of the chamber temperature. Number of flies emerged and time of emergence were noted precisely. All flies emerged during the light period. The time at which 50% of the newly emerged flies oviposited was taken as the developmental time. In a few experiments, 50% of the flies emerged immediately after the dark period. In such cases, it was assumed that these flies would have emerged earlier but were inhibited, by their photoperiodic rhythm, from emerging during darkness. Emergence time was then taken as the midpoint of the 8-hr dark period and developmental time was estimated to be 4 hr previous to the observed time of 1st oviposition.

Flies collected over 12 hr were used to determine

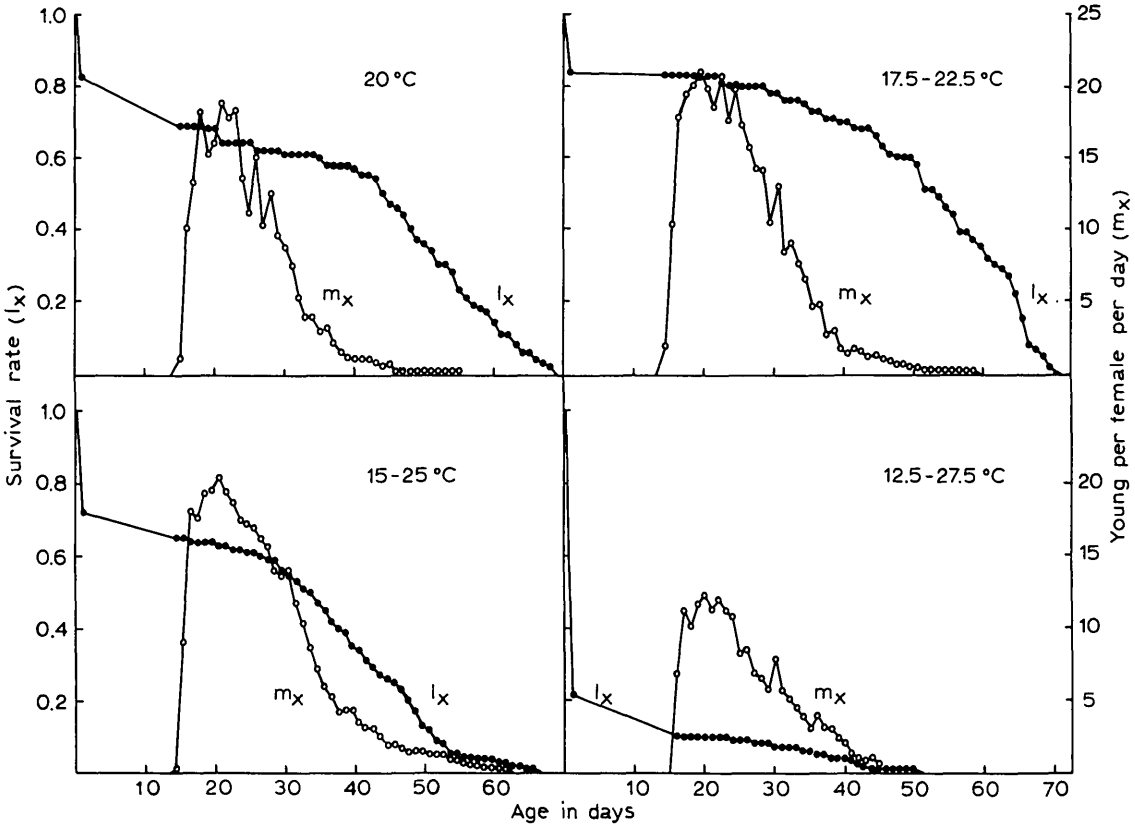

FIG. 1.—Survival rates and age-specific fecundity rates of *D. melanogaster* at constant and alternating temperatures of 20, 17.5–22.5, 15–25, and 12.5–27.5°C.

the time between emergence and 1st oviposition. The possible error is then considered to be ca. ±6 hr. Total maximum possible error in determining complete developmental time including egg age (±2 hr), larval age (±2 hr), time to 50% emergence (±0.5 hr), age of adults (±6 hr), and time of 1st oviposition is estimated to be ca. ±0.5 day.

Population performance was assessed by constructing life tables for populations at each temperature regime. From these data, the intrinsic rate of increase, r_m, was calculated from the equation $\Sigma e^{-r}m^x l_x m_x = 1$, where l_x is the survival rate of females and m_x is the age-specific fecundity rate. Derivation of r_m is discussed by Andrewartha and Birch (1954).

RESULTS

Longevity.—Age-specific survival (l_x) of females is shown in Fig. 1–4. The number of females alive each day is plotted as a proportion of the original complement of eggs. Time to 50% mortality and percent mortality of the immature stages are shown in Table 1.

Time to 50% mortality decreased with rising temperature at both constant and alternating temperatures. Generally, longevity was shorter at alternating temperatures than at the corresponding constant temperatures. The exception was longer survival of 50% of the population at alternations of 17.5–22.5°C than at 20°C. Time to 50% mortality at any temperature was shortest at alternations with the greatest amplitude. At alternations of 12.5–27.5°C about a mean of 20°C, 50% of the population died in less than 15 days during the immature stages. Mortality of immature stages increased with increasing constant temperatures and increasing amplitude of fluctuations about the same mean temperature.

Development.—Developmental times of populations at different constant and alternating temperatures are shown in Table 1. As temperature increased, developmental time decreased. Generally, developmental time tended to be shorter at alternating temperatures than at the corresponding constant mean temperature except when one of the alternations was 12.5 or 27.5°C. Alternations with 5° amplitude about any one mean resulted in the shortest developmental time and the time increased with increased amplitude of fluctuations. None of the flies completed development at 12.5°C constant and alternations of 5–20°C. Although a small number of eggs hatched at these temperatures, none of the larvae survived to the pupal stage.

Observed developmental times at alternating temperatures were compared with expected times determined from consideration of the proportion of development which occurred per unit time when the flies were reared at each of the temperatures constantly. For example, at 25°C, development was completed in 9.1 days, and in 32.0 days at 15°C. Therefore, the flies might be expected to complete 10.99% of their total development in one day at 25°C and 3.13% in one day at 15°C. Complete development at 12-hr alternations of 15 and 25°C would then be expected

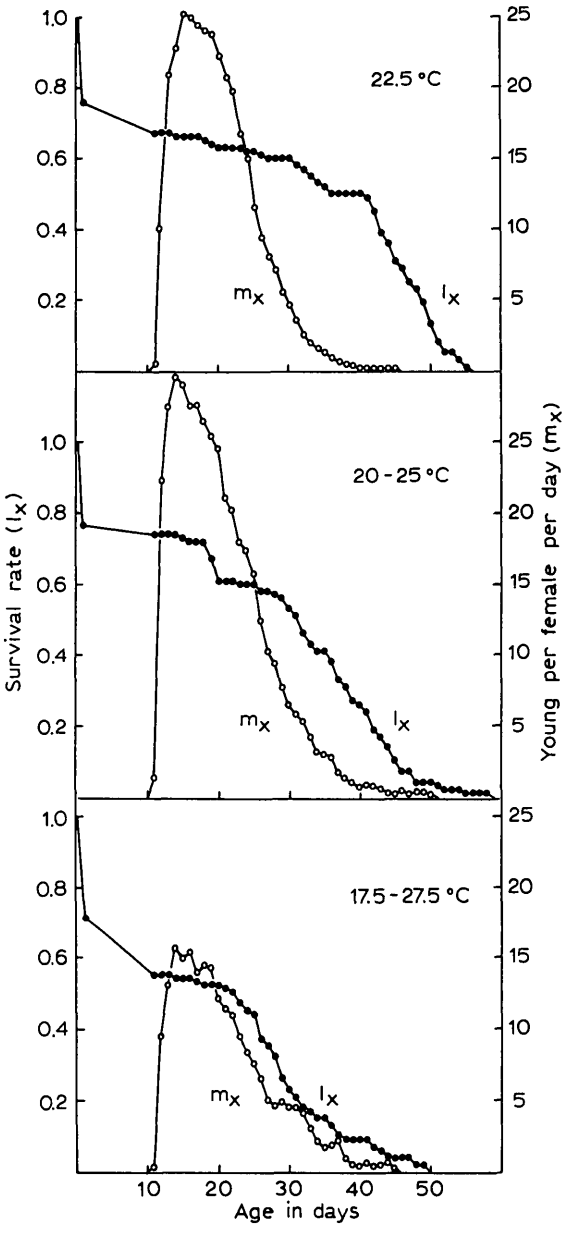

FIG. 2.—Survival rates and age-specific fecundity rates of *D. melanogaster* at constant and alternating temperatures of 22.5, 20–25, and 17.5–27.5°C.

in 14.2 days. Considering the possible maximum error of ±0.5 day in determination of developmental time, differences between observed and expected times were not sufficient to conclude whether alternating temperatures either accelerated or retarded development more than expected from a comparison of respective rates at the 2 alternations.

Relations between temperature and complete development are also shown in Fig. 5 and 6. Reciprocals of time taken to develop at each temperature were multiplied by 100 and also plotted against temperature so that values on the ordinate represent percent

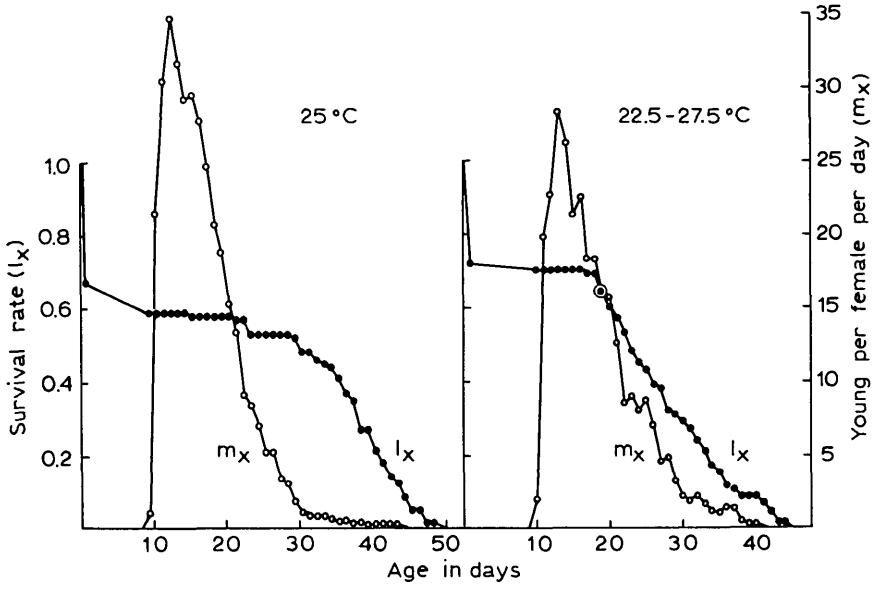

FIG. 3.—Survival rates and age-specific fecundity rates of *D. melanogaster* at constant and alternating temperatures of 25 and 22.5–27.5°C.

development per day or speed of development. Two functions were derived as empirical descriptions of the trends of developmental times and speeds at constant and alternating temperatures. These functions are of the form: $1/(Y) = Y_0 e^{-a(t_0-t)^2}$ where Y = developmental time at temperature t, Y_0 = highest value of 1/Y, e = constant = 2.718, a = constant, and t_0 = temperature corresponding to Y_0.

Derivation of these values is described by Pradhan (1945, 1946). To derive the function for alternating temperatures, the value t was taken as the mean of the 2 temperatures (Fig. 6).

A logistic equation of the form:

$$\frac{1}{Y} = \frac{K}{1 + e^{a - bx}}$$

fitted to the data as described by Davidson (1942) did not conform as closely to the observed values.

The trend of speed of development at constant temperatures was nearly linear between ca. 18 and

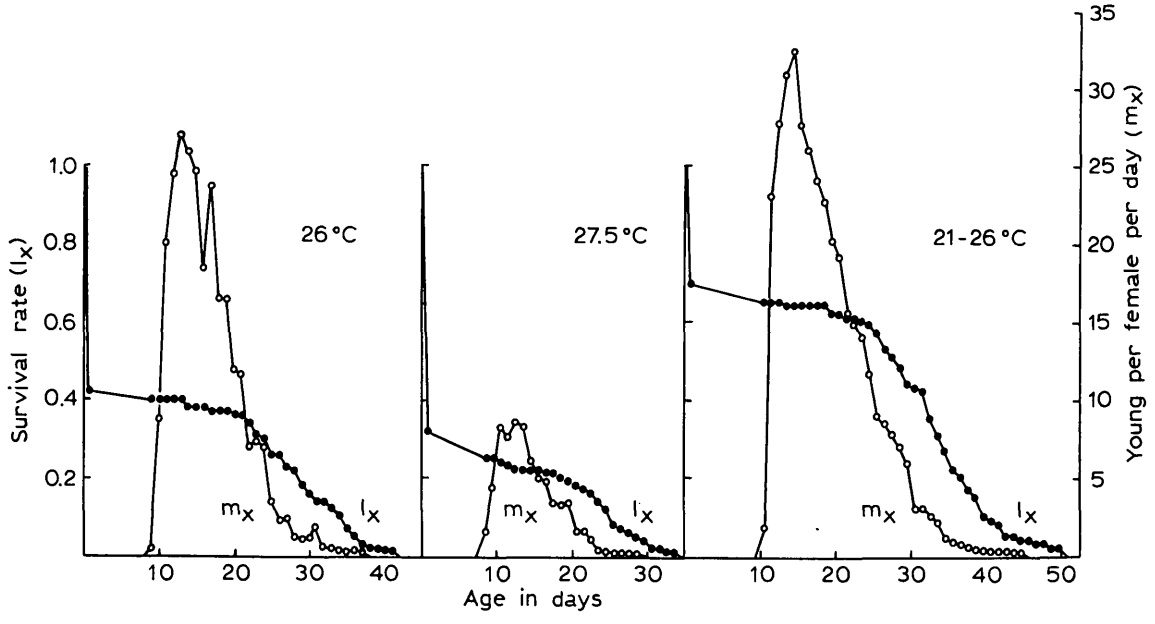

FIG. 4.—Survival rates and age-specific fecundity rates of *D. melanogaster* at constant and alternating temperatures of 26, 27.5, and 21–26°C.

Table 1.—Effects of constant and alternating temperatures on population parameters of *D. melanogaster*.

Temp (°C)	% mortality immature stages	Developmental time (days)	Time to 50% mortality (days)	Total fecundity	Innate capacity for increase (r_m)
12.5	100				
5–20	100				
15	...	32.0	...	...	...
17.5	...	22.2	...	...	...
20	31.3	15.0	44.0	22,791	0.239
17.5–22.5	17.0	14.5	52.0	31,805	.265
15–25	35.4	14.7	33.5	30,933	.248
12.5–27.5	90.5	15.6	...	15,497	.124
22.5	32.6	11.3	36.0	31,342	.320
20–25	26.5	10.8	31.0	36,074	.348
17.5–27.5	45.5	11.4	22.0	18,157	.278
21–26	35.4	10.6	26.0	33,996	.354
25	41.0	9.1	30.5	33,922	.376
22.5–27.5	29.8	9.7	23.0	25,400	.360
26	60.0	8.8	...	24,407	.326
27.5	74.0	8.4	...	5,890	.214

25°C. Within this range, an increase of 1°C produced an increase of ca. 0.85% in speed of development. Extrapolation of this part of the line to where it crosses the temperature axis gives the estimated threshold of development, in this case, ca. 12°C, the point on the temperature scale at which development would be initiated with rising temperature or halted with falling temperature. This value can be

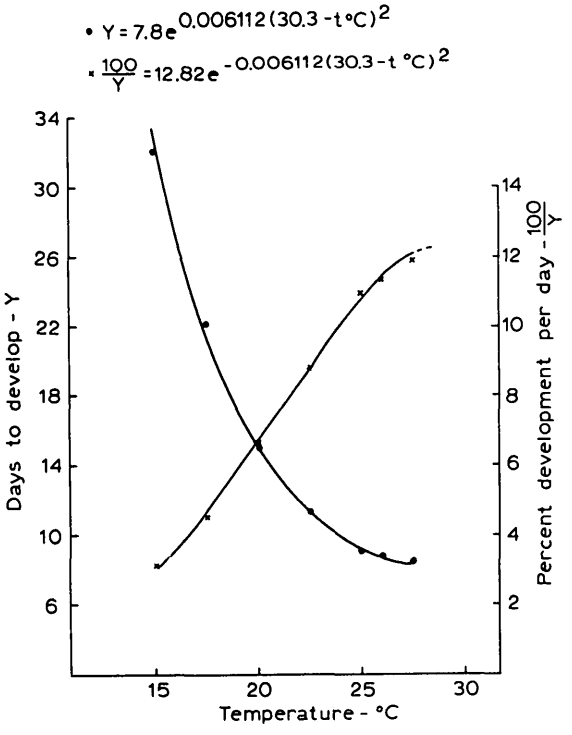

FIG. 5—Developmental time (Y) and speed of development [100/(Y)] of *D. melanogaster* at constant temperatures. The points plotted on the graph are observed values.

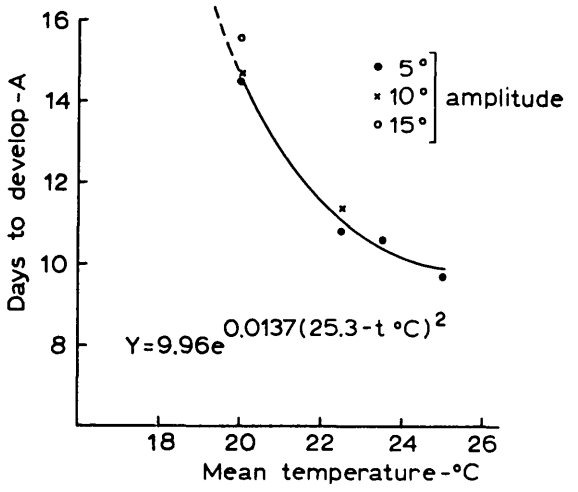

FIG. 6.—Developmental times of *D. melanogaster* at alternating temperatures. Curve calculated from means of the alternating temperatures with 5°C amplitude.

regarded only as purely theoretical because of the curvature of the temperature-velocity line at lower temperatures. However, it seems a reasonable estimate because none of the flies developed to maturity at 12.5°C although a few eggs hatched and some development followed.

Fecundity and Age Schedule of Births.—The greatest number of eggs was laid at alternating temperatures of 20–25°C and constant 25°C. Fecundity increased with increasing constant temperature between 20 and 25°C, above which it decreased. At a mean of 20°C, alternating temperatures with 5 and 10° amplitude resulted in greater numbers of eggs than at 20°C constant. At 22.5°C, only alternations of 5° amplitude resulted in more eggs than at constant temperature. Fecundity was lower at alternations of 5° amplitude about a mean of 25°C than at 25°C constant. Generally, more eggs were produced at alternating than at constant temperatures provided both alternations were favorable temperatures. Both 12.5 and 27.5°C were outside the favorable range.

Age schedules of births or age-specific fecundity rates (m_x) are illustrated in Fig. 1–4 as the number of young born per day per female alive each day. In bisexual populations, the total number of births in any period must be divided by a factor representing the sex ratio of the species because calculations are based on the female or reproductive unit of the population. In these experiments, the sex ratio was ca. 1:1 so the total number of eggs laid each day was divided by 2.

Oviposition began on the 2nd day after emergence. Peak fecundity was attained in 4 days at 25°C and alternations of 22.5 and 27.5°C but only after 7 days at 20°C and 15–25° alternations. Generally, fecundity rate rose with increasing constant temperature and mean of alternating temperatures up to 25°C.

Length of the reproductive period was also influenced by temperature. The higher the constant or

mean of alternating temperatures between 20 and 25°C, the sooner oviposition began and the shorter the reproductive period. Alternating temperatures usually slightly lengthened reproductive periods compared with corresponding constant temperatures which partly explains higher total fecundities at alternating temperatures.

Innate Capacity for Increase.—Values of r_m are listed in Table 1 and were computed on a daily basis. These values may be converted to finite rates of increase (λ) from the relation $\lambda = \text{antilog}_e\ r_m$. For example, at 20°C, $\lambda = \text{antilog}_e\ 0.239 = 1.27$, or the population has the capacity to multiply 1.27 times/female per day.

Values of r_m increased with increased constant temperature up to 25°C and decreased at 26 and 27.5°C. Within the favorable range, increased mean of alternating temperatures also produced higher innate capacities for increase. Rates of increase were higher at alternating than the corresponding constant temperatures except where one of the alternations was 27.5 or 12.5°C.

Different amplitudes of alternating temperatures also affected innate capacity for increase. Values of r_m decreased with increased amplitude of fluctuations. This decrease was related to higher rates of mortality in immature stages and slower production of eggs during early adult life.

Populations showed innate capacities for increase at all temperatures tested except 12.5 and 5–20°C, where finite rates of increase were 0 ($r_m = -\infty$). At these temperatures, populations were unable to maintain themselves and died out in the immature stages within the 1st generation. At 15° and 17.5°C, only developmental times were determined.

Population Growth Models.—Lewontin (1965) showed that the innate capacity for increase of a population is determined by 4 parameters of the function produced by plotting values of $l_x m_x$ against time. These parameters are: age at 1st reproduction, A; age at peak reproduction, T; age at last reproduction, W; and the multiplication per generation,

$$S = \int_0^\infty l_x m_x dx, \quad \text{approximated as} \quad \frac{(W - A)\ V_T}{2}$$

where V_T = the value of $l_x m_x$ at time T. Lewontin also showed that age at 1st reproduction was by far the most influential of these parameters.

Fig. 7 shows relations between each of these parameters and r_m for each temperature studied. Relations between r_m and A, T, and W were not close generally for constant temperatures above 25°C or for alternating temperature regimes in which one of the alternations was 27.5°C. This discrepancy occurred because of the overriding reduction of S at these temperatures caused by decreased survival rate (l_x), decreased fecundity rate (m_x), or both. These values were therefore excluded from subsequent calculations. The closest correlation (−0.98) was between r_m and A; the function is shown in Fig. 7. Relations between A, i.e., developmental time, and temperature are shown in Fig. 5 and 6. Because relations between r_m and A, and A vs. temperature could be accurately defined empirically by the stated functions, the equations were combined into 2 predictive, explanatory models expressing r_m at constant temperatures, $r_m = 0.587 - 0.0228(7.80e^{0.00712\,(30.3 - t°C)^2})$, and $r_m = 0.587 - 0.0228(9.96e^{0.0137\,(25.3 - t°C)^2})$ at alternating temperatures where t = the mean of alternations. Predicted values of r_m at favourable temperatures are shown in Table 2. The greatest deviation between predicted and observed values was 4.5%.

Table 2.—Empirical and predicted values of innate capacity for increase (r_m) of *D. melanogaster* at favorable constant and alternating temperatures.

Temp (°C)	r_m	
	Empirical	Predicted
20	0.239	0.246
22.5	.320	.329
25	.377	.376
17.5–22.5	.265	.253
15 –25	.248	.253
20 –25	.348	.334
21 –26	.354	.349
22.5–27.5	.360	.359

DISCUSSION

The number of alternating temperature regimes studied was too small to warrant extensive conclusions but the trend was for swifter development at alternating than at constant temperatures in the lower thermal range and relatively slower development at higher temperatures. This effect was predicted by Pradhan (1945) and observed for fruit fly eggs by Messenger and Flitters (1959). The Pradhan (1946) equation satisfactorily described the relation between temperature and rate of development and was a better fit than the logistic equation.

Time to 50% mortality of populations was generally shorter at alternating than at corresponding constant temperatures although total longevity was not consistently different.

As temperature increased up to 25°C, maximum fecundity was attained earlier. Peak fecundity was also reached sooner at alternating than at constant temperatures. Age at last reproduction decreased consistently with increased constant temperature and was usually greater at alternating temperatures except where one of the alternations was 27.5°C. Apparently, alternating temperatures generally result in earlier attainment of maximum fecundity and also extend the reproductive period. These changes resulted in greater total numbers of eggs laid at alternating than at constant temperatures except where one alternation was 27.5°C.

Strong and Sheldahl (1970) also found reduced fecundity at high temperatures. They concluded that the damage caused by exposure to 95°F could not be overcome by subsequent exposure to low temperatures either of 80 or 55°F, because there was a

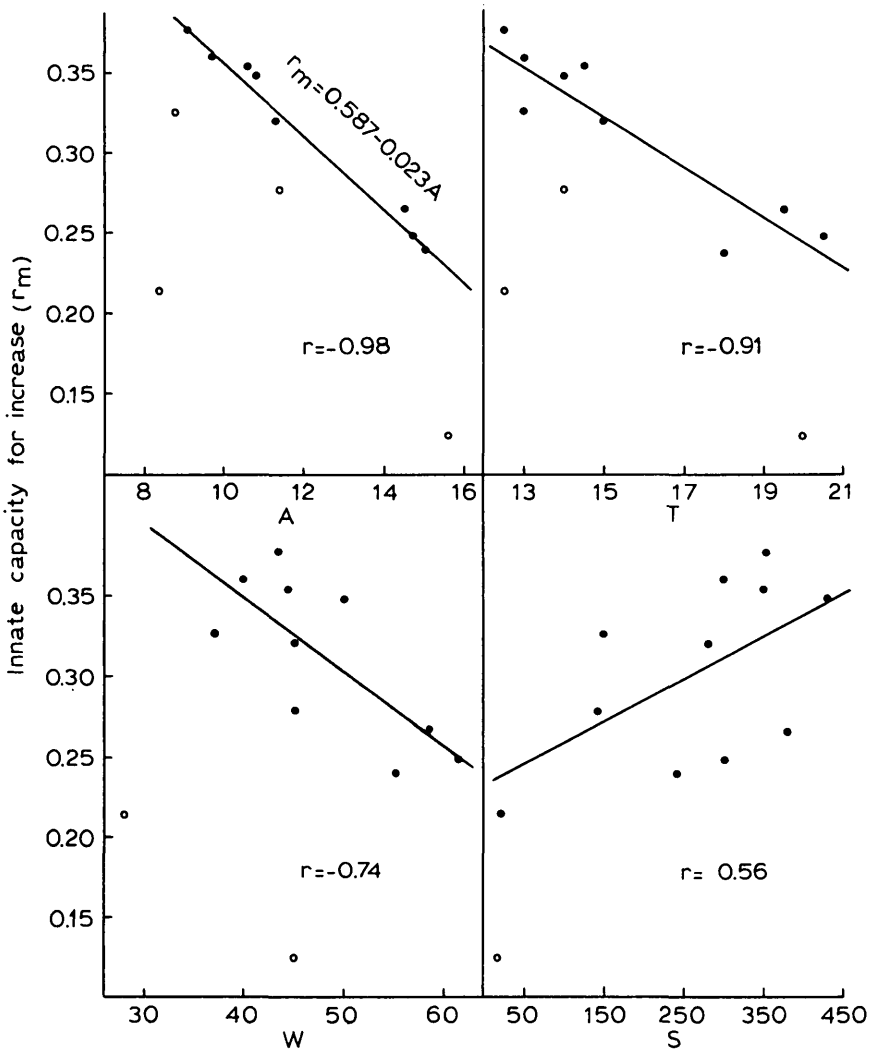

FIG. 7.—Innate capacity for increase of *D. melanogaster* in relation to developmental times (A), age at peak reproduction (T), age at last reproduction (W), and the multiplication per generation (S, see text) at constant and alternating temperatures. Points represented by open circles were not used in calculations.

significant reduction in the number of eggs when compared to the fecundity observed at either constant 70 or 80°F. Short exposures (4 hr each day) of females to 95°F had no effect on fecundity, which indicated that if damage did occur, it was not sufficiently great to be irreparable. In the present studies, lower fecundity at 26 and 27.5°C probably was a result of sterilizing and inhibitory effects of these temperatures. Young and Plough (1926) and Dobzhansky (1935) have also reported sterilizing effects of high temperature in *D. melanogaster* and *D. pseudoobscura* Frolova.

A comparison of rates of population growth of *D. melanogaster* and *Lygus hesperus* Knight (Strong and Sheldahl 1970) at various constant and alternating temperatures can not be made because the latter are based on parameters pertinent only to the adult, i.e., neither the developmental rate nor the mortality schedule of the egg or the nymphs were incorporated in the computation of r_m values. Immature mortality is definitely a contributing factor in limiting population increase. To ascertain the importance of immature mortality on the rate of population increase, Phillip and Watson (1971) treated their data, first, by taking the adult life only and assuming no immature mortality, and second, by considering immature mortality as one of the limiting factors. In the latter and more realistic approach they concluded that the intrinsic rates of increase decreased significantly compared to the first when only adult mortality was considered.

Thus, temperature affected developmental time, longevity, total fecundity, and fecundity rate, all of which influence the innate capacity for increase. However, Lewontin (1965) showed that the effect on r_m of changes in developmental time is greater

than the effect produced by proportional changes in any other parameter of population growth. In this work, between 15 and 25°C, values of r_m were correlated closely with developmental time. At higher and lower temperatures, other growth parameters were so drastically affected as to mask the otherwise dominant effect of developmental time. For example, at a constant 27.5°C, developmental time was shorter than at other temperatures but mortality in the immature stages was high and fecundity was severely reduced.

Consideration of values of r_m as true measures of rates of population growth may be unrealistic in the case of most species in nature because r_m is based on the assumption that the population is increasing in a nonlimiting environment and has attained a stable age-distribution, specifications which probably seldom occur. Messenger (1964) compared real and computed rates of population increase for the aphid *Therioaphis maculata* (Buckton) at 2 temperature regimes and found that computed rates were 9 and 16% lower than the empirical rates. Howe (1953) concluded that real rates of increase of the granary weevil, *Ptinus tectus* (Boieldieu), were lower than computed rates. However, even if actual rates are different from computed rates, r_m still provides the only viable means of comparing population growth rates under different conditions because it assumes a stable age distribution. At any other age distribution, growth rate will vary continuously. Because r_m is computed from observed values of survival rate and fecundity rate, it reflects the effect of environment on the potential growth rate of a population. Thus r_m serves as a quantitative index reflecting the relative effects of different environmental factors or different levels of the same factor on population dynamics.

The computed functions relating population growth rate to temperature are only preliminary models. Their efficacy is restricted to temperatures favorable for reproduction because at high temperatures, the relation between developmental time and r_m did not hold. Further, the relation between alternating temperature and developmental time (Fig. 6) was calculated for alternations of 5°C amplitude which provides a satisfactory empirical description of the trend of all the points. However, further values of fluctuations of different amplitudes might reveal that different equations would be required for additional accuracy depending on the amplitude of the alternations. Messenger and Flitters (1959) showed that curves of developmental time of eggs of *Dacus dorsalis* (Hendel), at cycling temperatures of different amplitudes, tended to coincide over only a relatively short range of medial temperatures and diverged at both higher and lower temperatures. Also, whether the functions are applicable to *D. melanogaster* generally is questionable but our observed developmental times at constant temperatures compare favourably with those of Powsner (1935), allowing for differences in experimental conditions and calculation of developmental time. However, as far as present data are concerned, the functions are adequate descriptions of the effect of temperature on the intrinsic rate of increase. Average deviation between empirical and computed values was only 2.3%.

Previously published work also shows close relations between r_m and developmental time. With *Sitophilus* (as *Calandra*) *oryzae* (L.) at constant temperatures between 18.2 and 29.1°C (Birch 1953), the correlation coefficient for the relation between $1/r_m$ and developmental time is 0.99. Pradhan's exponential function closely describes the relation between temperature and developmental time also in this case. Combining the 2 functions, the relation between r_m and temperature becomes

$$r_m = \frac{1}{0.507\ (3.99e^{0.00969(30.0 - t°C)^2}) - 0.345}$$

The average deviation between empirical and computed values of r_m is 3.9%. At temperatures higher than 29.1 and lower than 18.2°C, the relation does not hold because of drastic reduction of survival rate and fecundity rate.

Similarly with *P. tectus* (Howe 1953) the relation is $r_m = 0.529 - 0.0178\ (9.19e^{0.00469(27.7 - t°C)^2})$ with an average deviation between observed and computed values of 10%. Most of this deviation is caused by one very aberrant point.

It appears generally possible, therefore, to construct sufficiently accurate models of the effect of temperature on the innate capacity for increase of insect populations with reference to only the relation between temperature and developmental time and ignoring other population parameters. This generalization holds only for temperatures within the range favorable for reproduction.

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Soldier Differentiation, Survival, and Wood Consumption by Normally and Abnormally Faunated Workers of the Formosan Termite, *Coptotermes formosanus*[1,2]

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ABSTRACT

Normally faunated (NF) workers of *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae) fed more and survived better than did partially defaunated (PD; lacking only the protozoan *Pseudotrichonympha grassii* Koidzumi), or completely defaunated (CD) termites. Termite feeding and survival in the latter 2 groups were similar.

Total 8-week production and survival of soldiers for NF, PD, and CD termites was 91, 30, and 6, respectively (15:15:1), whereas the corresponding soldier ratios were 10.1, 9.7, and 2.9% (3.5:3.5:1). Thus, defaunation influenced soldier production and survival differently than it influenced overall termite feeding and survival.

Although the mutualistic relationship between the lower termites and some of their flagellate Protozoa has been reasonably well established for almost 50 years (Cleveland 1924, 1925), many unanswered questions remain. For example, the nutritional requirements of neither the termites, nor their intestinal Protozoa, nor the termite-protozoan complex are known, and the metabolic capabilities of individual protozoan species have not been determined.

Coptotermes formosanus Shiraki, harbors 3 species of Protozoa in its hindgut: *Pseudotrichonympha grassii* Koidzumi, *Holomastigotoides hartmanni* (Koidzumi), and *Spirotrichonympha leidyi* (Koidzumi) (Koidzumi 1921). The physiological importance of these Protozoa to their host has not previously been reported.

We report here the survival, feeding, and soldier differentiation capability of normally and abnormally faunated workers of *C. formosanus*. Because most symbiotic Protozoa from termites cannot yet be cultured in vitro, we felt that removal of certain species of Protozoa from the termite gut, followed by feeding, survival, and soldier differentiation studies would help demonstrate the importance of some Protozoa species for these normal termite functions. A companion study on the ability of similarly treated Formosan termites to degrade cellulose and to synthesize lipids using cellulose carbon is being published elsewhere (Mauldin et al. 1972[4]).

MATERIALS AND METHODS

Termites.—The termites were collected in August 1970 from a colony of *C. formosanus* infesting southern pine bait logs in Lake Charles, La. They were kept in the laboratory at 25°C for 3 weeks and were supplied with both southern pine sawdust and sapwood prior to testing.

Wood.—Woods of 4 species were selected for study: sugar maple, *Acer saccharum* Marsh.; black walnut, *Juglans nigra* L.; baldcypress, *Taxodium distichum* (L.) Rich; and slash pine, *Pinus elliottii* Engelm. var. *elliottii*. One hardwood, sugar maple, and one softwood, slash pine, are favorable for normal termite survival. The other hardwood and softwood, black walnut and baldcypress, respectively, are somewhat unfavorable. Previous unpublished work has shown that termites fed only baldcypress frequently lose their intestinal Protozoa, and black walnut has produced unusual results in other feeding studies (Smythe and Carter 1969, 1970a, b; Smythe et al. 1971).

Boards of sugar maple, black walnut, and baldcypress were acquired from commercial lumberyards in December 1968 and stored in an unheated building until the study began in August 1970. Because

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[4] J. K. Mauldin, R. V. Smythe, and C. C. Baxter. 1972. Cellulose catabolism and lipid synthesis by the Formosan subterranean termite *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae). Insect Biochem. (In manuscript.)