were removed, providing that the ovum with accompanying capsules was completely submerged during measurement. The clutches were then divided into groups of 25 eggs each, placed in fingerbowls with approximately 250 ml of 10% Holtfreter's solution (Hamburger, 1942) and kept at a constant 10 C (± 0.05 C). Approximately 25 developing embryos were then measured at various stages of development.

There were no significant intra- or interspecific differences (Kruskal-Wallis test) between the proportional increment in size between Harrison stages (Rugh, 1948) up to and including the gastrula stage among the embryos of all females, despite their being significant differences ($P \leq 0.01$; at both levels) in initial ovum size. (*A. tigrinum* produced ova with female-specific diameters ranging from 2.15 to 2.70 mm, while *A. maculatum*'s values ranged from 1.90 to 2.40 mm) The size changes for the embryos of one *A. tigrinum* female are presented in Figure 1. The appropriate factors by which embryo diameters should be multiplied in order to obtain initial ovum sizes are presented for specific Harrison stages in Table 1. These factors should prove useful for all *Ambystoma* species but care should be taken in applying them to other species where ovum size may differ appreciably and the generality of the conversion factors becomes questionable.

For ova of the size ranges found here, development through the gastrula stage results in approximately a 13% increase in the estimate of ovum diameter. This difference of approximately 0.3 mm, while seemingly slight (and previously ignored), has pronounced effects when such data are used to estimate ovum and clutch volumes. A diameter error of 13% is increased to a volume error of 43%. This large effect of ovum diameter differences on ovum volume emphasizes the need for considerable care being taken in obtaining intrapopulational ovum size measurements which are critical for the development of a reproductive strategy theory that relates to amphibians.

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POPULATIONS OF CRESTED NEWTS, *TRITURUS CRISTATUS*, IN OXFORDSHIRE, ENGLAND.—*Triturus cristatus*, the crested newt, is a large, strikingly colored newt which is widespread in Britain and continental Europe. Its ecology is little known, the only extensive work in the recent English literature being the account of variation given by Spurway (1953) and the description of Swedish material by Gislen and Kauri (1970). The purpose of this note is to provide a brief description of the distribution, abundance and population structure of crested newts in a small area of agricultural land in central England. The data were collected in 1972 and 1973 during a survey of smooth newt (*Triturus vulgaris*) populations, when all of the 34 ponds in an area 27 km^2 some 12 km SE of Oxford were located and their newt populations censussed by the use of underwater traps. Descriptions of the survey area, of the ponds themselves and of the techniques used to capture, mark and measure the newts are given by Bell (1977) and by Bell and Lawton (1975), and these papers should be consulted whenever details are lacking in the account below. The primary object of this survey was to study the ecology of smooth newts, but about 600 crested newts were also captured, and these form the basis of the present report.

Population structure.—After capture, newts were brought into the laboratory and anaesthetized in 1:8,000 solution of MS-222 before being measured with vernier callipers. The standard length frequency distributions of aquatic individuals (i.e., those found in the water during the breeding season) captured on the survey area in 1972 is shown in Fig. 1. These distributions are similar to those for smooth newts (although the large negative skew of the male distribution is surprising) and presumably bear a similar interpretation—that there are several year classes in the adult population, and that the age at maturity is variable—but it was not possible to collect from any single population a sample sufficiently large to establish these points beyond doubt. In one respect, the data of Fig. 1 are strikingly different from smooth newt length frequency distributions, and this is the long tail of the 'female' distribution. This comprises immature individuals, both male and female, which despite their presence in the water will not reproduce. Newts of less than 60 mm length are immature, while those of greater than 65 mm length are adult females; between the two lies a debatable region in which the reproductive status of individuals cannot be determined reliably without dissection. This behavior is unknown in the smooth newt populations on the survey area (all of 3,058 metamorphosed aquatic smooth newts were sexually mature), smooth newt juveniles ('efts') being exclusively terrestrial, and its function in crested newts is unknown. A possible explanation, which is consistent with current life history theory, is that growth rates are faster in the water than on land; certainly, some aquatic feeding is necessary for the maturation of oocytes in *T. vulgaris* (Bell, 1977) and in the related North American salamandrid *Notophthalmus viridescens* (Hurlbert, 1970). Because fecundity is proportional to body size in salamanders, a higher rate of growth will imply greater fecundity, and thus increased Darwinian fitness. At the same time, any increased risk of predation in the water would probably affect the conspicuous, distasteful crested newt juveniles less than it would the cryptic and relatively palatable smooth newt efts. Thus, a period of aquatic residence by postmetamorphosis juveniles might increase future fecundity in both smooth and crested newts, but has not evolved in the former because it involves a disproportionate increase in the risk of mortality.

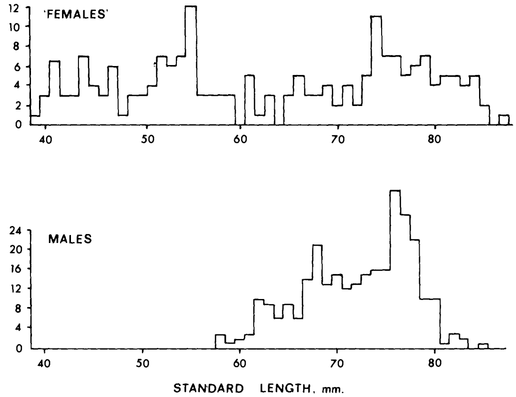

Fig. 1. Standard length frequency distributions of crested newts captured in the water during the breeding season, April–May 1972. 'Females' (N = 202) includes all individuals lacking male secondary sexual characters; this group comprises adult females and immature juveniles of both sexes. Males (N = 292) includes sexually mature males only.

The frequency of aquatic juveniles varies widely between populations. At the Arboretum pond, 50/70 (71%) of aquatic individuals trapped during the 1972 breeding season were juveniles, but only 8/63 (13%) of individuals trapped in other ponds. At a pond in Wytham Wood, Berks, only 2/56 (3%) of individuals caught in 1971, and 1/58 (2%) of those caught in 1972, were juveniles. There were no juveniles camong 144 crested newts caught in a pond at Drayton, Oxfordshire. The reasons for this extensive variation are unknown.

Abundance.—Altogether 580 crested newts were captured during 1972 and 1973, the bulk of them coming from the Arboretum (169) and Stadhampton Riccia (1976) ponds, which are the two points farthest to the right in Fig. 2. This figure plots the sample sizes (number of

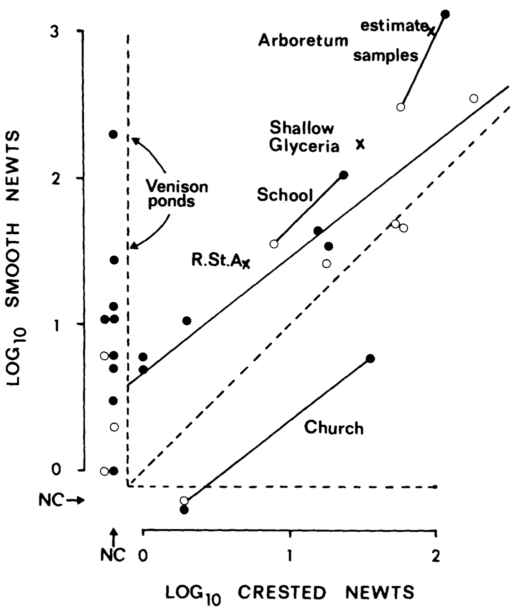

Fig. 2. Relationship between sample sizes of smooth and crested newts. Points outside horizontal and vertical broken lines are samples in which only one species was represented: N.C. means 'no captures.' Diagonal broken line represents samples in which the two species are equally abundant, among samples in which both species are represented. Solid line is regression of data, including only those samples in which both species were represented; the regression equation is: $Y = 0.787X + 0.667$, with $r^2 = 0.62$. 95% limits of slope coefficient are about 0.42, 1.14. Solid circles are 1972 samples; open circles are 1973 samples. Crosses represent direct estimates of population number, not sample size, as referred to in the text; they are not included among the data for computation of the regression equation. Solid and hollow points joined by unbroken lines are samples from three populations (Arboretum, School, Church) in successive years; there was a proportionate decline in the populations of both species between 1972 and 1973.

individuals captured in a given year) of crested newts against those of smooth newts. Since the trapping effort (number of trap-hours) is the same for both species in a given sample, the sample sizes are in direct proportion to the catch per unit effort. The graph therefore describes the relationship between population numbers in the two species, if they are sampled with equal efficiency by the traps. Although this will not be exactly true, the three instances in which a direct estimate of population number are available fall near the scatter of the data. At Rye St. Anthony (R.St.A. in Fig. 2) a very small artificial pond in the grounds of a private school was completely fenced around, so that all the newts entering or leaving the pond could be captured. This population comprised 26 smooth and 5 crested newts. At the Shallow Glyceria pond, almost the entire population of both species was removed by netting; this yielded 171 smooth and 30 crested newts, and since only 7 smooth and 2 crested newts were caught by intensive sampling in the following year, these figures cannot be far from the total population numbers. At the Arboretum pond, the recapture of marked individuals made possible estimates of population number by the method of Jolly (1966): the average of these estimates (for different dates during the breeding season) was 1,007 ± 220 smooth and 93 ± 71 crested newts. The estimates for Rye St. Anthony and for the Shallow Glyceria pond lie somewhat above the regression of sample sizes, and may indicate that the underwater traps caught crested newts rather more efficiently than smooth newts. The estimate of population numbers for the Arboretum pond lies well above the regression of sample sizes, but lies very close to the observed value of sample sizes for the pond. Thus, the regression of sample sizes appears to be proportional to the regression of population numbers in the two species, although it may slightly overestimate the relative abundance of crested newts.

In 7 of the 34 ponds (numbers 13, 20, 22, 23, 25, 32 and 34 of Bell, 1977) neither species was recorded in the two years of sampling. Five of these lacked macrophytes entirely; the remaining two had large populations of predatory fishes, in one case perch *Perca fluviatilis* (pond 23) and in the other sticklebacks *Gasterosteus aculeatus* (pond 32). Only smooth newts were found in 12 of the ponds (ponds 2, 3, 4, 8, 11, 12, 16, 17, 18, 19, 28 and 30), but 3 of these (ponds 16, 17 and 18) were inadequately sampled and may have supported crested newt populations. Of the remainder, all except two yielded very small (<15 individuals) samples of smooth newts. The two exceptions were the Venison ponds (ponds 2 and 3), where a total of 230 smooth newts were captured during the 1972 season; these two ponds were sampled intensively, and it is unlikely that even a very small population of crested newts would have escaped attention entirely. In one pond (pond 15), two crested newts but no smooth newts were captured. However, it is unlikely that these two newts represented a breeding population; the pond was grossly polluted by farmyard effluent and no larvae were seen in the two years of sampling. Moreover, three adult smooth newts were collected from underneath stones on the edge of this pond, although none were seen in the water.

In the remaining 14 ponds, both smooth and crested newts were captured. Fig. 2 shows that amongst these ponds there was a positive linear relationship between the logarithms of the sample sizes for the two species. The slope of the regression is 0.787 ± 0.180, so that it does not differ significantly from unity. It has been argued above that this regression is proportional to the regression of the logarithms of population number. It follows that throughout the range of populations censussed smooth newts are roughly 5 times more numerous than crested newts. Since the mean population number of smooth newts in these ponds was 72.5 (Bell, 1977), the average crested newt population comprised only 10–20 individuals of reproductive age. Curiously, since crested newts are on average some 3–5 times heavier than smooth newts (Smith, 1964; Bell, 1966), the adult biomass of the two species was nearly equal in most of the ponds.

The census data also provided information on sex ratios, but this is for the most part unreliable because the aquatic traps appear to capture males much more readily than females. Sampling with a dip-net is less selective: the two largest Oxfordshire samples were from the Shallow Glyceria pond (pond 31), where 13 males and 14 females were caught, and from the Wytham Wood pond, where 27 males and 27 females were caught. Dip net samples from various localities in Leicestershire yielded a total of 50 males and 59 females (Bell, 1970). These data do not allow us to reject the hypothesis that the adult sex ratio is near equality in crested newt populations.

Distribution.—These data suggest that smooth and crested newts are able to coexist, without either species excluding the other. Since smooth newts are on average so much more numerous than crested newts, the expected sample size of crested newts from ponds in which 15 smooth newts were captured is only two or three individuals, so that failure to record any captures of crested newts from many such ponds is not surprising. Nor is there any authentic example of crested newts occupying a pond to the exclusion of smooth newts. Only at the two Venison ponds were there unequivocally single-species populations, comprising moderately large numbers of smooth newts. Thus, the usual impression that crested newts are much more local in their distribution than smooth newts is mistaken; it has probably arisen because crested newts are much more difficult to capture with a dip net. Sampling with underwater traps shows that crested newts are nearly as widespread as smooth newts, but much less abundant.

Crested newts are often said to prefer deeper, clearer ponds than those inhabited by smooth newts (Smith, 1964; Steward, 1969), and there is some evidence for this view from collection in Leicestershire (Bell, 1970). However, it is not supported by the Oxfordshire data. The Church pond, which had the greatest ratio of crested newts to smooth newts, is a rather distrophic pond of medium size, dominated by *Typha*; and in general the data plotted in Fig. 2 suggest that as a pond becomes more suitable for crested newts it also becomes more suitable for smooth newts.

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