Group selection among laboratory populations of *Tribolium*

(extinction/colonization/population size)

MICHAEL J. WADE

Department of Biology, University of Chicago, Chicago, Illinois 60637

ABSTRACT   Selection at the population level or group se-
lection is defined as genetic change that is brought about or
maintained by the differential extinction and/or proliferation
of populations. Group selection for both increased and de-
creased adult population size was carried out among laboratory
populations of *Tribolium castaneum* at 37-day intervals. The
effect of individual selection within populations on adult pop-
ulation size was evaluated in an additional control series of
populations. The response in the group selection treatments
occurred rapidly, within three or four generations, and was large
in magnitude, at times differing from the controls by over 200%.
This response to selection at the populational level occurred
despite strong individual selection which caused a decline in
the mean size of the control populations from over 200 adults
to near 50 adults in nine 37-day intervals. "Assay" experiments
indicated that selective changes in fecundity, developmental
time, body weight, and cannibalism rates were responsible in
part for the observed treatment differences in adult population
size. These findings have implications in terms of speciation
in organisms whose range is composed of many partially iso-
lated local populations.

Much of the theoretical and experimental work in population
genetics has been concerned with genetic changes within single
panmictic populations or in a collection of permanent popu-
lations with some gene flow between them (1, 2). Such work
cannot be applied to those cases of biological interest in which
populations are going extinct and being recolonized at rates
comparable to the time scale of genetic changes within single
populations (3, 4).

Ecological theory, on the other hand, has attempted with
some success to predict the dynamics and the effects of subdi-
viding a species range into a large number of local habitats
(5–7). Although extinction and recolonization are important
factors in this work, it remains mainly nongenetic and theo-
retical in character.

Selection at the populational level or group selection is de-
fined as genetic change that is brought about or maintained by
the differential extinction and/or proliferation of populations.
Intergroup selection has been proposed by many workers on
theoretical grounds as a possible mechanism for the evolution
of altruistic and social behaviors (8–15). However, the evolution
of *any* trait, not necessarily social, that affects the likelihood
of a population becoming extinct or establishing colonizing
propagules will be influenced by intergroup selection (16,
17).

This report summarizes the major features of an extensive
empirical study of the genetical effects of extinction and re-
colonization in laboratory populations of the flour beetle, *Tri-
bolium castaneum* (18). The character chosen for group se-
lection was numbers of adults in a population at intervals of 37
days. Previous work (19–21) has shown that the number of adult
beetles at this time is highly correlated with the probability of
and time to extinction of a population and with the tendency
of adult beetles to emigrate. Standard conditions were observed
during the husbanding and censusing of the populations
(22).

The experiment consisted of four treatments (Fig. 1): treat-
ment A, group selection for high numbers of adults per popu-
lation; treatment B, group selection for low numbers of adults
per population; treatment C, no group selection; individual
selection within the populations was allowed to determine the
numbers of adults per population; and treatment D, random
group selection, i.e., selection and dispersion of populations by
means of a table of random numbers.

In treatment A, that population with the largest number of
adults at the 37-day census was selected and divided into as
many groups of 16 adults as possible. One new population was
then founded with each group of 16. The population with the
second highest number of adults was then chosen and likewise
divided into propagules of 16 adults. Group selection for large
numbers of adults was continued in this manner until 48 new
populations had been established. In treatment B, the procedure
was identical to that described for A except that the populations
with the lowest numbers of adults were selected and divided.
Treatment D was similar to A and B, but in this case a table of
random numbers was used to select the populations. Treatment
D permits a comparison of the effect of random with directed
extinctions (A and B).

Treatment C was designed to be a control treatment that
would indicate the effect of individual selection *within* popu-
lations upon adult numbers at 37 days. Accordingly, in this
treatment one group of 16 adults was chosen at random from
each of the 48 C populations and a new population was founded
with each group of 16. There could be no group selection in
treatment C because there was no differential extinction or
proliferation of the populations.

Changes in the mean number of adults produced in 37 days
occurred rapidly, within three or four generations, and the
differences between treatments were large in magnitude, at
times exceeding 100 adults per population (Fig. 2a). Group
selection in the opposite direction (Table 1, and see below) to
individual selection (compare A with C) produced an average
difference of over 100 adult beetles per population. Group se-
lection in the same direction as individual selection (compare
B with C) so accelerated the rate of change of adult numbers
that differences of over 60 adults per population were ob-
served.

Just as individual selection requires that there be differences
between individuals, group selection requires that there be
differences between populations. The origin of sufficient be-
tween-populations variance for group selection has been con-
sidered problematic in previous theoretical work (23, 24).
Analysis of the D treatment populations, among which there
were only *random* extinctions, revealed a heretofore unrec-
ognized source of between-populations variance. (It is em-
phasized that this between-populations variance is the *sine qua
non* of group selection.) A consequence of taking more than one
set of propagules from a single population is that in any gen-
eration some D populations are descended from the same
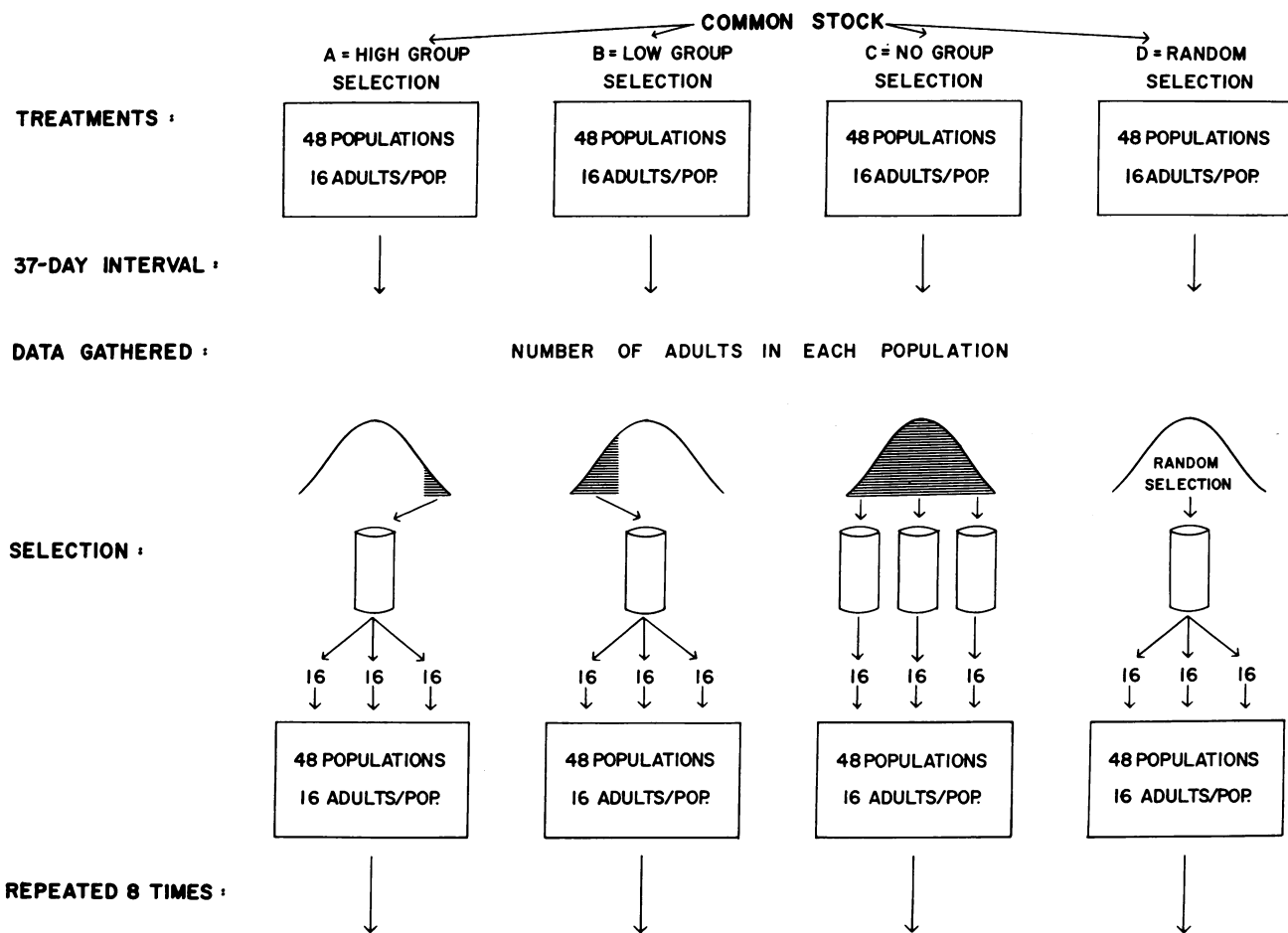"parent" population of the previous generation while other D

FIG. 1. The experimental design used in the study of group selection. The curves indicated prior to "Selection" represent smoothed histograms of the census data gathered for each treatment with numbers of adults on the abscissa and numbers of populations on the ordinate.

populations are descended from different parent populations. The total variance in adult numbers for a generation can be partitioned on the basis of the parents in the previous generation into *two* components: a within-populations component of variance and a between-populations component of variance. The within-populations component is evaluated by calculating the variance among D populations descended from the *same* parent in the immediately preceding generation. The between-populations component is evaluated by calculating the variance among groups of D populations descended from *different* parents. The process of random extinctions with recolonization (D) was observed to convert a large portion of the total variance into the between-populations component of the variance (Fig. 2b), the component necessary for group selection. This analysis indicates that group selection need only be a sporadic event in natural populations in order to bring about significant genetic change because a process of random extinctions with recolonization can create the ideal and favorable conditions for it to occur.

In addition, the process of speciation can be viewed as the conversion of variation within populations to variation between populations (25, 26). For this reason a process of random extinctions with recolonization may significantly accelerate the rate of speciation of organisms whose species range is composed of many partially isolated local populations. Sewall Wright, in several publications (16, 17), has strongly supported the view that such a population structure is most favorable to rapid evolutionary advance.

Several "Assay" experiments were conducted in an attempt to determine the mechanisms responsible for the observed changes in adult numbers. These experiments are designed to eliminate as far as possible all populational interactions except for the one under investigation (20). In addition, these assays were conducted in such a way as to permit the variance of each assayed character to be partitioned into within- and between-populational components (Table 1, column 5).

The assays show that the control (C) populations declined in mean adult population size (from over 200 adults in generation one to 50 adults in generation nine) primarily as a result of an increase in the voracity of C adults as cannibals of eggs and pupae [Table 1; c, the mean number of eggs eaten per adult per day, enters into models of *Tribolium* population growth as an exponent (27). The small numerical change in c in Table 1 is thus representative of a larger change at the populational level.]. The effectiveness of pupal cannibalism by C adults is further enhanced by a broadening of the range of initiation of the pupal stage from 2.36 days in the initial stocks to 4.09 days in the final C population assay. Thus each pupal cohort in C is exposed for a longer time to a more voracious population of adult cannibals, and this change can be attributed to individual selection within the C populations.

The high group-selected populations (A) exceeded the controls (C) in all assayed components expected to contribute to population size except larval egg cannibalism. The low group-selected populations (B) also exceeded or equalled the C populations in all components assayed, yet the B populations
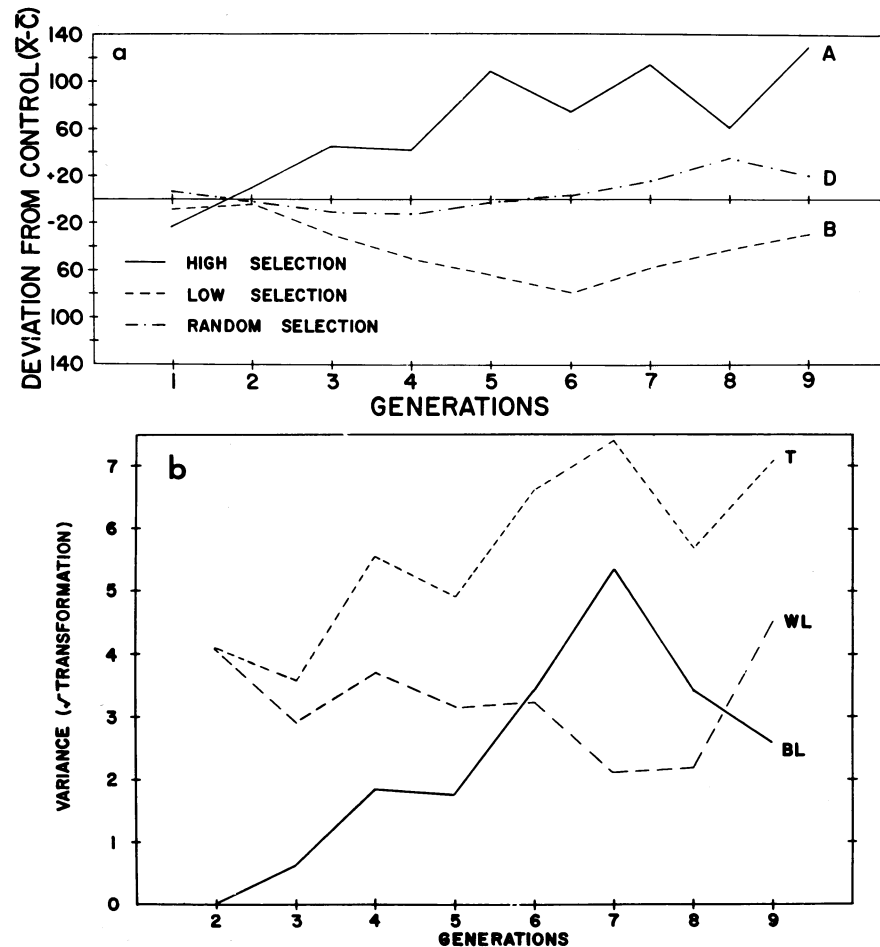
FIG. 2. (a) Deviations of the means of A, B, and D treatments from the C or control mean for each generation. The line at zero deviation represents the C or control treatment. For generations three through six, A > C = D > B with $P \ll 0.005$; for generations seven through nine, A > D > C > B with $P \ll 0.005$. (b) The analysis of the components of variance for the D treatment populations. The between treatments component of variance (BL) represents a significant portion of the total variance for generations three through nine ($P_3 < 0.025$, $P_{4-9} \ll 0.005$). T, total; WL, within lines; BL, between lines.

maintained much lower adult numbers. This unexpected result can be explained by examining the mean of each B population separately rather than the grand mean. In the B treatment, there is a significant between-populations variance for five of the nine traits assayed (Table 1, column 5; $P < 0.025$). That is, some of the B populations enjoy a higher cannibalism rate than the controls while other B populations have a longer mean developmental time or a lower average fecundity relative to the controls. Unidirectional group selection for lower adult population size resulted in a multivarious response among the B populations because there are many ways to achieve low population size. It can reasonably be assumed that individual selection within the B populations was operating in a manner similar to the individual selection in the control C populations. Thus, the decline in mean population size in the B treatment (from over 200 adults in generation one to 19 adults in generation nine) is the result of both group selection between populations and individual selection within populations favoring characters responsible for low population size. It is clear from inspection of Table 1, columns 2 and 3, that group selection and individual selection operating in the same direction (B) can produce results different from individual selection operating alone (C). All previous theoretical work (8–14) has ignored this aspect and implicitly or explicitly considered the case of group selection in the opposite direction to individual selection to be the only important case of biological interest.

In summary, these results indicate (*i*) that group selection in the opposite direction to individual selection can produce significant genetic change, (*ii*) that group selection in the same direction as individual selection can produce results very different from individual selection acting alone, and (*iii*) that a process of random extinctions with recolonization can establish conditions favorable to the operation of group selection.

1. Crow, J. F. & Kimura, M. (1970) *An Introduction to Population Genetics Theory* (Harper and Row, New York).
2. Wright, S. (1951) *Annals of Eugenics* 15, 323–354.
3. MacArthur, R. H. & Wilson, E. O. (1967) *The Theory of Island Biogeography* (Princeton University Press, Princeton, N.J.).
4. Simberloff, D. S. & Wilson, E. O. (1969) *Ecology* 50, 278–296.
5. Levin, S. (1974) *Am. Nat.* 108, 207–228.
6. Levins, R. & Culver, D. (1971) *Proc. Natl. Acad. Sci. USA* 68, 1246–1248.
7. Slatkin, M. (1974) *Ecology* 55, 128–134.
8. Boorman, S. A. & Levitt, P. R. (1973) *Theor. Pop. Biol.* 4, 85–128.
9. Levin, B. R. & Kilmer, W. L. (1974) *Evolution* 28, 527–545.

Evolution: Wade

Proc. Natl. Acad. Sci. USA 73 (1976) 4607

Table 1. Primary characteristics of the group-selected populations

Trait assayed	Treatments				Between-populations variance	Significance of comparison ($P < 0.001$)
	A	B	C	D		
Fecundity[a]	53.5	52.7	43.1	52.3	B	A = B = D > C
Fertility(%)[b]	90.1	86.0	88.7	85.6	D	A = B = C = D
Larval survivorship to adulthood(%)[c]	95.5	83.3	82.7	83.4	None	A > B = C = D
Sex ratio[d]	1:1	1:1	1:1	1:1	None	A = B = C = D
Developmental time[e]						
♂♂	24.7	24.8	26.1	25.4	B	A = B < C = D
♀♀	24.8	25.7	25.7	25.6	None	A < B = C = D
Body weight[f]						
♂♂	2.01	2.25	2.09	2.18	B	A = C < B = D
♀♀	2.31	2.33	2.16	2.23	B	A = B > C = D
Cannibalism rate						
Larvae on eggs(%)[g]	47.8	44.6	42.3	48.4	B,C,D	A = D > B > C
Adults on pupae(%)[h]	52.4	51.1	64.6	66.9	B	A = B < C = D
Adults on eggs[i]	3.7	3.3	5.1	6.7	C	D > C > A = B

Summary of the data of the assay experiments. Each table entry in columns 1 through 4 is the mean of 24–48 observations, depending upon the assay.

[a] Fecundity = mean number of eggs laid per ♀ per 3-day interval during adult ages 7–31 days.
[b] Fertility = % of eggs hatching.
[c] % of first instar larvae surviving to adulthood.
[d] Sex ratio was determined on pupae surviving adult cannibalism, larvae surviving to adults, and developmental time adults.
[e] Days from first instar larva to fully sclerotized adult.
[f] Table entry = mg $\times 10^{+2}$.
[g] % of 100 eggs cannibalized in a 2-day interval by a uniformly aged cohort of 50 larvae.
[h] % of 30 pupae eaten by a cohort of 16 adults.
[i] Table entry = $c \times 10^2$, where c = mean number of eggs eaten per adult per day.

10. Levins, R. (1970) *Am. Math. Soc.* **2**, 75–108.
11. Sturtevant, A. H. (1938) *Q. Rev. Biol.* **13**, 74–76.
12. Gadgil, M. (1975) *Proc. Natl. Acad. Sci. USA* **72**, 1199–1201.
13. Wilson, D. S. (1975) *Proc. Natl. Acad. Sci. USA* **72**, 143–146.
14. Wright, S. (1945) *Ecology* **26**, 415–419.
15. Wynne-Edwards, J. C. (1962) *Animal Dispersion in Relation to Social Behavior* (Hafner Publishing Co., New York).
16. Wright, S. (1931) *Genetics* **16**, 93–159.
17. Wright, S. (1956) *Am. Nat.* **90**, 5–24.
18. Wade, M. J. (1976) *Evolution*, in press.
19. Nathanson, M. (1975) *Bull. Entomol. Res.* **65**, 1–12.
20. Park, T. (1954) *Physiol. Zool.* **27**, 177–238.
21. Ziegler, J. (1972) Doctoral dissertation, University of Chicago.
22. Park, T. (1948) *Ecol. Mongr.* **18**, 265–308.
23. Smith, J. M. (1964) *Nature* **201**, 1145–1147.
24. Williams, G. C. (1966) *Adaptation and Natural Selection* (Princeton University Press, Princeton, N.J.).
25. Darwin, C. (1878) *The Origin of Species* (D. Appleton & Co., New York).
26. Lewontin, R. C. (1974) *The Genetic Basis of Evolutionary Change* (Columbia University Press, New York).
27. Neyman, J., Park, T. & Scott, E. L. (1956) *Proceedings of the Third Berkeley Symposium on Mathematical Statistics and Probability*, Vol. 4, 41–79.