occurred terminally on the two largest acrocentric chromosome pairs in the red deer and the fallow deer. The same chromosomes and localizations have been reported to be NOR-carrying in the sika deer\(^1\), reindeer, and scandianvian moose\(^2\). However, in the roe deer only one of these largest acrocentric pairs was a NOR carrier (no. 1), while the other NOR was localized on a medium sized chromosome (no. 13). In an previous experiment\(^3\), the order of deer chromosomes from left to right is red deer, fawllow deer, and roe deer. B—comparison of the biarmed chromosome 13 of red and fallow deer with its corresponding uniairned equivalents in the roe deer and cattle karyotype (Robertsonian translocation).

**ABSTRACT.** In a line artificially selected for high melanogaster chromosomes (d = deer, c = cattle), the order of deer chromosomes from left to right is red deer, fallow deer, and roe deer. B—comparison of the biarmed chromosome 13 of red and fallow deer with its corresponding uniairned equivalents in the roe deer and cattle karyotype (Robertsonian translocation).

**Notes**


**Balanced polymorphism at the selection limit in Drosophila melanogaster**

**Aurora García-Dorado and Carlos López-Fanjul**

**ABSTRACT:** In a line artificially selected for high sternopleural bristle score, a lethal-inversion complex with an effect on this trait reached a stable frequency of around 0.5. This complex determined the establishment of an effective balanced system where no further response to selection could be obtained and relaxation of selection would not restore fitness.

**Materials and Methods**

In a previous experiment\(^1\), 36 lines of *Drosophila melanogaster* were selected at varying intensities for high bristle score on the two sternopleural plates. One of these lines (C\(\beta\)) shows a delayed and pronounced response to selection starting at generation 9, largely surpassing the performance of the remaining lines. C\(\beta\) was selected with an average intensity of 1.44 and a maximum effective size of 6.9 during 38 generations.

Several tests were carried out at different times to investigate the possible causes of that unexpected response: 1) a subline (C\(\delta\)) derived from C\(\beta\) at generation 26, was selected by the same procedure as the latter until the end of the experiment (generation 38). 2) Relaxed-selection sublines were split from C\(\beta\) at generations 20 and 33, and from C\(\eta\) at generation 33. Their performances were evaluated after one generation in the first case, and after five generations in the other two instances. 3) Chromosomes 2, 3, 4, and 5 were screened for lethals by using the Cy \(\text{Srr}/\text{Xa stock}\) at generations 22, 29, and 37. Five to 10 males were taken from C\(\beta\) and a random sample of five chromosomes 2 and five chromosomes 3 for each male were tested for lethality. Therefore, the probability of not detecting a lethal carried by one male was around 1/32. Lethal chromosomes were isolated and their allelic relationships tested within and between males. 4) The effect of a lethal on bristle score in the heterozygote was estimated in C\(\beta\) males at generation 29. Forty-two males were scored and each was progeny-tested in order to classify them as either homozygous nonlethal or heterozygous. 5) C\(\delta\) larvae were examined cytologically for inversions at generation 23.

**Results and Discussion**

The changes of the mean and the phenotypic variance of females of line C\(\beta\) are shown in Figure 1. The realized heritability estimated over the first three generations of selection (0.44 ± 0.03) was smaller but not significantly different (P > 0.05) from the base population.
estimate (0.61 ± 0.09). An accelerated response to selection was observed starting at generation 9, which was accompanied by an abrupt increase in the variance. From generation 26 onwards, line C1 reached a plateau characterized by an oscillating variance. Subline C1, initiated at generation 26, did not respond to selection and its variance also fluctuated widely.

Only one lethal was detected, associated with the terminal inversion 3R which prevents crossing over along the whole right arm of chromosome 3. The frequency of this lethal was 0.5 in the selected males at generation 22, and 0.44 ± 0.02 and 0.45 ± 0.05, respectively, in the males scored at generations 29 and 37.

The high frequency attained by the lethal-inversion complex and its subsequent maintenance in the line, strongly suggests that this complex has an effect on bristles. These results therefore can be interpreted as a consequence of antagonism between natural and artificial selection forces. In this sense, a significant downward trend after one generation of relaxation starting at generation 20 was found (8.24 ± 1.49 bristles). Populations of Drosophila consisting chiefly of heterozygotes for a certain inversion have been previously reported1, but in this case the maintenance of this type of balanced polymorphism could only be ascribed to natural selection.

Continued artificial selection favoring heterozygotes for the complex, also will especially at low effective sizes, protect all deleterious recessives linked in disequilibrium to it from natural selection. These will subsequently accumulate along the right arm of chromosome 3. Eventually, the effects on fitness of the complex — carrier chromosome and its homologue will tend to be similar and an effective balanced lethal system will then be established. In accordance with this prediction, the effect of five generations of relaxation starting at generation 33 (0.34 ± 1.09 bristles in C1 and 2.40 ± 1.44 bristles in C1) was found to be nonsignificant (P > 0.05). This also is in agreement with the standard chromosome behaving as a recessive semilethal, as found in an independent test carried out at generation 37.

On the other hand, genes increasing bristle score also will accumulate in the homologue chromosome, although the maintenance of the complex at high frequency would correspondingly reduce the selection pressure exerted on other loci. Consequently, the effect of the complex on the trait will be expected to decrease as selection progresses. This effect was estimated in males at generation 29 (1.25 ± 0.74), after a plateau was reached, and was nonsignificant (P > 0.05). At these stages both chromosomes had about the same effects on bristles and on fitness and will be maintained at the intermediate frequencies attained previously, as the inversion inhibits crossing over.

Our results therefore are in sharp contrast with most previously reported work2. It is a common feature of long term selection experiments that relaxed selection results in a considerable decline of the mean previously attained, particularly when the lines carry lethals with a pleiotropic effect on the selected trait. Increasing opposition of natural selection will then cause a cessation of response to artificial selection and a limit will eventually be reached characterized by an unstable equilibrium between these two forces. However, in the present case, the presence of the inversion determines the establishment of an effective balanced lethal system where no further response can be obtained and relaxation of selection will not restore fitness.

References