EGG PRODUCTION IN THE SMOOTH NEWT (TRITURUS VULGARIS)

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ABSTRACT

The relationship between body size and fecundity in female smooth newts *(Triturus vulgaris)* was examined by counting the numbers of eggs oviposited, to resolve several controversies. First, whether body size is positively correlated with fecundity. Second, whether ovarian oocyte counts represent the numbers of ova oviposited by females in any particular year. In addition, the hypothesis that body size is positively related to the rate of ovipositon was tested. Female body size was positively correlated with clutch size and rate of oviposition. Numbers of ova oviposited by individuals were of a similar order of magnitude to the estimates of clutch size obtained from ovarian oocyte counts in previous studies. A median oviposition rate of 7.2 ova per day was recorded during the oviposition period.

INTRODUCTION

Among amphibians, clutch volume or mass has been shown to be positively related to female body size, which has lead to the conclusion that female body size constrains clutch size (Crump & Kaplan, 1979; Kaplan & Salthe, 1979). Within species it has become axiomatic that large female body size is naturally selected due to the associated fecundity advantage (e.g. Howard, 1988; Woolbright, 1989).

Smooth newts produce many single eggs over a long period of time and wrap each egg within vegetation (Smith, 1973), so that precise counts of numbers of eggs produced by individual females are difficult to obtain. Hence investigations of fecundity the smooth newt have relied on ovarian oocyte counts, making the assumption that the yolked ova in the ovaries immediately prior to mating represent the reproductive potential of an individual for that year (Bell, 1977). Bell (1977) found that larger females contained more ovarian oocytes than small females. Verrell (1986) and Verrell & Francillon (1986) have found that female body size is positively correlated with number of ovarian oocytes. However, Hagström (1980) was not able to find any relationship between body size and clutch size, in Norwegian smooth newts.

The assumption that ovarian oocyte number represents actual clutch size may not be justifiable. Hagström (1980) reported that female smooth newts that he captured in ponds, after he assumed that oviposition had ceased, still contained yolked oocytes. It is possible that not all females complete oviposition synchronously, so that these newts may have still been ovipositing. However, Harrison (1985) found that females moving away from a breeding pond in July also contained yolked oocytes.

To resolve the above controversies, actual clutch size records are needed. In addition to the problems of prolonged oviposition periods and cryptic deposition of ova, work in this area has also keen hampered by the fact that, once removed from their natural breeding ponds, female smooth newts tend to lose reproductive condition and cease oviposition (pers. obs.). This may explain why attempts to investigate ovipositional parameters within this species and other congenerics, in an aquarium situation, have produced results that are at odds with the ovarian clutch size counts. Ovarian oocyte counts predict that *Triturus* species should oviposit several hundreds of eggs (100-400, *T. vulgaris*, (Bell, 1977); approximately 200-300, *T.*

vulgaris and *T. cristatus* (Hagström, 1980); 100-500, *T. vulgaris* (Verrell, 1986); 130-470, *T. vulgaris* (from graph in Verrell & Francillon, 1986); 240, *T. vulgaris* (Harrison, 1985)).

However, only very low numbers of ova have actually been deposited in aquaria Wimpenny (1951) recorded mean values of 2.75 and 0.76 ova for *T. cristatus and T. vulgaris,* and Verrell (1986) recorded counts of 25-80 for *T. vulgaris.* There is clearly a discrepancy between ovarian clutch sizes and oviposited clutch counts. Verrell (1986) explains his low clutch sizes as being the number of ova produced on a single insemination only.

Another anomaly is that the rates of oviposition recorded in aquaria are lower than might be expected. oviposition periods of natural populations last between approximately 75 and 125 days (90 days for *T cristatus, T. helveticus* and *T. vulgaris* (Smith, 1973); 125 days for *T. vulgaris* (Bell & Lawton, 1975); 75-90 days for *T. marmoratus* (Diaz-Paniagua, 1989)) and so the rate of oviposition should fall within the range of 0.8 (100 ova in 125 days) and 6.7 (500 ova in 75 days) ova per day. However, Arntzen & Hedlund (1990) found rates of 0.33 for *T. cristatus* and 0.74 for *T: marmoratus.*

The present study records actual clutch sizes of individual female smooth newts, selected to represent the full body size range of a natural population. They were maintained under semi-natural conditions to avoid loss of reproductive condition during the course of the study. The study was performed to test the hypothesis that clutch size is positively related to maternal body size and to establish whether oviposited clutch counts are similar to ovarian counts from previous studies.

This study also allowed an examination of rates of oviposition and hence the testing of a second hypothesis, that rate of ovipositon is positively related to female body size. In an observational study, Diaz-Paniagua (1989) found that large female *Triturus marmoratus pygmaeus* were more efficient at oviposition than small females, in terms of ova produced per oviposition attempt, and they also invested less time in failed attempts than smaller females.

Costs associated with ovipositional behaviour of Triturus species have not been investigated, but observation of smooth newts in a natural pond in the Milton Keynes area suggests that such costs may exist. I Towards the end of one reproductive period (May 1990), females were seen ovipositing during daylight

hours, so that females in this particular pond were easily visible in shallow water, at the pond's edge searching for oviposition sites and were also seen ovipositing just below, or at, the water's surface. This latter operation sometimes involved individuals rolling onto their sides and backs, clearly exposing the non-cryptically coloured ventral surfaces. Such behaviour may expose females to a greater risk of predation than does their otherwise secretive nature. Diaz-Paniagua (1989) sees the potential advantages of efficient oviposition in large female *Triturus marmoratus pygmaeus* as being energetic savings and as leaving more time in which to search for new oviposition sites. However, if there are increased chances of predation associated with ovipositional behaviour, then efficient oviposition may also be advantageous in minimising these dangers. Diaz-Paniagua's work predicts that the more efficient ovipositors will be large females.

METHODS

To ensure that females were captured before the start of oviposition, newts were collected at a drift fence, as they migrated towards a pond in Milton Keynes (7.3.89 - 27.3.89). Twelve females, selected by eye to cover a wide range of body sizes, were individually maintained outside in plastic aquaria, measuring (39 x 20 x 25 cm). These aquaria were placed in a larger tub of water (see Fig. 1) to ensure that the newts experienced a temperature regime similar to that of a small pond. Each tank was furnished with one clay pot refuge and two pieces of 'weed'. This 'weed' consisted of strips of polythene (20 x 2 cm) which were cut along one edge to create a fringe. This design allowed females to carry out their normal oviposition behaviour of wrapping ova in some flexible material, which also prevented the newts from eating the ova, and at the same time facilitated ease of collection of ova. Weights were placed on one end of each strip to anchor the 'weed' to the substrate, so that the polythene strips spanned the whole depth of the aquarium. The newts were fed on an *ad libitum* basis on zooplankton that was cultured in the large tub and *Tubifex* obtained from a commercial supplier.

Males, captured in funnel traps at the same breeding pond, were introduced every week, for two or three days, to ensure that all oocytes were fertilised. After the two or three days these males were returned to the pond.
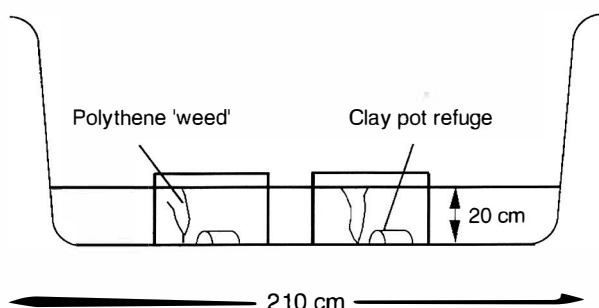

Fig. 1. Diagram of aquaria containing individual females, within a larger tub of water.

Tanks were inspected for ova daily. As soon as any ova were seen in any tank, that individual female was weighed (to 0.1 g). After this, ova were collected every 1-3 days, removing them from the substrate by gently peeling away the polythene. Females were judged to have oviposited a complete clutch on the basis of changes in external characters and behaviour. On completion of oviposition the tail fin decreases in size, the skin becomes granular rather than smooth, the cloaca becomes reduced in size and dome-shaped rather than flat-topped, dome-shaped, and the newts often float at the water surface. These characteristics are also associated with the resumption of terrestrial life.

Once a female had completed oviposition she was anaesthetised in MS-222 (Sandoz) and snout-vent length (SVL) and total length (TL) were measured to the nearest 0.5 mm. Newts were anaesthetised only after oviposition, to ensure that any possible adverse effects of anaesthesia could not act on oviposition.

RESULTS

FEMALE BODY SIZE AND CLUTCH SIZE

Ten of the twelve females produced ova. Descriptive data of the body sizes and clutch sizes of these newts is given in Table 1. In the following statistical analyses, data from only the ten ovipositing newts were used. Pearson product-moment correlation analyses were used to detect whether there was a relationship between both female mass and the number of ova produced and between SVL and the number of ova produced. One-tailed tests were adopted because of the uni-directional nature of the hypotheses being tested.

There were significantly positive correlations between both measures of female body size and the numbers of ova produced. For female body mass and clutch size $r=0.61$, $P<0.05$, 8 d.f. For SVL and clutch size, $r=0.60$, $P<0.05$, 8 d.f..

RATE OF OVIPOSITION

To test the hypothesis that larger females are able oviposit faster than small females, a measure of oviposition rate was needed. This was calculated by dividing the clutch size by the number of days between the first and last ova produced (oviposition period), for each individual female. Descriptive data on oviposition period and oviposition rate are given in Table 2. A Pearson product-moment correlation analysis showed that female body mass was significantly positively correlated with oviposition rate ($r=0.89$, $P<0.01$, 8 d.f.). Larger females were able to oviposit at a faster rate than small females. Data on the maximum number of ova produced per night, by each female, are also given in Table 2, as 'peak rate oviposition', to show the maximum rate at which the females in the present study were able to oviposit.

DISCUSSION

The present study confirms the results of Bell (1977), Verrell (1986) and Verrell & Francillon (1986) that there is a positive association between female body size and clutch size in smooth newts. Larger females oviposited more ova than did small females. It is also notable that the two newts that did not oviposit were both particularly small, weighing 1.1 and 1.7 g. It is possible that these two females were immature, being below the

	Mean	Median	S .D.	Range
SVL (mm)	45.9	45.3	3.816	40.0 - 52.0
TL (mm)	85.5	85.2	8.82	70.0 - 99.5
Mass (g)	2.7	2.4	0.822	1.6 - 4.2
No. ova oviposited	300	252	189.4	88 - 637

TABLE 1. Mean, median, standard deviation and range of body sizes and numbers of ova produced by ten *T. vulgaris*.
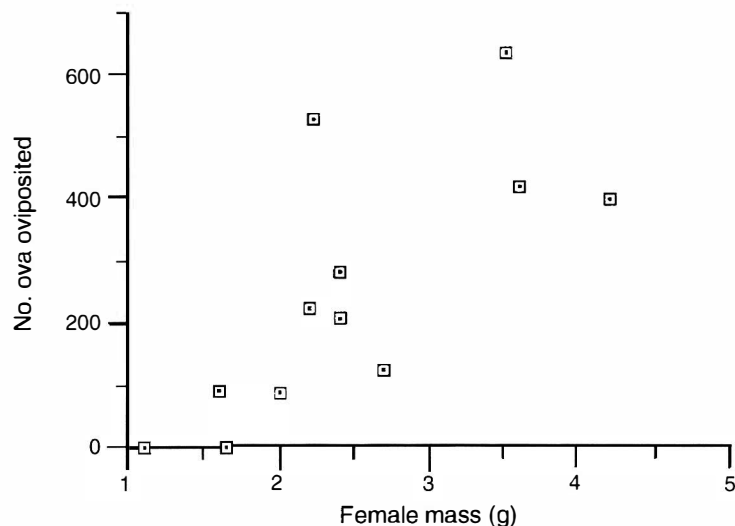

Fig. 2. Relationship between female body size (mass) and the number of ova oviposited. Data from the two non-ovipositing females were not included in the statistical analysis.

minimum body size for sexual maturity. It has previously been thought that juvenile smooth newts do not migrate to ponds (Verrell, 1985). It is possible that juvenile smooth newts have not been recognised as inhabiting the aquatic environment because only the largest juveniles adopt this strategy and the size range of these newts tends to be similar to the small end of the adult body size range.

The clutch size data of the present study also suggests that the assumption that ovarian oocyte counts represent actual clutch sizes is valid. The numbers of ova oviposited by newts in the present study (88-637 ova) are of a similar order of magnitude to estimates of clutch size generated from previous ovarian oocyte counts, from populations in Oxfordshire or Buckinghamshire, made at the beginning of breeding seasons (approximately 100-400 recorded by Bell (1977), 100-500 recorded by Verrell (1986), 130-470 from graph in Verrell & Francillon (1986)). Thus I would conclude that female *T. vulgaris* from local populations are quite able to oviposit all ova yolked at the beginning of a season, during that season.

Harrison (1985) working on *T. vulgaris* at Llysdinam, mid-Wales, recorded mean clutch sizes of 239 (yolked ova carried by immigrating females) or 190 (obtained by subtracting the number of yolked ova in emigrating females from the number in immigrating females) which seem much lower than the mean in the present study (300). However the Llysdinam newts are smaller than those found in the Milton Keynes area, with mean

total length (TL) of 79 mm for immigrants and 76 mm for emigrants. Hence the difference in clutch sizes between local newts and those from mid-Wales may be a reflection of differences in body size. Hagström's (1980) low ovarian counts of approximately 200 may reflect the shorter foraging and/or breeding seasons of *T. vulgaris* in Sweden.

Harris (1987) notes that female *Notophthalmus viridescens dorsalis* actually oviposit rather more ova than ovarian oocyte counts would predict. Harris interprets this observation as evidence that females may be able to yolk up ova during the oviposition period, depending on food availability. If female *T. vulgaris* can adopt a similar strategy of vitellogenesis then this would explain the presence of yolked ova in the ovaries immediately after the breeding period, as found by Hagström (1980), Harrison (1985) and Verrell et al. (1986). This does not seem an unreasonable possibility, when it is considered that adult smooth newts are reported to perform most feeding and annual growth, as well as courtship, during the aquatic phase (Verrell, 1987).

The mean and median rates of oviposition (8.7 and 7.2 ova per day) are higher than values predicted using data from ovarian oocyte counts and records of the lengths of population oviposition periods (0.8 to 6.7 ova per day). The relatively high daily rate of oviposition recorded in the present study is probably an accurate measurement of natural oviposition rates of females in the field, and is higher than estimated by dividing

	Mean	Median	S.D.	Range
Oviposition period (days)	36.9	40.0	19.69	11 - 74
Mean oviposition rate (ova per 24 hours)	8.7	7.2	4.64	3.9 - 17.3
Peak rate oviposition (ova per 24 hours)	32.3	32.0	13.07	16 - 54

TABLE 2. Mean, median, standard deviation and range of ovposition periods, mean rates of oviposition and peak rates of oviposition for ten female *T. vulgaris*.

clutch sizes by oviposition periods of whole populations, because oviposition is not exactly synchronous. Mean and median oviposition periods for individual newts are 36.9 and 40 days respectively (see Table 2), whereas the length of time that elapsed between the first and last ova produced by the sample as a whole was 84 days. Thus, an individual female actually oviposits over only a fraction of the population oviposition period.

The finding that oviposition rate is positively correlated with female body size is consistent with the results of Diaz-Paniagua (1989) that large female newts can oviposit at a higher rate than small females. Diaz-Paniagua found that this difference occurred because small female *T. marmoratus pygmaeus* were less efficient at oviposition behaviour. It is not known whether this is also true of *T. vulgaris*, or whether small females are physiologically and/or energetically less able to sustain a high rate of oviposition.

ACKNOWLEDGEMENTS

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