Acknowledgments.—I would like to thank Dr W. Z. Lidicker, Jr., for the use of the specimens and many useful comments on the manuscript. Dr R. J. Berry, Dr C. J. Krebs, and Randall Peterman criticised the manuscript.

4. REFERENCES

- BERRY, R. J. 1963. Epigenetic polymorphism in wild populations of *Mus musculus*. *Genet. Res. Camb.*, **4**, 193-220.
BERRY, R. J. 1964. The evolution of an island population of the house mouse. *Evolution*, **3**, 468-483.
BERRY, R. J., AND SEARLE, A. G. 1963. Epigenetic polymorphism of the rodent skeleton. *Proc. Zool. Soc. Lond.*, **140**, 577-615.
GRÜNEBERG, H. G. 1952. Genetical studies on the skeleton of the mouse. IV. Quasi-continuous variation. *J. Genet.*, **51**, 95.
LIDICKER, W. Z., JR. 1963. The genetics of a naturally occurring coat-color mutant in the California vole. *Evolution*, **17**, 340-346.
LIDICKER, W. Z., JR., AND ANDERSON, P. K. 1962. Colonization of an island by *Microtus californicus*, analysed on the basis of runway transects. *J. Anim. Ecol.*, **31**, 503-517.

CHANGES IN THE BEHAVIOUR OF INDIVIDUAL MEMBERS OF A *DROSOPHILA* POPULATION MAINTAINED BY RANDOM MATING

JOHN ANGUS

[Departments of Genetics and Psychology, University of Birmingham, England]

Received 15.ii.74

SUMMARY

It has been inferred from the genetical architecture of spontaneous locomotor activity in *Drosophila melanogaster* that natural selection has favoured a relatively high level of activity. To test this inference, a population was set up from a cross between two inbred lines, and maintained by random mating. Successive samples taken from the population showed an increase of the activity level of individual flies. This result confirms the prediction made from the genetical architecture, provides further justification for the behavioural measures, and indicates that a high level of activity is advantageous to the organism.

1. INTRODUCTION

In an earlier paper (Angus, 1974a), it was suggested that the genetical architecture for spontaneous locomotor activity in *Drosophila* males implied a history of natural selection for a relatively high level of this trait. The present experiment was designed to test this inference. It was intended to study the changes, if any, in the activity of individuals of a population during an extended period of maintenance by random mating in competitive conditions, thus determining whether natural selection acts in the predicted manner in these circumstances.

2. METHODS

A population was initiated from the F_2 of a cross between two inbred lines, Edinburgh and 6C/L. The two lines were crossed reciprocally, and approximately 500 of each sex of each reciprocal F_2 were placed in a

population cage. This cage was maintained at 25° C. as described by Barnes (1968). Fresh culture vials are introduced to the cage in a cyclical system, such that any vial remains in the cage for 17 or 18 days. The initiating size of 2000 flies corresponds to the observed average size of a population maintained under these conditions (Barnes, 1968).

Samples were taken from the cage at regular intervals, and an F_2 between Edinburgh and 6C/L was produced on each occasion to emerge simultaneously. This F_2 may be regarded as having the same genetical constitution as the base population, and so can be used as a control with which the cage population may be compared. The simplest method of sampling from the cage would be to remove some vials, and employ the flies emerging from them. However, the egg and larval density of culture vials in the population cage tends to fluctuate over time and space, and it is possible that culture density may affect subsequent adult behaviour. All samples, therefore, were raised at a controlled low density. On each occasion eggs were collected from the cage and raised at approximately 100 eggs per culture vial. Eggs were also collected from vials containing an equal number of flies of each reciprocal F_1 and cultured at the same low density. Adults were collected within 24 hours of emergence and transferred to fresh culture vials, 10 females and 10 males per vial, and kept at 25° C. for 7 days.

Behavioural measurement was carried out by a form of time-sampling technique which has been described in detail elsewhere (Angus, 1974*a, b*). Individual flies were placed in glass tubes in which they could walk, run, turn round, but could not fly. In this situation, their behaviour could be separated into three mutually exclusive categories, namely, locomotor activity, preening, and inactivity. Each measurement involved briefly observing a fly on each of five occasions within 1 minute. Flies were observed for 1 minute immediately before and after a momentary reduction in the intensity of overhead illumination (which may be referred to as a shadow stimulus). Thus, data were obtained on both spontaneous behaviour and on the reaction to a simple stimulus. It was found that the scores could most usefully be summarised as the proportion of flies which were active (or preening).

On each of two occasions on each of 2 days, the behaviour of 20 males of both the control F_2 and the cage population was tested. Thus a total of 40 flies was scored in a random order on each occasion, and 80 flies of each population were scored in each sample (*i.e.* a total of 320).

Starting from the 11th month after initiation of the population, the cage was sampled four times at intervals of approximately 3 months, and compared with the F_2 . A fifth sample was tested after a further interval of 12 months. The population may be regarded as having passed through about 75 generations.

3. RESULTS

The activity results are presented in table 1, as the proportion of each group which were active on any of the five observations made within 1 minute, both before and after the stimulus. The differences (after minus before) are also given to show the reaction to stimulation. The data were analysed as a five-dimensional chi-square (Kendall and Stuart, 1961; Crawford-Sidebotham, 1970), and the significant items are given in table 2.

The ED $\times$ 6C/L cage population is shown to have a significantly greater level of activity than that of the F_2 . The data indicate that the significance of the population $\times$ sample item is at least partially due to the gradually increasing difference between the populations over successive samples. The stimulus item, and the difference between the scores before and after stimulation, show that there is a significant decrease in activity in response to the shadow stimulus, as found previously (Angus, 1974a), but there is no apparent change in the size of this reaction over the five samples.

TABLE 1
Activity scores for five successive samples from F_2 and 6C/L $\times$ ED population, raised at a density of approximately 100 eggs per vial

Population	Stimulus	Sample number				
		1	2	3	4	5
Cage	Before	0.649	0.687	0.862	0.850	0.926
	After	0.550	0.712	0.675	0.665	0.785
	Difference	-0.099	+0.025	-0.187	-0.185	-0.141
F_2	Before	0.684	0.562	0.500	0.700	0.637
	After	0.618	0.500	0.525	0.575	0.587
	Difference	-0.066	-0.062	+0.025	-0.125	-0.050

The predictions (Angus, 1974a) to be tested in this experiment are primarily concerned with spontaneous activity of male flies, and so the relevant data (the mean scores before stimulation) are given in fig. 1. Although the values for the F_2 fluctuate, the mean of the five samples is approximately the same as that obtained previously.

TABLE 2
Significant items in analysis of table 1

Items	d.f.	χ^2	P
Population	1	33.20	$< 10^{-6}$
Stimulus	1	12.53	3.99×10^{-4}
Samples	4	10.86	2.82×10^{-2}
Populations $\times$ samples	4	20.11	4.74×10^{-4}

The combination of the data, the analysis, and the graph clearly indicates that the activity level of flies in the population cage has increased during the period of sampling, and that the mean level in the cage is consistently higher than that of the F_2 from which the population was derived.

Preening behaviour was also measured in these samples. The data did not indicate any effect of natural selection on this trait, but one was not really expected from the genetical control (Hay, 1972; Angus, 1974a).

4. DISCUSSION

It would appear from these results that there has been a change towards an increased level of activity in the random mating population. As the population has been maintained in a constant environment it seems reasonable to suppose that this change is due to natural selection. If this interpretation is correct, these results are in accordance with the inference made from the genetical architecture. It was suggested (Angus, 1974a) that the

FIG. 1.—Mean activity scores before stimulation, for four samples taken at 3-month intervals and for a fifth sample taken after a further 12-month interval from the 6C/L × ED population, and from the F₂ from which it was initiated. Each point is a mean of 80 males. At sample 0 are given the scores of Edinburgh, 6C/L, and their F₂ (Angus, 1973a), each based on 200 males. The activity scores is the proportion of flies active on any of five momentary observations made within a 1-minute period.

genetical control of the character indicated a history of natural selection for a high level of activity in the population from which the lines were derived. These results, therefore, give further support to the arguments of Mather (1960, 1966, 1967) regarding the relationship between the genetical architecture of a character and the type of natural selection which has been acting upon it.

Also these results provide additional support for the validity of the technique of behavioural measurement used (Angus, 1973b). Thus the ability of the technique to detect a change in the activity of flies in the population cage, indicates that the behavioural trait measured is of some relevance to the survival of individual flies in a competitive situation, or at least is closely related to such a trait. The genetical dominance and apparent selection for a relatively high level of activity suggest that this level is most advantageous for the organism. These experiments have thus put into practice the suggestions made by Roberts (1967) concerning the use of genetical architecture to identify the significance of behavioural traits, and their most advantageous form of expression.

The above interpretation of the results is, of course, not necessarily correct, as the change in the activity of the population may have been due to genetic drift rather than selection. This explanation is less likely, and can only be tested by further study of the population, and of other populations.

Acknowledgments.—I am very grateful to Dr M. J. Kearsey for his advice, and to Professor P. L. Broadhurst for his comments on the manuscript. This work was carried out during tenure of a studentship from the Science Research Council, and was further supported by a grant from the Medical Research Council to Professors P. L. Broadhurst and J. L. Jinks for work on psychogenetics.

5. REFERENCES

- ANGUS, J. 1974a. Genetic control of activity, preening, and the response to a shadow stimulus in *Drosophila melanogaster*. *Behav. Genet.* 4, 317-329.
- ANGUS, J. 1974b. Measurement of locomotor activity in *Drosophila*. *Anim. Behav.*, in press.
- BARNES, B. W. 1968. Stabilising selection in *Drosophila melanogaster*. *Heredity*, 23, 433-442.
- CRAWFORD-SIDEBOTHAM, J. T. 1970. Differential susceptibility of species of slugs to metaldehyde/bran and to methiocarb baits. *Oecologia (Berl.)*, 5, 305-324.
- HAY, D. A. 1972. Genetical and maternal determinants of the activity and preening behaviour of *Drosophila melanogaster* reared in different environments. *Heredity*, 28, 311-336.
- KENDALL, M. G., AND STUART, M. A. 1961. *The Advanced Theory of Statistics Vol. 2, Inference and Relationship*. Griffin, London.
- MATHER, K. 1960. Evolution in polygenic systems. *Int. Colloquium on Evolution and Genetics, Rome, Acad. Naz. dei Lincei*.
- MATHER, K. 1966. Variability and selection. *Proc. Roy. Soc. B.*, 164, 328-340.
- MATHER, K. 1967. Complementary and duplicate gene interactions in biometrical genetics. *Heredity*, 22, 97-103.
- ROBERTS, R. C. 1967. Some evolutionary implications of behavior. *Canad. J. Genet. and Cytol.*, 9, 419-435.

THE BIAS IN THE REGRESSION OF Δq ON q

G. C. KIRBY

Department of Genetics, University of Adelaide, Adelaide, South Australia

Received 20.xi.73

SUMMARY

It is shown that when the regression of Δq (the change in gene frequency) on q (gene frequency) is calculated from data obtained from a sequence of censuses of one population, the regression coefficient does not provide an unbiased estimate of the amount of immigration or selection maintaining an equilibrium gene frequency in the population. Also, the equilibrium gene frequency estimated from the regression will be biased towards the observed gene frequency in the first census.

THE relationship between the gene frequency in a population at time $t(q_t)$ and the change in gene frequency (Δq_t) over the next time interval is useful for locating gene frequency equilibria in theoretical models of population genetics (Li, 1955). At an equilibrium point, $\Delta q_t = 0$. If there is a stable equilibrium gene frequency ($\bar{q}$) maintained by recurrent mutation, frequency dependent selection or immigration from a source population with constant