

## CYCLIC OSCILLATIONS IN POPULATION SIZE OF *Drosophila sturtevantii*

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### ABSTRACT

This paper presents a study of 38 experimental populations of *Drosophila sturtevantii* which exhibit cyclic oscillations in size. On the average, each cycle lasts 12 weeks and comprises four distinct phases (contraction, ascent, explosion, and descent) which occur in a regularly repeating fashion. In the explosion phase the population size, 300 to 400 flies, is about tenfold that of the contraction phase. Alternating phases of strong and weak adult and larval competition regulate population size. Natality, mortality, descendants-per-parent ratio, fecundity and fly biomass, acting as density-dependent factors, vary regularly.

### INTRODUCTION

Laboratory studies of population size using *Drosophila* species have utilized either population cages or the serial transfer technique in bottles. In either case vital space is constant and a constant food supply is provided at regular intervals. After a few generations the populations usually reach an equilibrium size. Thereafter population size varies around a mean equilibrium level and the birth and death rates are equal. This pattern has been observed for nearly 30 different species (e.g. Dobzhansky and Pavlovsky, 1961; Carson, 1964; Ayala, 1968a, 1968b; Mourão *et al.*, 1972; Benado *et al.*, 1976).

This paper discusses populations of *D. sturtevantii* with cyclic oscillations.

lations in population size. Preliminary reports on these populations have been presented by Tadei (1974, 1975, 1979a, 1979b) at annual meetings of the Sociedade Brasileira para o Progresso da Ciência (SBPC).

## MATERIALS AND METHODS

*Drosophila sturtevantii* from four localities were used: three from Brazil (São José do Rio Preto-SP, Mirassol-SP and Campo Grande-MS) and one from Mexico (Veracruz). Eighteen isofemale strains were established for each locality.

Experimental populations were maintained in 250 ml bottles with about a 2 cm layer of corn and wheat flour-agar medium. A 4.5 x 17 cm piece of paper towel partially pressed into the medium provided additional surface for the flies.

The serial transfer technique, modified from Buzzati-Traverso (1955) by Dobzhansky and Pavlovsky (1961), is shown in Figure 1. Founder flies are introduced in bottle number 1. After 7 days the survivors are transferred to bottle number 2, and so on. When the flies begin to emerge in the bottles in which the eggs have been deposited (bottle number 1 in the 3rd week, bottles 1 and 2 in the 4th week, and so on), they are collected and added to the new bottle together with the adult survivors of the previous census. Each bottle is discarded on the 35th day. Each population consists of five bottles: one bottle contains the adults (population size) and the other four contain eggs, larvae, pupae and newly emerged flies (population productivity). The number of flies introduced in the new bottle in one census, minus the survivors in the next census gives the mortality during that week. In each census (made every Thursday) adult survivors and newly emerged flies were counted by sex and weighed. Individual biomass can be obtained by dividing the total biomass by the number of flies weighed.

In *D. sturtevantii* the flies emerge on the 21st, 28th and 35th day. It is therefore necessary that each bottle be counted during three successive weeks in order to obtain the number of flies produced by a given number of adults. When the newly emerged flies per bottle are counted separately, this number can be obtained directly. In the present case two expressions were developed to obtain this kind of data, using the two frames of Figure 1.

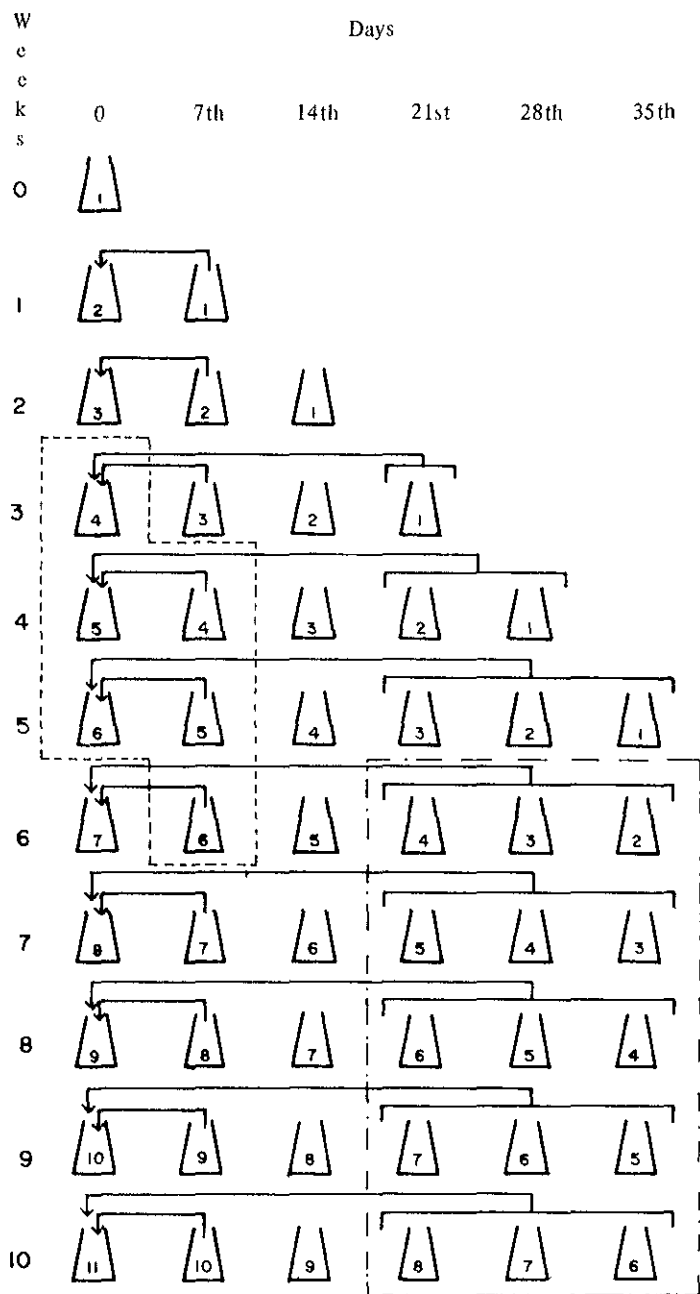


Figure 1 - Diagram of the serial transfer technique.

The frame on the left side (dashed line) of Figure 1 gives the number of parents as

$$P_I = \frac{(A_4 + S_4)/2 + (A_5 + S_5)/2 + (A_6 + S_6)/2}{3} \quad (1)$$

where A is the number of adults on the census day and S is the number of respective survivors on the 7th day in the bottle indicated by the subscript. Flies of bottles 4 to 6 emerge in weeks 6 to 10. Moving the frame one week below,  $P_{II}$  is obtained, and so on.

The frame on the right side (dash-pointed line) of Figure 1 gives the descendants of  $P_I$  as

$$D_I = \frac{(D_6 + D_7 + D_8)/3 + (D_7 + D_8 + D_9)/3 + (D_8 + D_9 + D_{10})/3}{3} \quad (2)$$

where D is the number of flies emerged in the week indicated by the subscript.  $D_6$  are the flies emerged in bottles 2, 3 and 4 during the 6th week. Moving the frame one week below,  $D_{II}$  (descendants of  $P_{II}$ ) is obtained, and so on.

For both expressions it is assumed that the flies emerge in equal numbers in the three bottles and that the three sets of parents give equal numbers of descendants. The expressions are usable for any species, changing the frames according to the weeks of emergence of the flies.

When the populations were discarded, samples of females were put individually in vials and transferred twice after 48-hour periods; those which yielded progeny were considered fertile females. Males were also put individually in vials, together with three virgin females from the stock and those which yielded progeny were considered fertile males.

A total of 38 populations, designated S1 to S38, were founded with different numbers of flies and different sex ratios and were maintained for about 30 to 110 weeks. The founder flies were mixtures of strains from a single locality. The populations were maintained on the same shelves in a constant temperature room (25°C) and counted and weighed once weekly in the same sequence and at approximately the same time.

## RESULTS

These are partial results based on the analysis of the 38 populations.

Figures 2 and 3 present graphs in which the censuses of 14 of the 38 populations have been plotted. These populations illustrate four distinct situa-

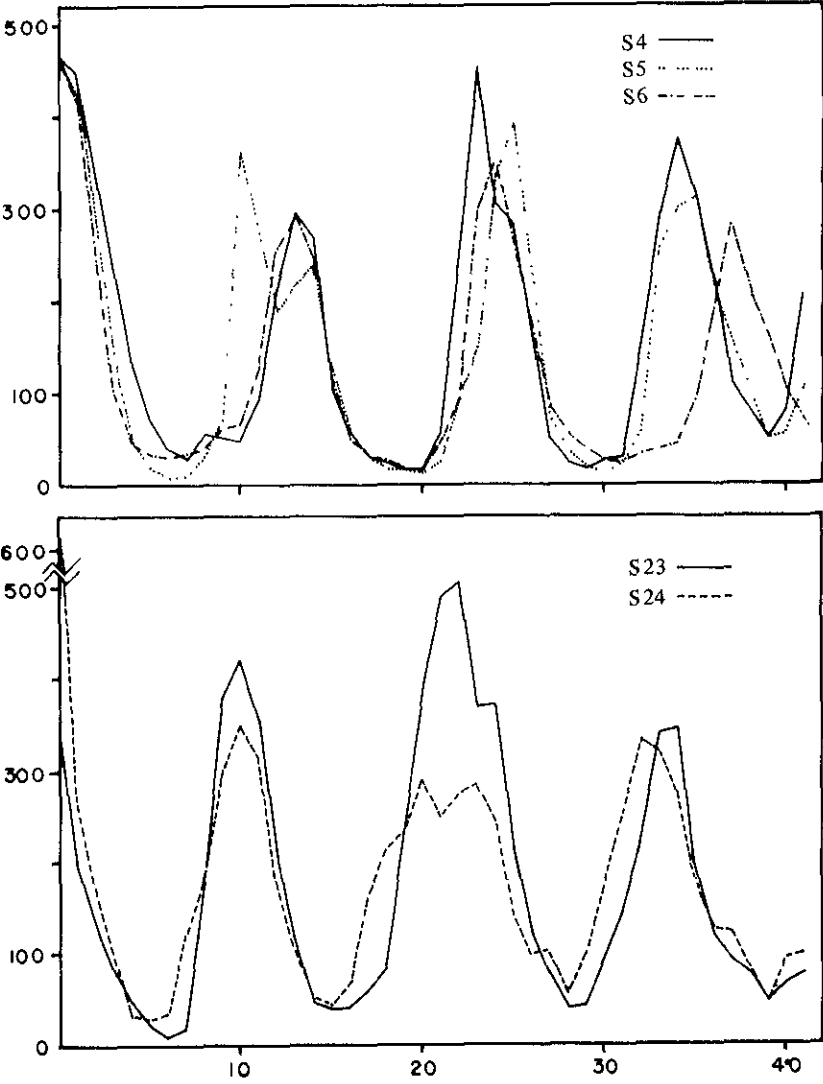


Figure 2 - Size of 5 populations. Ordinate: numbers of flies. Abscissa: weeks.

tions which were observed in the 38 populations: a) oscillations continuously recurring, as S4 (Figure 2), observed in 28 populations (74%); b) oscillations temporarily interrupted, as S37 (Figure 3), observed in 5 populations (13%); c) oscillations permanently interrupted, as S27 (Figure 3), observed in 3 populations (8%); and d) oscillations never occurring, as S28 (Figure 3), observed in 2 populations (5%).

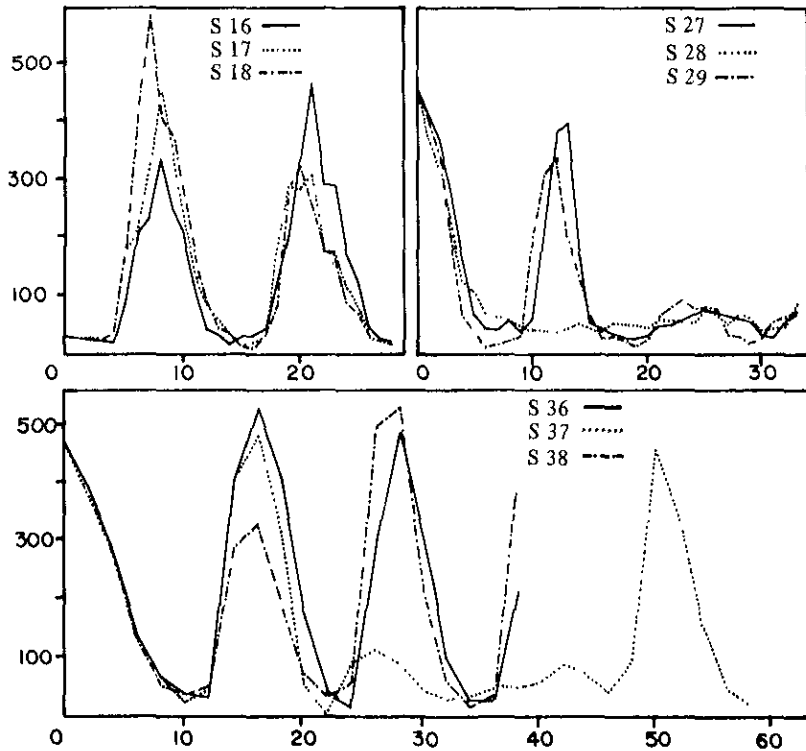


Figure 3 - Size of 9 populations. Ordinate: numbers of flies. Abscissa: weeks.

The populations with continuously recurring oscillations (situation a) should be considered the standard for the population dynamics of *D. sturtevanti*. These cyclic oscillations can be characterized as follows: a) each cycle comprises four distinct phases (contraction, ascent, explosion and descent) which occur in a regularly repeating fashion; b) the average cycle length is 12 weeks and c) the explosion phase population size, about 300 to 400 flies, is about tenfold that of the contraction phase.

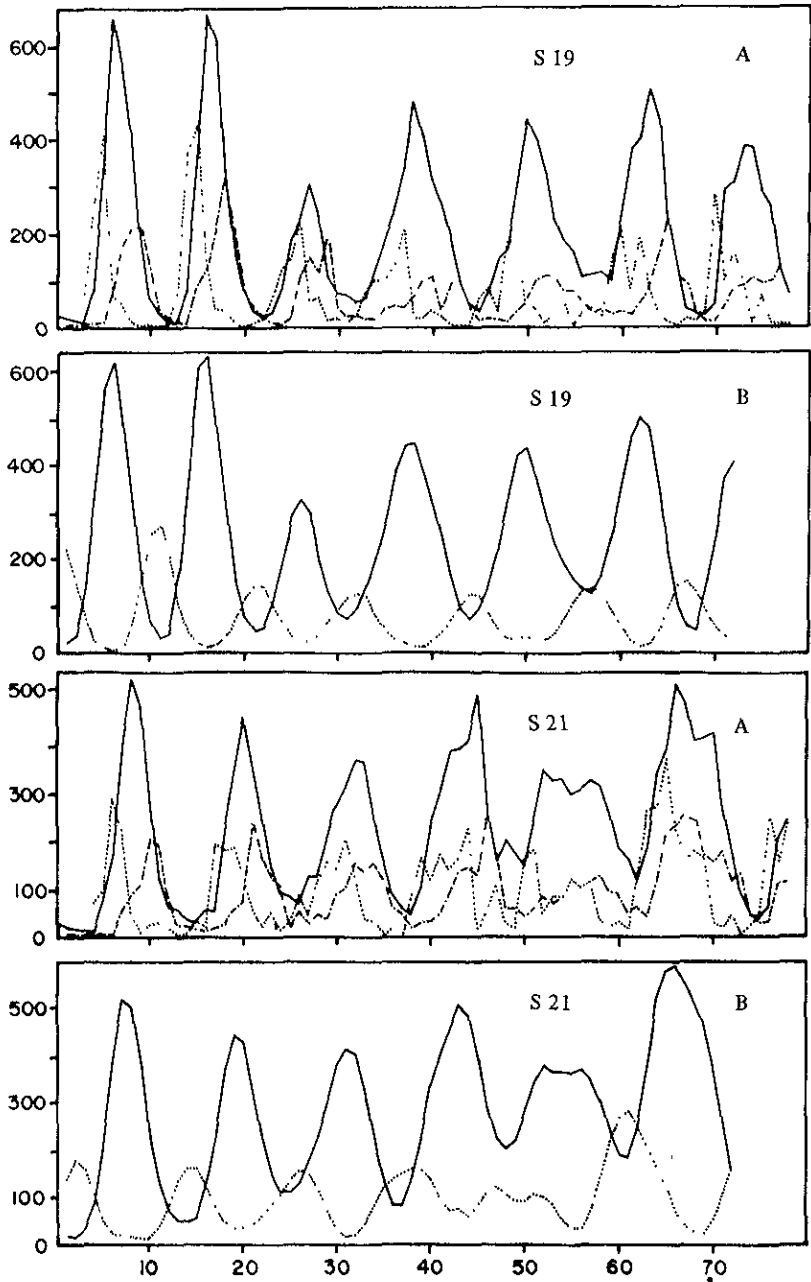


Figure 4 - Numbers of size (———), natality (---) and mortality (-.-) in A and of parents (———) and descendants (---) in B, of populations S19 and S21. Ordinate: numbers of flies. Abscissa: weeks.

Figure 4 (panels A) shows the variations for population size, productivity and mortality observed in populations S19 and S21, and reveals that the maximum values for these parameters are separated by intervals mostly of one or two weeks. For these same populations, Figure 4 (panels B) shows the variation in numbers of parents and their respective descendants, the values plotted having been calculated with the expressions presented in Materials and Methods. A pattern of cyclic variation is evident for the number of parents and descendants as well as for productivity and mortality.

Table I - Means and standard errors of size, productivity and mortality and of numbers of parents and descendants of populations S19 and S21 in 79 weeks (A = average for means of 5 populations).

Parameter	S19	S21	A
size	227 ± 17	210 ± 19	165 ± 7
productivity	102 ± 10	80 ± 11	62 ± 4
mortality	93 ± 8	76 ± 7	61 ± 3
parents	279 ± 18	255 ± 18	193 ± 7
descendants	100 ± 7	78 ± 7	60 ± 2
desc./parents	0.36	0.30	0.31

Table I presents the means for population size, productivity, mortality, parents and descendants which were used in making the graphs in Figure 4. The mean number of parents is equal to mean population size plus 50% of mean mortality, and the mean number of descendants is equal to mean productivity, for either population S19 and S21 or for the average of five populations. The descendants-per-parent ratios indicate an average of three parents to one descendant.

The graphs presented in Figure 4 (panels B) permit the determination of descendants-per-parent ratios in each of the four phases of the cycle through the selection of appropriate points belonging to the respective phases of the cycle. The results are given in Table II. In both populations there is a predominance of female parents in each of the four phases. Descendants-per-parent ratios below unity (as occurs in ascent, explosion and descent) indicate that the emerged flies are descendants of only a fraction of the parents. In the contraction phase each parent produces an average of two or more descendants.

Table II - Means and standard errors for numbers of parents and descendants and ratios descendants/parent in the four phases of populations S19 and S21.

population	No. of censuses	parents		descendants	descendants per	
		females	males		female	male
S19						
contraction	19	82 ± 12	38 ± 5	157 ± 12	1.91	4.13
ascent	18	182 ± 20	98 ± 9	120 ± 13	0.66	1.22
explosion	18	291 ± 16	165 ± 6	53 ± 7	0.18	0.32
descent	17	201 ± 20	103 ± 8	64 ± 9	0.32	0.62
S21						
contraction	18	38 ± 4	33 ± 4	154 ± 12	4.05	4.67
ascent	18	142 ± 14	93 ± 10	73 ± 7	0.51	0.78
explosion	19	269 ± 13	188 ± 12	22 ± 2	0.08	0.12
descent	17	132 ± 12	100 ± 8	67 ± 10	0.51	0.67

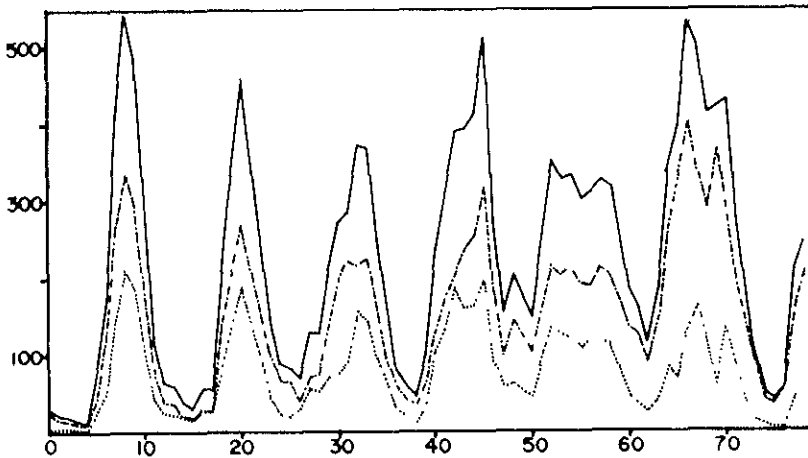


Figure 5 - Numbers of females (---), males (---) and total (—) in size of population S19. Ordinate: numbers of flies. Abscissa: weeks.

Population S19 was used to plot the total size and numbers of both sexes in each census. A predominance of females occurs in every census (Figure 5). Among the newly emerged flies (productivity) the numbers of females always exceeded the number of males; averages of means of 24 populations, with standard errors, are  $41 \pm 2$  for females and  $24 \pm 1$  for males ( $t_{46} = 6.38$ ,  $P < 0.001$ ).

The graphs presented in Figure 4 (panels A) also permit an analysis of the sex frequencies in the population during each phase of the cycle. The results are presented in Table III. In all phases of populations S19 and S21 females are approximately 1.5 to 2.0 times as frequent as males. The  $t$  values for the means of females and males were all significant. Correlation coefficients between means of females and males for 17 populations are: for contraction

Table III -Means and standard errors, in the four phases of the cycle, of frequencies of females and males in the size of populations S19 and S21, (A = average for means of 17 populations).

Populations	No. of censuses	females	males	$\frac{\text{females}}{\text{males}}$
<b>S19</b>				
contraction	20	$63 \pm 9$	$27 \pm 4$	2.33
ascent	18	$158 \pm 17$	$79 \pm 10$	2.00
explosion	19	$250 \pm 14$	$147 \pm 7$	1.70
descent	17	$168 \pm 21$	$75 \pm 9$	2.24
<b>S21</b>				
contraction	21	$34 \pm 4$	$24 \pm 4$	1.42
ascent	16	$145 \pm 16$	$90 \pm 10$	1.61
explosion	16	$291 \pm 23$	$180 \pm 16$	1.62
descent	21	$124 \pm 12$	$79 \pm 10$	1.57
<b>A</b>				
contraction		$22 \pm 1$	$13 \pm 1$	1.69
ascent		$104 \pm 5$	$57 \pm 4$	1.82
explosion		$216 \pm 8$	$138 \pm 8$	1.56
descent		$87 \pm 4$	$57 \pm 4$	1.53

$r = 0.549$  ( $t_{15} = 2.54$ ,  $P < 0.05$ ), for ascent  $r = 0.771$  ( $t_{15} = 4.69$ ,  $P < 0.001$ ), for explosion  $r = 0.858$  ( $t_{15} = 6.47$ ,  $P < 0.001$ ) and for descent  $r = 0.410$  ( $t_{15} = 1.74$ ,  $P > 0.05$ ). For totals of all phases  $r = 0.895$  ( $t_{15} = 7.77$ ,  $P < 0.001$ ).

Table IV -Numbers of fertile females and their progeny (mean and standard error) and of fertile males in samples of ten populations in the four phases of the cycle.

population	size at discard	females				males	
		No.	fertile	progeny		No.	fertile
				females	males		
contraction							
S2	74	20	18	20 ± 5	21 ± 5	14	11
S3	61	21	19	15 ± 4	15 ± 4	11	11
S21	78	43	33	17 ± 2	16 ± 2	7	6
ascent							
S23	148	86	82	46 ± 3	43 ± 2	34	30
S25	105	42	41	45 ± 4	41 ± 3	25	23
explosion							
S1	332	131	130	66 ± 2	56 ± 2	72	71
S20	454	99	82	46 ± 3	42 ± 2	—	—
S22	339	125	123	43 ± 2	39 ± 2	94	89
descent							
S19	247	108	94	24 ± 2	23 ± 2	28	28
S24	136	66	45	16 ± 2	18 ± 2	6	6

Table IV gives data on the fertility and fecundity of samples of flies from ten populations which were individually separated in vials. More than 90% of both the females and males studied were shown to be fertile, and the fertility frequencies in the populations during any given phase are mostly above 80%. The  $t$  values for the means of females and males produced were all nonsignificant, except for population S1 ( $t = 3.43$ ,  $P < 0.001$ ). However mean female progeny during the contraction and descent phases are about half those of explosion and ascent.

Table V - Means and standard errors of individual biomass ( $\text{mg} \times 10^{-3}$ ) for flies of size and productivity and of parents and descendants of populations S19 and S21 in the four phases.

population	No. of censuses	size	productivity	No. of censuses	size	productivity
S19						
contraction	20	1.014 $\pm$ 0.025	0.666 $\pm$ 0.033	19	0.986 $\pm$ 0.029	0.827 $\pm$ 0.036
ascent	18	1.090 $\pm$ 0.030	0.829 $\pm$ 0.036	18	1.018 $\pm$ 0.033	0.773 $\pm$ 0.029
explosion	19	1.142 $\pm$ 0.036	0.732 $\pm$ 0.042	18	1.073 $\pm$ 0.032	0.589 $\pm$ 0.012
descent	17	1.064 $\pm$ 0.032	0.595 $\pm$ 0.021	17	1.068 $\pm$ 0.034	0.690 $\pm$ 0.022
F		3.17 *	7.94 **		1.71	15.74 **
S21						
contraction	21	0.914 $\pm$ 0.030	0.629 $\pm$ 0.042	18	0.967 $\pm$ 0.033	0.949 $\pm$ 0.019
ascent	16	1.209 $\pm$ 0.042	0.960 $\pm$ 0.019	18	1.108 $\pm$ 0.036	0.811 $\pm$ 0.027
explosion	16	1.265 $\pm$ 0.037	0.767 $\pm$ 0.040	19	1.212 $\pm$ 0.032	0.597 $\pm$ 0.021
descent	21	1.188 $\pm$ 0.027	0.601 $\pm$ 0.024	17	1.132 $\pm$ 0.030	0.766 $\pm$ 0.037
F		23.41 **	22.85 **		9.68 **	30.41 **

F = homogeneity

\*  $P < 0.05$

\*\* $P < 0.01$

The graphs in Figure 4 (panels A and B) also permit an analysis of individual biomass in each phase. The results are presented in Table V. Except for the biomass of the parents of population S19, the significant F values indicate heterogeneity of the means. The following rankings for biomass are observed in both populations in the phases of contraction (C), ascent (A), explosion (E) and descent (D): size:  $E > A > D > C$ ; productivity:  $A > E > C > D$ ; parents:  $E > D > A > C$ ; and descendants:  $C > A > D > E$ .

A remarkable contrast is evident: the explosion flies are the heaviest but produce the lightest descendants, whereas the lightest flies, those of contraction, produce the heaviest descendants. The heaviest newly-emerged flies (productivity) occur in the ascent phases and the lightest ones in the descent phases.

## DISCUSSION

The variables analyzed (fertility, fecundity, fly biomass, natality, mortality, population size, ratio of females to males and the number of descendants per-parent) permit the characterization of the oscillations and some of their interrelations, as well as the relationship of the variables with the environmental conditions (amount of food and space), which produce the oscillations. In three populations the oscillations were interrupted and in two others they never occurred. It might be expected that the oscillations could have occurred if the observations had been extended over a longer period, considering the temporary interruption of oscillations observed in five other populations.

Ultimately, the cyclic oscillations are caused by regular variations of natality, mortality, ratio of descendants-per-parent, fecundity and fly biomass. Two further variables, fertility and sex ratio, can be disregarded: there is a permanent predominance of females, among both adult survivors and newly-emerged flies and the frequency of sterile flies in the four phases is nearly constant, mostly less than 20%.

The fecundity of the females in the four phases, as investigated by separating samples of the populations in vials, revealed an initially unexpected result: the lowest fecundity occurred among the contraction females and the highest among the explosion females. Developmental conditions should be considered to be nearly optimal in the vials, or at any rate more nearly optimal than in the population bottles, since larval competition is weaker in the vials.

A second, initially unexpected, result is the lower biomass of contraction parents in comparison with explosion parents. Furthermore the largest flies produce the smallest descendants and vice-versa.

This apparent contradiction becomes understandable when the relationships between the variables studied are considered. During the explosion phase the bottles are crowded, thereby causing a strong competition for food and space. Nevertheless, oviposition increases as a consequence of the larger number of more highly fecund females (indirect evidence was provided by the vial tests) and hence the number of larvae increases (a thick layer of larvae could be easily observed, subjacent to which a more or less thin layer of food remained practically untouched). Strong larval competition reduces natality. Simultaneously, the mortality rate increases in crowded bottles. Decreased natality and increased mortality reduce the population size, resulting in a

relative increase in the amount of food and space available. Oviposition is reduced as a consequence of the smaller number of less fecund females (indirect evidence from vial tests) and this in turn causes a reduction in the number of larvae and a relaxing of larval competition. Natality increases and the mortality rate decreases, producing a new explosion and a consequent reduction in the amount of food and space. A new cycle begins.

Alternating phases of strong and weak adult and larval competition regulate population size. Natality, mortality, number of descendants per parent, fecundity and fly biomass act as density-dependent factors.

The apparent contradiction presented by fly biomass is explained by the fact that the contraction flies are mostly descendants of explosion adults which in turn are mostly the descendants of contraction adults. The inverse relationship between the biomass of the parents and descendants in these phases is associated with the degree of larval competition.

The partial results presented here seem sufficient to conclude that there is a genetic basis which interacts with the experimental environmental conditions to produce regular, cyclic oscillations in population size. Flies with different levels of fecundity, biomasses and survival rates vary in frequency with variations of population density. Dobzhansky and Spassky (1944) demonstrated that in *D. pseudoobscura* some genotypes survive relatively better than other genotypes at higher population densities; conversely, certain genotypes show better survival at lower densities and still others show no density effect. Lewontin (1955) provided experimental evidence in *D. melanogaster* that selection on different genotypes can vary with population density. The problem of density-dependent selection of genotypes was analytically studied by Anderson (1971). The clear repetition of oscillations in nearly all the populations of the present study leads to the conclusion that, independent of the geographic origin, number, and sex ratio of the founder flies, a genetic basis characteristic of *D. sturtevantii* is involved in the dynamics of the cyclic oscillations observed for population size in this species.

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## RESUMO

Foram estudadas 38 populações experimentais de *Drosophila sturtevantii* com oscilações cíclicas do tamanho populacional. Cada ciclo tem duração média de 12 semanas e compreende quatro fases (contração, ascensão, explosão e descensão) que se sucedem de modo regular. Nas explosões, o tamanho das populações (300 a 400 moscas) é cerca de 10 vezes maior que nas contrações. O tamanho das populações é regulado por uma alternância de fases de competição fraca e forte, de adultos e larvas. A natalidade, a mortalidade, a razão pais-descendentes, a fecundidade e a biomassa das moscas variam de modo regular, atuando como fatores dependentes da densidade.

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