Selection in natural populations

V. INDIAN RATS (*RATTUS RATTUS*)

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1. INTRODUCTION

One method of studying natural selection in a free-living population is to use a character that is variable in the population but that does not change ontogenetically within an adequately long proportion of the life cycle. Such characters are relatively rare in the animal kingdom (and even rarer among plants), but they do exist. One such set of characters is the structure of the unworn parts of the enamel surface of those mammalian teeth that do not grow continuously. If a cohort is sampled randomly at two more or stages of its life cycle, any difference in the distributions of the character in the two samples will indicate the action of differential mortality (or, exceptionally, differential migration).

In the present case it is not cohorts that were sampled but populations containing rats of various ages. In such cases an unambiguous interpretation of any difference between the age groups may not be possible, because environmental influences may have been different between the times of enamel formation in the rats of different ages. In the present study, however, as in some others on mammalian teeth (Kurtén, 1953, 1957, 1958; Van Valen, 1963, 1966), there is evidence that any such environmental differences are not of major importance for at least some of the differences found.

2. MATERIAL AND MEASUREMENTS

The rats measured belong to the species *Rattus rattus* and were collected in November and December, 1961, and January 1962, by a party led by H. Grüneberg. These rats have been the subject of another study (Grüneberg *et al.*, 1966).

Sixteen populations were used in the present study, with sample sizes varying from 50 to 68. These are all from the state of Kerala, in southern India, and consist of all the samples used by Grüneberg *et al.* (1966) that have over twenty specimens.

Measurements of anteroposterior length and labiolingual width of each left lower molar (occasionally a right one) were made by Weiss, using a measuring microscope, and are accurate to 0·01 mm. In a series of duplicate measurements the standard

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error of the difference was 0·0077 mm. The width measurements were taken perpendicular to the longitudinal axis of the tooth and parallel to the occlusal surface. The plane of the occlusal surface changes very little if at all with age, and there are no obvious interindividual differences in it. In addition, the base of the tooth is rounded, so that any change in the occlusal plane would have a disproportionately small effect on the measurement. Most of the characters measured are not constant over a sufficiently long range of tooth wear for use in the present study, because the base of the enamel is narrower and shorter than some or all of the rest of the tooth. In mature individuals the teeth become worn below the level of the maximum value of most measurements. Only the widths of M_2 and M_3, of the characters used, have their maxima sufficiently near the base of the crown to be suitable, and even with these measurements 53 of the 899 individuals had teeth too worn for one or both of these measurements to be used. In all old individuals, M_2 and M_3 were examined to see if they were, or could be, worn below the point of maximum width. Six individuals had teeth too incompletely erupted for measurement.

Age was estimated by tooth wear. The specimens were divided by Van Valen into five arbitrarily delimited age groups. The youngest and oldest pairs of these groups were relatively small and were combined for the analyses, which were thus made on three age groups. The way in which the teeth have been worn shows some variation between individuals. The same boundaries between groups were used for both sexes and for all populations. These boundaries were based on ratios of the maximum length (with anteroposterior and vertical components) of the wear facet on one loph of an upper molar to the maximum length of the surface of the next loph that was exposed above this wear (cf. Van Valen, 1966). Individuals with a mean ratio less than or equal to 1 were placed in the young age group (S), those with a mean ratio of at least 2 were placed in the old age group (H), and the remainder comprised the middle age group (M). The occasional individuals with total wear equivalent to one age group but with a mean ratio characteristic of another, were placed in the former group. The number of measured individuals in each age group in each sex can be seen in Table 1. There is no adequate calibration available for determination of the absolute ages of these groups, and undoubtedly there is some overlap between adjacent groups. There is significant, but relatively small, heterogeneity among the age distributions of the samples from different populations.

The statistical methods used have been described elsewhere (Van Valen, 1965, 1966), except as noted below.

3. RESULTS

Table 1 gives the statistics from which comparisons can be made. Although there is heterogeneity among the populations in the measurements, it is shown below that no heterogeneity is detectable for the ratios of the variances of the age classes. Grouping of the populations as in Table 1 therefore does not distort any difference between the age classes. The various significance tests used are nevertheless performed on the data before such grouping.

The following questions can be asked of the measurements: (1) Is there a signi-

Table 1. *Means and variances (in mm.) of tooth width in three age groups*
(S, young; M, middle; H, old), for all populations combined

		N	Weighted mean of $s^2 \times 10^4$	Weighted $\bar{x}$	Unweighted $\bar{x}$
Males					
M_2	S	117	41·34	1·700	1·697
	M	195	42·91	1·707	1·706
	H	101	32·77	1·714	1·713
M_3	S	117	46·93	1·477	1·473
	M	196	46·14	1·486	1·486
	H	97	31·53	1·491	1·486
Females					
M_2	S	122	35·71	1·713	1·713
	M	201	40·56	1·697	1·698
	H	117	41·38	1·706	1·703
M_3	S	120	59·51	1·478	1·480
	M	201	53·97	1·483	1·486
	H	117	37·14	1·473	1·471

ficant average decrease of the variance with age? (2) Is there a significant average change of the mean with age? (3) Does the amount of either or both of these possible changes differ among the populations, between the teeth, or between the sexes? The last question will be discussed first, with reference to the variance.

There is no detectable heterogeneity among populations, between sexes, or between the two teeth in the ratio of the variance in one age class to the variance in another age class. The test for heterogeneity between teeth is the same as that for heterogeneity between sexes. The tests on sex and tooth were made separately for each tooth and sex respectively, and that for populations was made separately for each combination of tooth and sex. The probabilities resulting from these tests were combined to produce one value each for tooth, sex, and population heterogeneity. All tests were made for each pair of the three age groups; as only one of the nine combined probabilities was below 0·1 (it was about 0·06) and most were much higher, further manipulation seemed unnecessary.

The correlation (weighted $\bar{z}$) between M_2 and M_3 is 0·771 for males and 0·641 for females. These are not clearly different ($P = 0·07$) and give a joint estimate of $z = 0·704$ or $r = 0·607$. The calculated variance among the z correlations was divided by the weighted mean theoretical error variance of the z's to give, for each sex, an approximately χ^2/d.f. variate with 15 degrees of freedom for the sixteen populations. Neither of the probabilities from this test for interpopulation heterogeneity of the correlations was below 0·1, so the correlations may be assumed homogeneous among populations as well as between sexes.

The most direct test for a uniformly directional difference in the variances with age would be to use regressions of variance on age. This proved impractical because the correct number of degrees of freedom was not evident in part of the analysis.

An alternative method was then used, testing each pair of age groups and combining the results with due regard for their lack of independence. The weighted mean variance for each combination of age group, sex, and tooth was determined, each estimated variance being weighted by one less than its sample size. These variances are the ones given in Table 1. For each combination of tooth and sex, the ratios of the variances for the three pairs of age groups were then determined, and from these the one-tailed probabilities of the variance decreasing. By the method of Yule & Kendall (1950, p. 330), it can be seen that these three ratios are equivalent to $1 \cdot 75$ independent ratios. To combine the three probabilities in each group, then, we have

$$\chi^2 = \tfrac{7}{6} \sum (-\ln P)$$

with $3 \cdot 5$ degrees of freedom. The combined probabilities are $0 \cdot 19$ for male M_2, $0 \cdot 05$ for male M_3, $0 \cdot 76$ for female M_2, and $0 \cdot 017$ for female M_3. The male and female probabilities are independent under the null hypothesis and give joint estimates of $0 \cdot 45$ for M_2 and $0 \cdot 007$ for M_3. The estimated correlation of $0 \cdot 607$ shows that about $0 \cdot 63$ of the variance of each tooth is determined independently from the other, so the two teeth represent $1 \cdot 63$ independent variates. Combining the probabilites for the two teeth within each sex, using the estimated correlations for each sex, gives joint probabilities of $0 \cdot 07$ for males and $0 \cdot 08$ for females. Combining either pair of probabilities gives a final probability of $0 \cdot 03$ for no decrease of variance with age. The ostensible decrease of variance with age is therefore probably real.

For the means, there is no detectable average difference between the means of any pair of ages. Such a result could come about by a uniform lack of difference or from differences in opposite directions that cancel out each other, so heterogeneity among populations, between sexes, and between the teeth was also tested. No heterogeneity was found for sexes or teeth, but there is significant heterogeneity among populations (final $P = 0 \cdot 02$, combined from four separate tooth-sex classes as for the variance). This heterogeneity among populations with respect to the mean is in the difference between age groups, not in the measured characters themselves. Grüneberg et al. (1966) have found heterogeneity among populations for the latter aspect also.

4. DISCUSSION

It is possible that the heterogeneity among populations in the differences of means is a result of heterogeneity in local sequences of weather or other environmental influences. Tooth size may depend to some degree on, e.g., temperature or level of nutrition. If different localities had sequences of temperatures, or sequences of the degree of approach of population size to carrying capacity (the population size at which some environmental resource becomes limiting), that were different in direction between two populations, then in one population the rats developing earlier could have larger teeth than those developing later, while the reverse could be true in the other population.

Moreover, individuals developing in unusual or unfavourable environments are often more variable than those developing in more common or more favorable

environments. A change in environment producing a change in mean would also then produce a change in variance without the action of selection. For such an effect to be operative in the present case, the range of environments would have to extend some distance beyond the range of reduced response to environmental influence (if this reduction or canalization exists here) in both directions. The environments of the several populations would have to be about optimal initially, then deteriorate in both directions as the younger rats passed the developmental interval when molar size is determined. The samples were not collected quite simultaneously, but the absence of detectable heterogeneity in the variance ratios suggests that region-wide environmental changes were not involved. This lack of appreciable heterogeneity is also evidence against the mean difference in variance being due to direct environmental effects at all, because about the same degree of environmental change in each population would be required, some in one direction and some in another, and these changes would have to be considerable in order to extend in both directions beyond any zone of canalization. Alternatively, if the environment itself were more variable at a later time in each population, the lack of heterogeneity is again a difficulty, particularly because of the somewhat different times of collection.

It is therefore probable that the differences in variances are the result of stabilizing selection, while no conclusion can be reached on the cause of the differences in mean.

The stabilizing selection is descriptively on molar width, but it is entirely possible that its primary effect is on some correlated character such as body size. In such a case the intensity of selection on this other character would have to be greater (by a factor of $1/r^2$) than that found for molar width. The strong selection intensities found for tooth dimensions in two other mammals (Kurtén, 1957, 1958; Van Valen, 1963, 1966), as well as the multiplicity of adaptive trends in the paleontological record of teeth, suggest that selection can be on tooth dimensions directly, although it is impossible to say whether this is the case in the present instance.

The mean reduction in variance between age groups M and H is 0·211, and that between S and H is 0·188. These correspond respectively to selection intensities of 0·041 and 0·035 if the initial populations were normally distributed (Van Valen, 1965). The combined probability from Kolmogorov-Smirnov tests of the combined distribution of S and M against the normal distribution, separately for each population and sex, is 0·09 for M_2, so any non-normality is presumably not serious. The individual samples are too small to estimate selection intensities on the mean, if in fact the differences of means are due to selection, because of a bias defined elsewhere (Van Valen, 1963).

The work of Lloyd (1909, 1910) on color patterns and of Grüneberg (1961) on skeletal variants has shown that there is much local differentiation within the rat populations of single Indian cities, with some variants extending for only a house or two. Grüneberg (1961) has interpreted his results as indicating action of genetic drift by recolonization, because of the general similarity of the shops where he captured his samples. This interpretation is very possibly correct, but no firm conclusion can be reached without information on such possibly important selective

agents as parasites, carrying capacity, resident or transient predators, and condition of food. Only information on the history of population size, such as that given by Berry (1963) for housemice and Goodhart (1962) for *Cepaea*, provides good evidence as to the action of drift. Strong differences among generally similar localities in the amount, and probably in the direction, of selection have been shown elsewhere (Van Valen, 1966) for housemice, and if the differences in the means found in the present study are due to selection this would provide another instance of the same phenomenon.

Perhaps as important as stabilizing selection in the maintenance of genetic variance in a species as a whole are differences in direction (and therefore intensity) of selection between different localities and at different times. This is the say that local optima often differ. Such differences in selection may be responses to environmental factors that are not at all obvious. They may indeed not be responses to environmental differences at all, if selection is operating toward different genotypic adaptive peaks in different populations with the same effective environment (Wright, 1965 and earlier).

SUMMARY

In samples of sixteen populations of *Rattus rattus* from southern India, the oldest individuals have less variable molar widths than the younger ones. This is probably due to stabilizing selection by mortality. There is no detectable heterogeneity between sexes or teeth or among populations in this selection. Although there is no average difference between age classes in mean tooth width, the difference between age classes is heterogeneous among populations. This heterogeneity may reflect heterogeneity in directional selection or in direct environmental effects. The selection intensity on the variance is about 0·04.

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