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THE REDUCTION OF MORPHOLOGICAL VARIATION IN NATURAL POPULATIONS OF SMOOTH NEWT LARVAE

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INTRODUCTION

Normalizing selection acting on continuous variation, although often invoked in theoretical discussions, has only rarely been observed in natural populations. The possibility of studying its action in populations of smooth newt (*Triturus vulgaris* (Linn.)) larvae was raised when a collection was taken from a pond near Nuneham Courtenay, Oxfordshire. The net used on this occasion was made of rather harsh material, and as a result about half the animals died before they could be measured in the laboratory. It was clear from the length-frequency diagram of dead and living larvae (see Fig. 1) that the larger (and older) larvae were much less likely to be killed than the smaller ones, but it also seemed possible that mortality was less near the major mode of the distribution. To test this idea, the data were regrouped at 5-mm intervals, which are sufficient to bridge the mode, and a line drawn through the plot of the proportion of animals dead in each group. This line was considered to estimate the proportion of animals expected to be dead in each 0.5-mm group, if simple physical size were alone responsible for differences in mortality. The actual proportion dead in each 0.5-mm group is known from the original data, and so the ratio of observed to expected mortality can be calculated. When this is drawn out (see Fig. 1), it is found to decline towards the centre of the major length mode, and to rise again on the other side. This suggests that animals nearer to the average in length are being selected for under conditions of stress, and this would constitute an example of normalizing selection. However, the analytical procedures involved are rather suspect, and a more rigorous analysis is not possible. It was decided, therefore, to measure the change in morphological variability amongst populations of these larvae by measuring surviving animals, and to attempt to eliminate by experiment or induction the action of factors other than selection. At the same time, an attempt was made to relate the intensity of selection in different populations to the more conventionally ecological parameters of survival and growth, and to study in detail the time-course of selection during the whole of the life-history.

PROCEDURE

The two characters chosen for study were standard length (often referred to as head + body length, or h + b), which is the distance from the tip of the snout to the posterior margin of the cloaca; and head width, which is the greatest width of the head behind the eyes. Larvae were captured by netting in the field and taken into the laboratory, where they were anaesthetized in a 1:20,000 solution of MS-222 (a soluble anaesthetic) and measured to an accuracy of 0.1 mm under a binocular microscope. Because the animals could not be aged other than by their length, the variation of standard length

and of head width was expressed at 0.5-mm intervals of total length (the distance between the tip of the snout and the tip of the tail). These graphs can be converted into time-curves through a knowledge of the growth-rate. The variation statistic used in all cases is Pearson's coefficient of variation:

$$CV = 100s/\bar{x}.$$

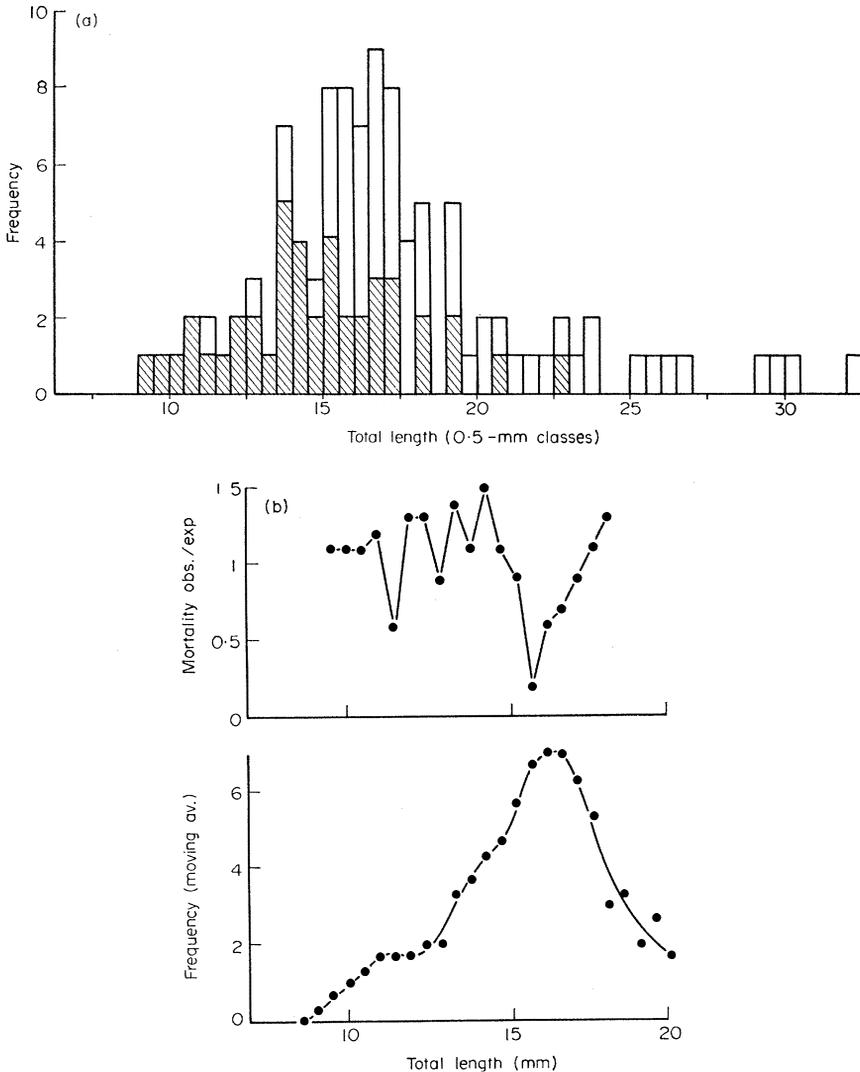


FIG. 1. Apparent normalizing selection caused by stress-induced mortality. Data from Nuneham Courtenay Arboretum, 5 August 1971, $n = 97$. (a) Length distribution of live (unshaded) and dead (hatched) animals. (b) Decline in mortality near the centre of the size mode.

This parameter will be referred to as 'variation', as opposed to variance. The variance of a measurement will increase as the mean value of that measurement increases, whereas the coefficient of variation (under certain circumstances) will maintain a constant value.

Collections were taken on about two dozen occasions from three small ponds near Nuneham Courtenay.

If normalizing selection were acting on either character, the variation of that character would be expected to decrease with increasing total length. Such a reduction would not, however, necessarily imply the presence of normalizing selection; in a rather similar study, Berry & Crothers (1970) discovered a reduction in the variation of body-weight ratios in populations of the dog-whelk, but failed to eliminate the possibility that other factors may produce the same result. It is known, for example, that the variation in human I.Q. declines with increasing age, but this is not primarily the result of any contemporary selective process. Rather, it is because the epigenetic system is so constructed that individuals which are originally quite different tend to become more similar as their development proceeds. This phenomenon, which was first identified by Waddington (1948), is called 'developmental canalization', and will readily mimic normalizing selection. To discover whether, or to what extent, canalization was responsible for the decline in morphological variation observed in wild populations, two groups of larvae, the progeny of about 150 females, were reared in the laboratory under conditions which were made as nearly optimal as possible. Since these survived much better than animals in the field, the intensity of any selective process was expected to be much lower; canalization, on the other hand, would be expected to take much the same course.

Nor are canalization and selection the only ways in which variation can be reduced. In many species of anurans it is known that when many larvae are grown together in a crowded culture, the larger larvae secrete a substance which tends to inhibit the growth of the smaller larvae (e.g. Lynn & Edelman 1936). This will normally result in an increase in the variation of any particular continuous character associated with growth, but it is easy to envisage a situation in which the mutual effects of crowded larvae may slow the growth of each larva to more or less the same extent, and thereby reduce the variation of such characters. The usual method of detecting mutual growth inhibition is to culture different numbers of larvae in equal volumes of water, the expectation being that those in the most crowded cultures will exhibit the lowest average growth rates. There are a number of difficulties with such designs: it is hard to be sure that food-levels are exactly comparable, for example, and in the more crowded cultures the larvae often attack one another. I therefore decided to use a different design. Six glass dishes, each containing 1 litre of water, were arranged at different levels, so that water could be slowly siphoned from the top dish to the bottom dish, through every intermediate dish. Four larvae were placed in each bowl; as far as possible, larvae of the same size were used. If any growth-inhibiting substances are produced by the larvae, these should become progressively more concentrated down the gradient of dishes, and the larvae should show a corresponding cline in growth rate.

Finally, it must be shown that any decline in variation is not the result of a statistical artefact. For example, if the rate of growth decreases with age, so that size reaches a plateau at some given age, then the variance of the growth measurement will tend to decrease with age too. The regressions of length on age, and of standard length and head width on total length, must therefore be rectilinear if complicated corrections are to be avoided.

RESULTS

Fig. 2 shows the relationship between variation and increasing total length in the three

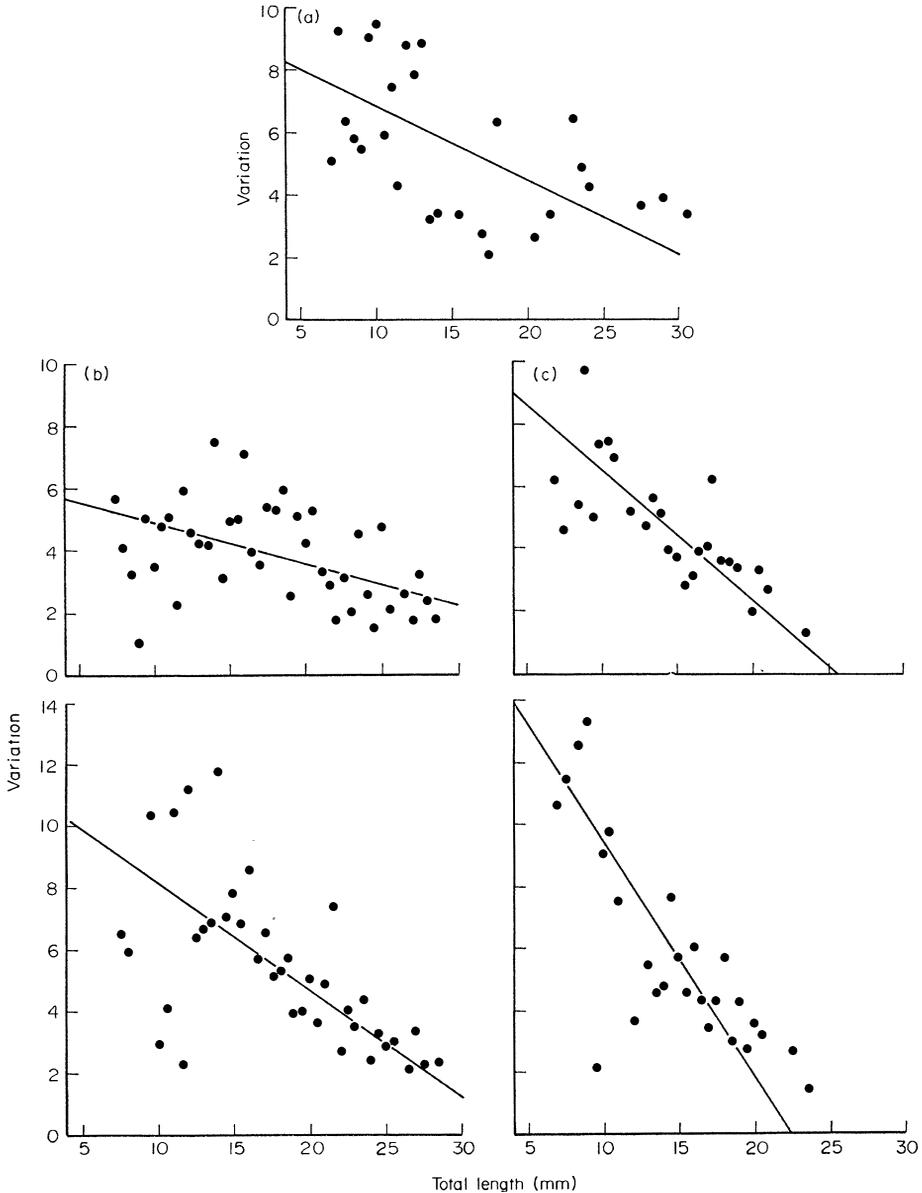


FIG. 2. The reduction of morphological variability in the three Oxfordshire localities. (a) Head+body variation against total length, Nuneham Courtenay Arboretum, $n = 191$. $b_{yx} = -0.1025 \pm 0.0846$ when $P = 0.01$. (b) Head+body variation against total length (above) and head width variation against total length (below), Nuneham Courtenay Venison South, $n = 277$. Above: $b_{yx} = -0.1025 \pm 0.0846$ when $P = 0.01$. Below: $b_{yx} = -0.2694 \pm 0.2000$ when $P = 0.001$. (c) As (b) but locality Stadhampton, $n = 173$. Above: $b_{yx} = -0.3096 \pm 0.2107$ when $P = 0.001$. Below: $b_{yx} = -0.5533 \pm 0.4595$ when $P = 0.01$.

populations. In all cases a highly significant reduction in variation can be demonstrated. The cause of this reduction was then investigated by attempting to eliminate explanations other than natural selection.

Firstly, larvae were reared under nearly optimal conditions in the laboratory. Because mortality was low the intensity of selection was expected to be low, so that any reduction in variation would be ascribed largely to canalization. The results, set out in Fig. 3, show that the decline in variation in these controls is much less than in the wild populations, and is in fact non-significant. The difference between controls and the field

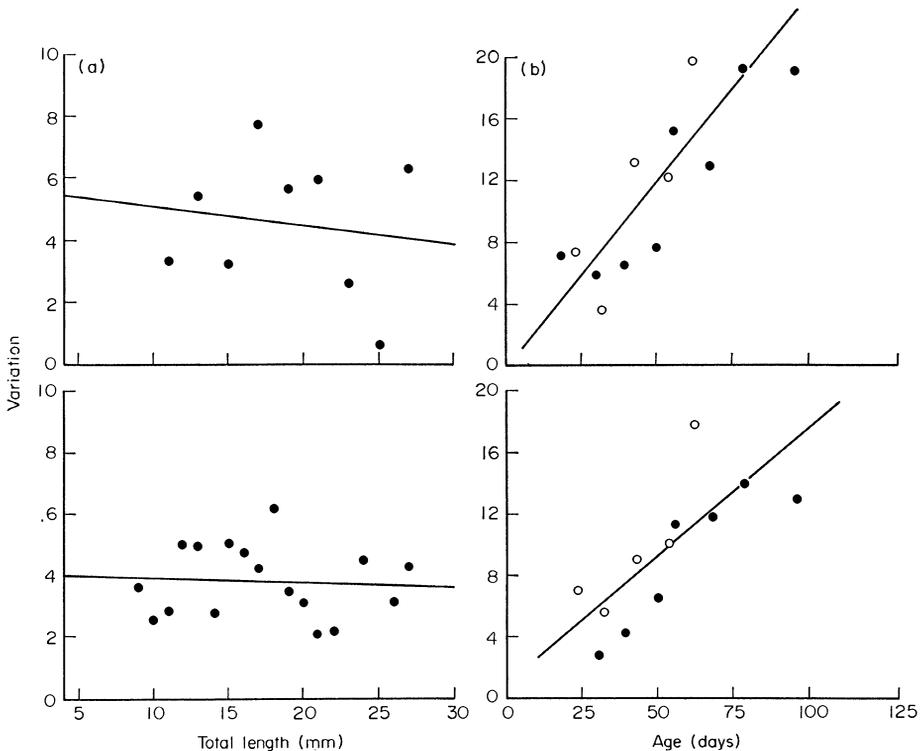


FIG. 3. Change in morphological variability in two laboratory populations maintained under nearly optimal conditions. The two cultures show no significant differences and have been lumped for the purposes of analysis. Total length variation, $n = 152$; standard length variation, $n = 49$; head width variation, $n = 121$. (a) Head + body variation (above) and head width variation (below) against total length. Above: $b_{yx} = -0.0474 \pm 0.4040$ when $P = 0.80$. Below: $b = -0.0133 \pm 0.0140$ when $P = 0.80$. (b) Total length (above) and head width (below) against age in days. Open and filled circles, two different replicates.

populations with respect to variation in standard length is significant only for the Stadhampton animals; this is perhaps because the sample size of the controls is rather small in this case. For head width, where many more of the controls were measured, the differences are significant beyond the 5% level in all cases (Table 1). Another control is possible. The laboratory animals were hatched from eggs which are known to have been laid on the same night, and so their age is known precisely. When the variation of total length or of head width is plotted against age, there is a steep positive regression; not only is canalization not acting, but morphological variation is able to increase

Table 1. Significance of the differences between linear regression coefficients for the reduction of variation

| Population | <i>b</i> | Venison South | Arboretum | Stadhampton |
|----------------------------------|----------|---------------|-----------|-------------|
| (a) Variation in standard length | | | | |
| Laboratory | -0.0474 | $P > 0.6$ | $P > 0.4$ | $P < 0.05$ |
| Venison South | -0.1025 | | $P > 0.2$ | $P < 0.01$ |
| Arboretum | -0.1763 | | | $P < 0.10$ |
| Stadhampton | -0.3096 | | | |
| (b) Variation in head width | | | | |
| Laboratory | -0.0133 | $P < 0.01$ | - | $P < 0.01$ |
| Venison South | -0.2694 | | | $P < 0.05$ |
| Arboretum | - | | | |
| Stadhampton | -0.5533 | | | |

sharply. The reason that this is not shown when standard length or head width variation is plotted against total length is presumably that animals which are aberrant in one of the test measurements are likely also to be aberrant in total length; plots of this sort tend to underestimate the degree of change in variation. These data do not exclude the possibility of interaction between canalization and major environment (e.g. Rasmusen 1960), although the conditions of culture were made as close as possible to natural conditions by using fresh pondwater as a medium and pond zooplankton as a food source. The most important differences between the laboratory and the natural environments were the absence of predators, the smaller volume and the slightly more stable temperature maintained in the culture vessels.

Secondly, the siphon experiment was set up to investigate the possibility that newt

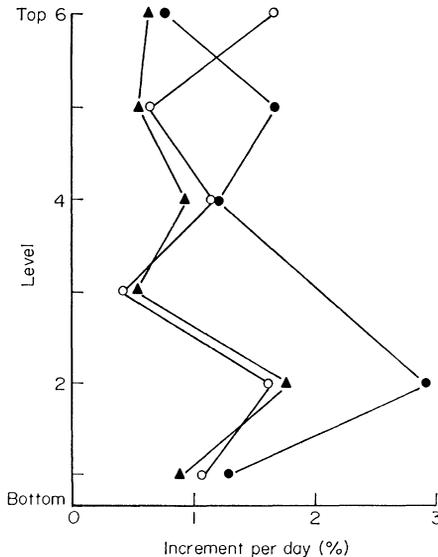


FIG. 4. Results of the siphon experiment. Water is siphoned down a gradient of dishes from level 6 (top) to level 1 (bottom). Any inhibitory substances should show a progressive concentration down this gradient. There is no obvious cline in growth-rates. Experiment run for 4 weeks, n (measurements) = 96, n (larvae) = 24. ●, Total length; ○, standard length; ▲, head width.

larvae exhibit mutual growth inhibition. Fig. 4 shows that there is no obvious cline in growth-rate down the gradient of dishes, and that consequently mutual growth inhibition cannot, in this case, be invoked as a mechanism tending to reduce morphological variation. It is necessary to add one qualification: the same results could be obtained if an inhibitor were capable of acting at densities much lower than 4 larvae/l, or if an inhibitor decayed rather rapidly, or both. However, the growth rate of larvae in culture at densities of about 20 larvae/l was not found to be significantly different from the growth rates measured at Nuneham Courtenay Arboretum and Nuneham Courtenay Venison South.

Finally, the demonstration of a real reduction in variation teems with statistical traps, even when biological alternatives have been eliminated. Fortunately, the nature of the data makes it possible to evade these pitfalls. The use of a coefficient of variation, rather than the variance or the standard deviation, is commonplace. Further, there is in every case a significant decline in the untransformed standard deviation of the two

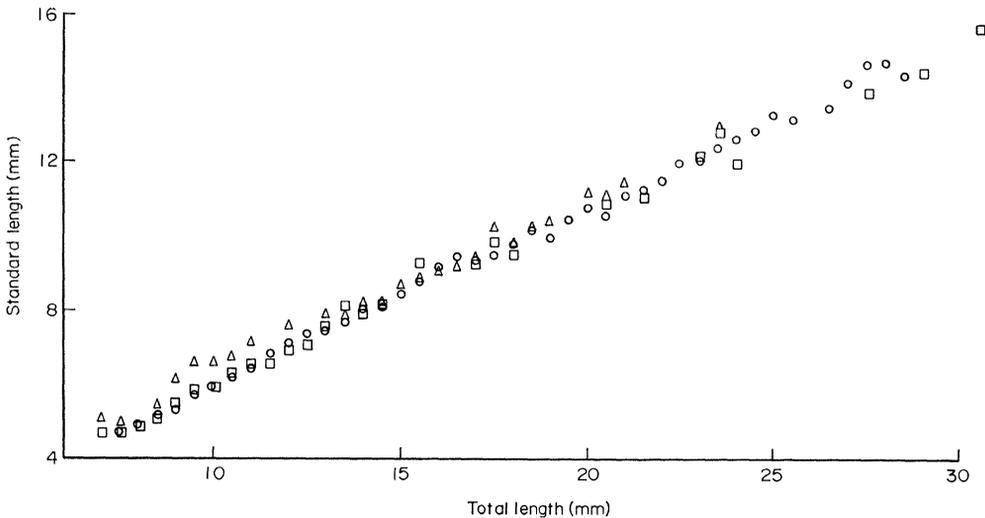


FIG. 5. The relationship between standard length and total length at the three Oxfordshire localities, $n = 641$. \square , Nuneham Courtenay Arboretum; \circ , Nuneham Courtenay Venison South; \triangle , Stadhampton.

measurements in the natural populations. The dependent variable in the variation regressions (Fig. 2) is the variation of a measurement rather than of the ratio of that measurement to total length; thus the possibility of autocorrelation is avoided. In animals whose rate of growth declines with age, the variation of a growth measurement will decline with age. Surprisingly, however, the growth in length of newt larvae is rectilinear, at least until shortly before metamorphosis (Fig. 11, and G. Bell, unpublished). An allied phenomenon would be a decline in variation at metamorphosis, caused by the loss of animals from the larval population. To eliminate this possibility, the largest larvae represented in the regressions of Fig. 2 were less than 30 mm in total length, whilst immediately pre-metamorphosis larvae are on average 35 mm in length. Finally, the regression of the test measurements on total length, which is analogous to a growth curve, should be rectilinear. This is shown in Fig. 5 for standard length, and is also true for head width.

I would conclude, therefore, that normalizing selection is probably responsible for the observed decline in variation.

DISCUSSION

The characters used in this study were chosen quite fortuitously; they happened to be useful for the purposes of a life-table study. The fact that both characters are found in all five cases to respond to selection might imply that selection of this sort is a very common event. Moreover, the intensity of normalizing selection on either character corresponds fairly closely to the overall survival rate (Table 2). This suggests two things. If each character were selected independently, the overall rate of survival would be much lower, and there must therefore be a considerable degree of functional, and possibly of genetical, association between them. This co-adaptation makes possible the production of a harmoniously balanced phenotype which is unlikely to be extreme in any respect; the possession of such a phenotype as a starting-point may be important in the second round of selection that the animal enters after metamorphosis. Secondly, it suggests that selection and survival may be equal phenomena, in the sense that the survivors of a population which has experienced any kind of mortality whose intensity is neither

Table 2. *Total survival at 30 days after hatching, compared with the amount of reduction in morphological variation*

| Locality | Arboretum | Venison South | Stadhampton |
|---|-----------|------------------|-------------|
| Overall survival | 0.87 | 0.43 | 0.36 |
| Reduction of variation in h + b length | 0.72 | (0.75) | 0.37 |
| Reduction of variation in head width | — | 0.66 | 0.17 |

zero nor one will not be a random sample of that population. This is a speculation familiar to population geneticists, but I do not believe that it is always appreciated by population ecologists.

In the examples described here, canalization does not seem to be an important factor in reducing morphological variability. The smooth newt inhabits small field ponds, a notoriously unstable habitat, produces a relatively large number of offspring (between 100 and 300), and is able to colonize new ponds rather rapidly (Warwick 1949). To this extent it can be considered an '*r*-selected' animal in the sense of MacArthur & Wilson (1967; cf. '*b*-selection' of Hairston, Tinkle & Wilbur 1970). In *r*-selected animals, which are capable of a high maximal rate of increase in unexploited habitats, it is supposed that the production of a large number of offspring necessarily involves a decline in the 'quality' of the offspring. It may be that selection and canalization are alternative ways of producing optimal phenotypes in surviving offspring. In *r*-selected animals, survival is usually sufficiently poor to allow considerable selection during the lifetime of the cohort, whereas in *K*-selected animals, which produce few offspring each of which has a high probability of survival, an alternative, developmental mechanism must be evolved to ensure that surviving offspring have nearly optimal phenotypes. Normalizing selection may occur under either regime, of course, but will be much slower in the latter.

The selective reduction in variation has so far been expressed as a simple linear re-

gression. There is some indication from Fig. 2 that this is not the case. The earliest points, before about 15 mm total length, seem to show a greater scatter about the mean, and may reflect a constant, or even increasing, amount of variation. This is especially well shown by the variation of standard length at the Venison South locality (Fig. 6), where variation quite clearly rises at first before declining beyond a total length of about 15 mm. This may be associated with a change in the behaviour of the larvae at this time. When the larvae first hatch, they are disruptively coloured with a pattern of longitudinal black and yellow stripes, and they cling to aquatic weeds until they have exhausted what remains of their yolk. At about 9 mm total length this coloration fades to a cryptic fawn, and at the same time the forelimbs appear. The larva now lies passive on the bottom or amongst the weeds, preying on any small cladocerans or chydorids which come within reach. At about 15 mm total length, the hind-limbs appear and the larva begins to search actively for prey; for the first time, chironomid larvae and small gammarids can be found in the gut. Larvae of this size can be seen prowling amongst the weeds and even on the open bottom of ponds, which smaller larvae never do. Selection

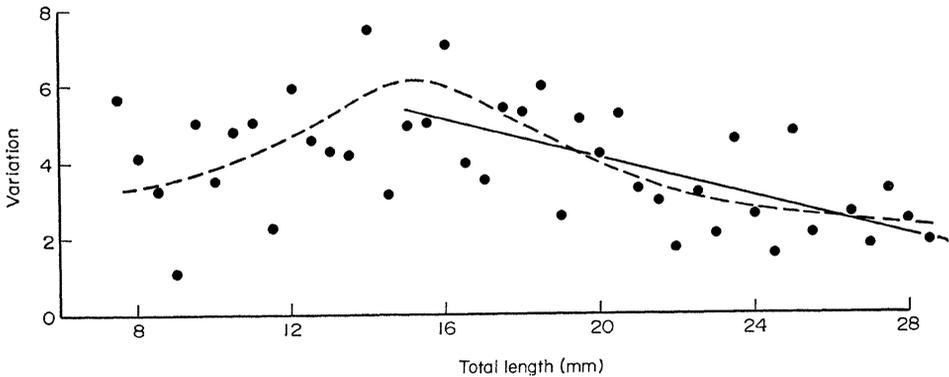


FIG. 6. Details of the selective reduction in variability of standard length at Nuneham Courtenay Venison South, 1972. Broken line drawn by eye to give the best fit to the plotted points. The regression line is for animals 15 mm and over. $b_{y,x} = -0.2517$.

pressures relating to prey capture and to predator avoidance must differ considerably between these two behaviours and I would suggest that optimal body proportions are likely to be more stringently selected in the older, actively hunting animals.

The mean value of the ratio of standard length: total length falls during larval life from about 0.68 immediately after hatching to about 0.47 shortly before metamorphosis. Immediately after metamorphosis, however, the mean rises to about 0.54, remaining at this value for immature animals and declining somewhat in mature newts (Fig. 7). Only a part of this change is explained by the resorption (in the larvae) or regrowth (in the adult male) of the caudal crest. The problem is that by the end of larval life the variation of the ratio has fallen to such low values that it is no longer possible to select for the optimal adult phenotypes from within the larval range. It was found that at metamorphosis the variation of the ratio suddenly increases from about 2.5 to about 6.0 (Fig. 7b), later declining, perhaps again under normalizing selection, both in mature and in immature animals. I do not suggest that this increase in variation is a function of metamorphosis, but only that it is a consequence, and perhaps an inevitable consequence, of the changes in gene expression occurring at this time.

Normalizing selection in newts

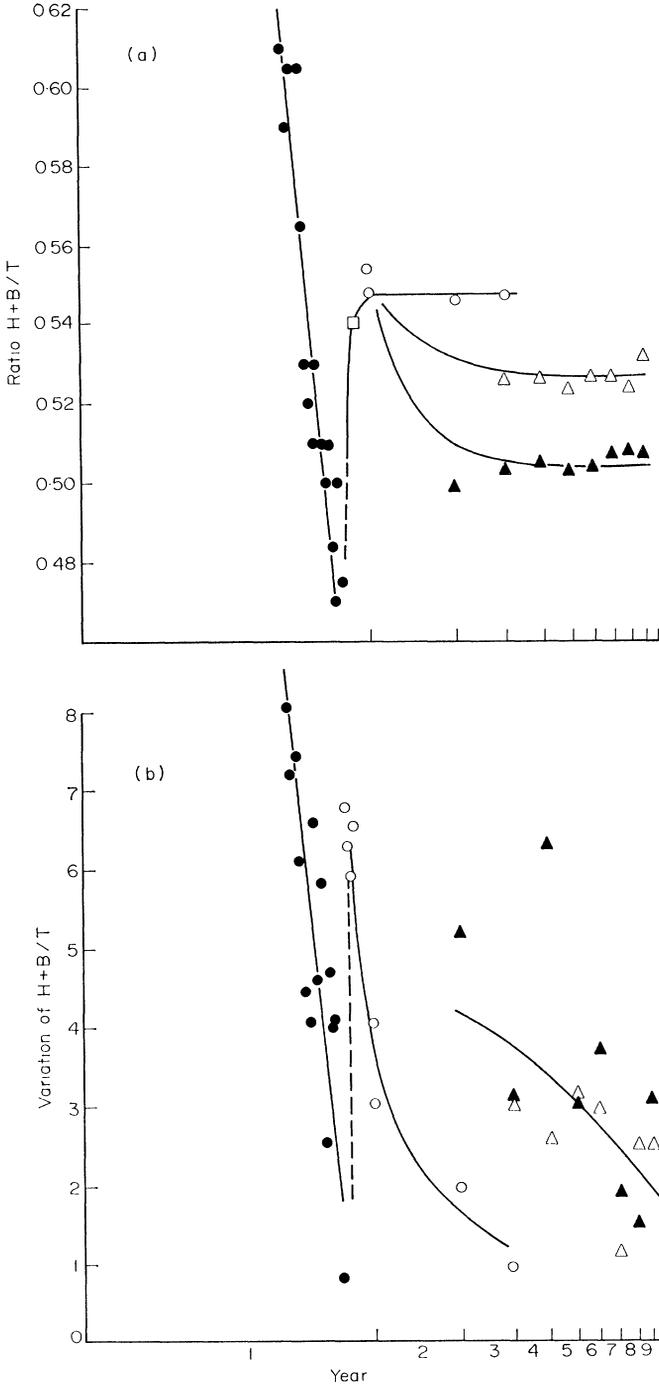


FIG. 7. Change in (a) the mean and (b) variance of the ratio of standard length : total length during life. Larvae from Nuneham Courtenay Arboretum, $n = 191$ (●), post-metamorphosis animals from Nuneham Courtenay Arboretum, $n = 179$ (□), immature animals from Drayton ($n = 65$) and Appleton ($n = 22$), both in north Berkshire (○) and adults from Nuneham Courtenay Arboretum $n = 690$ (▲, males, △, females).

Differences between the three populations in the rate at which variation is reduced presumably reflect differences in the intensity of selective forces in the three environments. Moreover, different selective pressures will reflect corresponding differences between populations in other, more conveniently ecological, population parameters. The most obvious of these is survival; the rate of survival strongly influences the amount of selection that can take place within a population, and more strongly selected populations would be expected to show poorer overall survival. Fig. 8 shows that this is true. The differences in survival are not inconsistent with the character of the ponds. For example, the pond at Stadhampton, where survival was worst, is a small, shallow, nitrogenous body of water which is rapidly approaching the terminal stages of succession. It dries up almost completely before any other pond in the district, and is very easily accessible to amphibious predators such as aquatic birds; in addition it is disturbed by cattle. These three populations do not appear to differ in adult survival or in fecundity (G. Bell, unpublished), so that any differences in demographic parameters must be

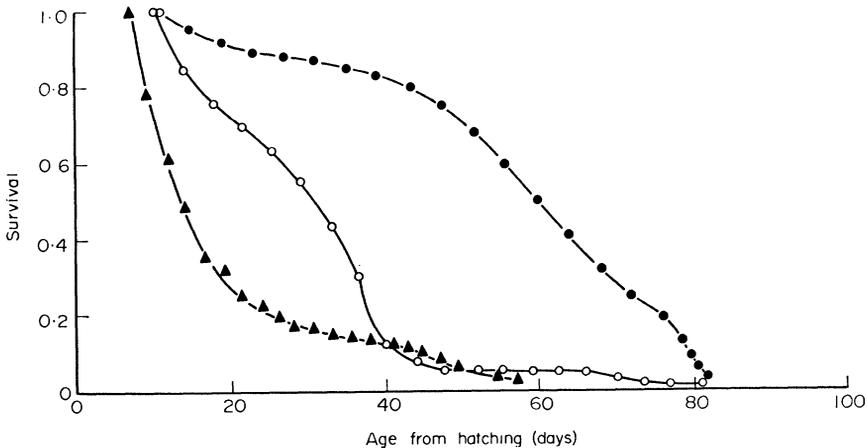


FIG. 8. Larval survival. Smoothed curves, derived mainly from length-frequency data, but checked independently at Stadhampton and Nuneham Courtenay Venison South. ●, Nuneham Courtenay Arboretum, 1971; ○, Nuneham Courtenay Venison South, 1972; ▲, Stadhampton, 1972.

ascribed chiefly to differences in egg and larval survival. For example, the history of the differences in larval survival will be revealed by differences in the adult age-structure. In general, heavy mortality of the younger stages will bias the population age-structure towards older age-classes. This shift will take place over a period of time corresponding to longevity, which is about 12 years. Fig. 9 shows the age (as standard length) structures of a number of adult populations near Oxford, ranked from top to bottom in order of increasing senility. The Arboretum population seems to be near equilibrium; the Venison South population is slightly more senile, but has an irregular age-structure which suggests that survival is much poorer in some years than in others; Stadhampton is a decidedly senile population. The only two populations more senile than Stadhampton are known to have nearly zero larval survival. The differences in early survival cannot cause different stable population sizes, but they can cause differences in the rates at which populations are increasing relative to one another. The age-structures of the populations suggest that the Arboretum population is stationary or slightly increasing, the Venison South population fluctuating and perhaps slightly decreasing, and the Stadhampton

population going quite rapidly to extinction. These differences are reflected in the observed population sizes, the Arboretum population being the largest and Stadhampton the smallest. The differences in larval survival also cause differences in the apparent larval growth-rate; small larvae survive less well than large larvae, and so heavier mortality, causing the differential removal of smaller larvae, will bias the growth-curve up-

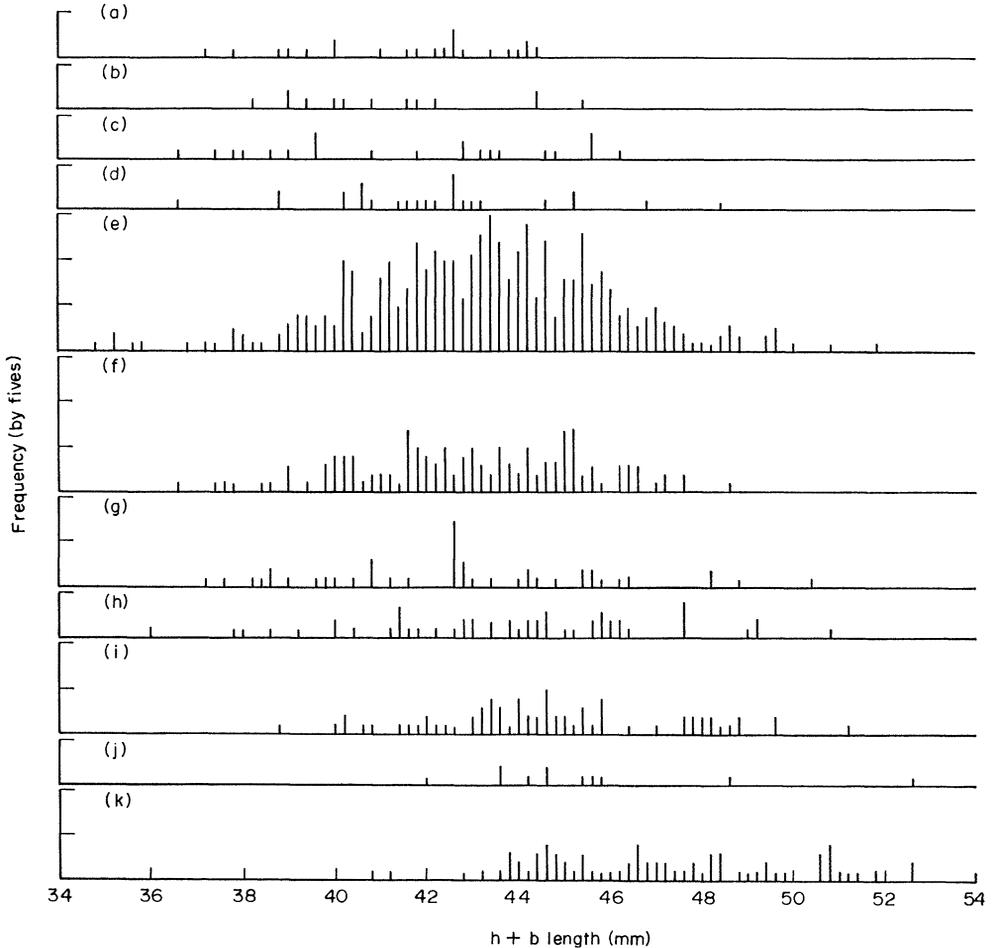


FIG. 9. Age-structure (as standard-length frequency) at a number of Oxfordshire and Berkshire localities. This refers to breeding males only, captured in 1972 (ranked from the most juvenile populations at the top to the most senile populations at the bottom). (a) Nuneham Courtenay Venison North, (b) Wytham Duck, (c) Nuneham Courtenay Bramble, (d) Nuneham Courtenay Cattle, (e) Nuneham Courtenay Arboretum, (f) Nuneham Courtenay Venison South, (g) Drayton, (h) Appleton, (i) Stadhampton, (j) North Oxford, (k) Marsh Baldon School.

wards, when growth is measured as the increase in mean size between sampling dates (Fig. 10). These relationships between demographical parameters and the intensity of selection are summarized in Table 3.

If the decline in variation is plotted against the estimated age, rather than against total length, the differences between the localities, and between the localities and the controls, are even more marked.

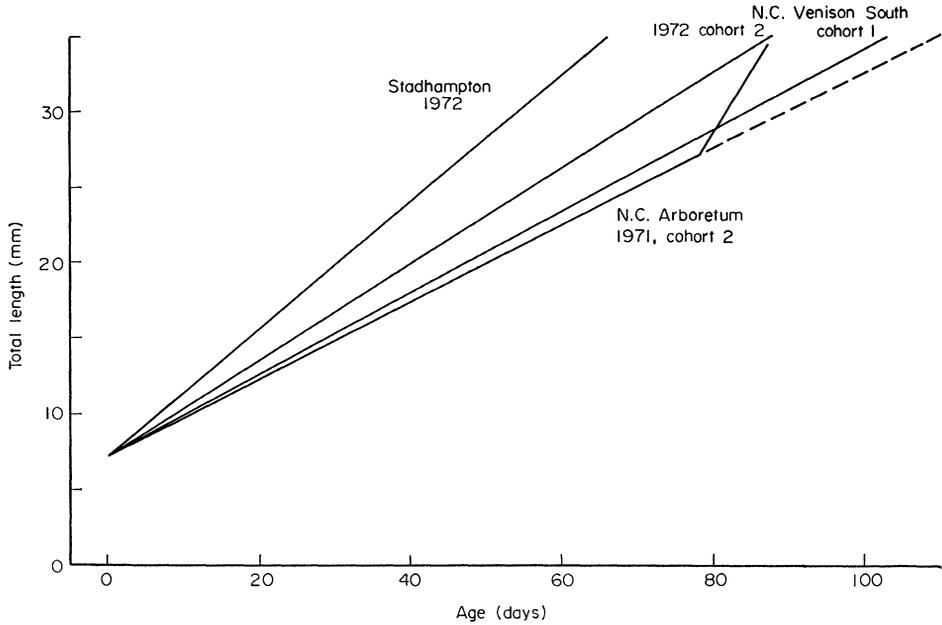


FIG. 10. Larval growth in total length. The linear regressions are calculated; there is no evidence of curvilinearity. It is known from field and laboratory observations that metamorphosis occurs at a larval length of about 35.0 mm.

Table 3. *Relationship between certain population parameters*

| Locality | Arboretum | Venison South | Stadhampton |
|---|--------------|-------------------|-------------|
| Larval growth-rate (total length) (b_{yx}) | 0.2481 | 0.2709* 0.3209 | 0.4218 |
| Time to metamorphosis (days) | 87.4 (112.1) | 103.0* 87.4 | 66.1 |
| Larval survival at 30 days of age | 0.87 | 0.43 | 0.36 |
| Larval survival to metamorphosis | 0.055 | 0.033 | 0.025 |
| Adult age-structure | Equilibrium | Slightly senile | Senile |
| Adult population size | 1007 | 243 | 180 |
| Selective reduction in h + b variation (b_{yx}) | -0.1763 | -0.2517 | -0.3096 |
| Selective reduction in hw variation (b_{yx}) | - | -0.2694 | -0.5533 |

* Two values given refer to two separate larval cohorts.

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SUMMARY

(1) A significant reduction in the variability of two morphological measurements was observed in three populations of smooth newt (*Triturus vulgaris* (Linn.)) larvae inhabiting small ponds in Oxfordshire.

(2) Neither developmental canalization nor mutual growth inhibition nor statistical artefact appeared to contribute significantly to this decline, which was therefore attributed to natural selection.

(3) The time-curve of selective response is complex. Morphological variability lost by the larvae under selection was restored by metamorphosis, allowing further selection in post-metamorphosis newts.

(4) Differences between populations in the rate of selection was associated with corresponding differences in larval survival, larval growth, adult age-structure and population size.

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The Colonization of Bomb-Crater Ponds at Marlow, Buckinghamshire

Tom Warwick

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