HERPETOLOGICAL JOURNAL, Vol. 9, pp. 1-8 (1999)

# ABUNDANCE AND SURVIVAL RATES OF GREAT CRESTED NEWTS (*TRITURUS CRISTATUS*) AT A POND IN CENTRAL ENGLAND: MONITORING INDIVIDUALS

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A population of great crested newts (*Triturus cristatus*) in central England was monitored from 1988-1995. Recognition of individuals was used to quantify population dynamics. Adult annual survival varied from 31-100%. Long-term members of the breeding population had a significantly higher rate of annual survival (65%) than individuals breeding for the first time (57%). The population showed variable patterns of recruitment. A period of six years with little recruitment was followed by a rapid increase in population size, more than three-fold, over two years. The change in the population characteristics coincided with a crash in the population of predatory three-spined sticklebacks (*Gasterosteus aculeatus*), raising the possibility that newt recruitment was held in check by predation. Juveniles were rarely captured, but their recapture rate between years (49%) indicated that the rate of annual survival for juveniles in this population could be relatively high (estimated as 59%). Most juveniles matured at two years of age. The study population thus consisted of long-lived adults, showing variable survival, and erratic recruitment. The longevity of adults enabled the population to persist under adverse conditions until beneficial circumstances could be exploited by rapidly increasing the population size. These demographic traits may be common in *T. cristatus* populations.

*Key words*: *Triturus cristatus*, population dynamics, mark-recapture

## INTRODUCTION

Concern over the issue of declining populations of amphibians (e.g. Blaustein & Wake, 1995) has focused attention on the need for greater understanding of amphibian population dynamics. In this respect the population dynamics of *Triturus cristatus* are of particular conservation interest. Although it is widespread throughout its British range, the species has been in decline since before the 1960s and it is the most rapidly declining amphibian in Britain (Beebee, 1975; Cooke & Scorgie, 1983; Hilton-Brown & Oldham, 1991; Beebee, 1994).

Long-term studies (twelve and nine years) have demonstrated that amphibian populations may naturally show large fluctuations (Pechmann *et al.*, 1991; Woolbright, 1996), apparently driven by stochastic, climatic events, such as variable patterns of rainfall (Pechmann *et al.*, 1991; Banks, Beebee & Denton, 1993; Woolbright, 1996) or extreme weather conditions (Woolbright, 1996). However, not all amphibian populations are unstable. Amphibians may have high survival rates and be long-lived (e.g. *Ambystoma talpoideum* [Raymond & Hardy, 1990], *Triturus alpestris* [Schabetsberger & Goldschmid, 1994], *Bombina variegata* [Plytycz & Bigaj, 1993]).

Great crested newts (*Triturus cristatus*) have a wide distribution over northern Europe (Griffiths, 1996) and population data from a number of sites have been summarized by Arntzen & Teunis (1993). The data suggest that population processes vary between sites. Adult *T. cristatus* can be long-lived. Skeletochronological estimates indicate that individuals can live for as long as 14 to 17 years (Hagström, 1977; Dolmen, 1983*a*; Francillon-Vieillot, Arntzen & Géraudie, 1990; Miaud, Joly & Castanet, 1993). Although adult annual survival varies between sites, it is fairly stable within sites (49% to 78%) (Arntzen & Teunis, 1993). This longevity and constant rate of adult survival create the potential for population stability, which has been recorded for some populations. For example, Glandt (1982) estimated that the size of a breeding population in Germany stayed between 89 and 108 individuals over a four-year period. Hedlund (1990), found that a population on the island of Öland in the Baltic, was relatively stable, staying between 150 and 223, over a five-year period.

However, population fluctuations do occur in this species. Hagström (1979) recorded a halving of population size (500 to 230 adults) between two consecutive breeding seasons, at a site in south-west Sweden, while Miaud *et al.* (1993) noted a doubling of population size (209 to 434) over an equivalent interval at a site in eastern France. Two long-term studies have also detected population fluctuations in this species. Arntzen & Teunis (1993), studying a population in north-west France, estimated that although adult survival was fairly constant (33-57%) over a six-year period, population size ranged from 16 to 346 individuals. Similarly, in England, Cooke (1995) recorded annual mean counts of 3 to 183 for a population over an 11-year period. Although Cooke did not directly measure population size, he concluded that fluctuations in visual counts mirrored changes in population size.

This paper reports the results of a long-term study of a population of great crested newts, *Triturus cristatus*, to provide information on the dynamics of a population, using recognition of individuals to quantify population demography.

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## MATERIALS AND METHODS

### Study Site

The Walton Hall Pond is on the campus of the Open University (52°1'N,00°42'W, Ordnance Survey grid reference SP 886369), Buckinghamshire, England. It measures 400 $m^2$ and is up to 2.5 m deep. It is heavily vegetated and can be regarded as a permanent pond, although it dried out in a drought year, 1976 (Bielinski, 1986). Map records show that the pond has been in existence since at least 1925 (Bielinski, 1986). A steep bank around the pond supports relatively unmanaged vegetation. Beyond this the pond is bordered on three sides by lawns and beyond these, office buildings. There is a road and car park on the fourth side. The pond is the breeding site of the four amphibians indigenous to the area; *Rana temporaria*, *Bufo bufo*, *T. cristatus* and *T. vulgaris*. A population of three-spined sticklebacks (*Gasterosteus aculeatus*) was present in the pond from at least 1980 (Bielinski, 1986) until 1990, spanning the first three years of this study.

The study population was considered to be isolated, with little or no newt movement between this and other ponds. The nearest neighbouring breeding site is 500 m away. Although this falls within the dispersal range of this species (Oldham, 1994) it is separated from the study pond by a main road, and drift fencing erected in 1989 did not detect any newt migration from this direction in 1989.

### Capture and Identification of Newts

The objective of this study was to capture and identify as many individual newts as possible each year. Procedures for capturing and identifying newts were modified over the course of the study, as the most efficient sampling techniques for this particular population became evident (drift fence/pitfall trapping was eventually abandoned in favour of the use of funnel traps). In 1988 newts were captured in funnel traps placed in the pond, during a pilot study of the monitoring program. From 1989 to 1991 newts were captured by the use of both a drift fence/pitfall trap system and by the use of funnel traps. In 1992 only 16 newts were captured at the drift fence, so it was assumed that the population had diminished and that aquatic trapping was not merited. From 1993 to 1995 newts were captured solely by the use of funnel traps in the pond.

The drift fence/pitfall trap system was put in place to coincide with the newts' spring migration to the breeding pond, but was dismantled before emigration, to avoid the disruption of dispersal into the terrestrial habitat. The formally-managed grounds beyond the immediate pond border appear to provide little "newt-friendly" terrestrial habitat, as described by Oldham (1994). Emigrants were not captured to avoid the possibility that trapping and release might have disorientated or detrimentally delayed newts navigating a seemingly harsh terrain. Hence, the drift fence was completed by the end of January, and dismantled as the arrival of immigrants ceased (2 March to 5 May). The fence was constructed of 3 mm plastic mesh, stapled to wooden stakes. Since the pond is located in a public area, the fence was designed to be inconspicuous. The fence was 15 cm high, with another 10 cm below ground. The top of the fence was folded at an angle of 90° to the vertical, to provide an 8 cm lip, facing outwards. Pitfall traps were emptied daily.

The population was also sampled later in the season, by trapping aquatic individuals in funnel traps. These were box-like traps (50 x 25 x 25 cm), made from perforated aluminium, with a funnel entrance at one end. The large size of these traps and their placement in shallow water allowed newts to rise to the surface to breathe within the trap. Additionally, each trap had a "chimney" to allow newts access to the water surface should the traps be placed in deeper water. These funnel traps were chosen in preference to the more widely used plastic drinks bottles (Griffiths, 1985) to avoid the possibility of drowning newts, a risk that would be significant over the course of a long-term sampling study such as this. Two to four funnel traps were set at the western end of the pond, the only edge easily accessible due to emergent vegetation (*Carex riparia* and *Sparganium erectum*) surrounding 80% of the pond perimeter. Funnel traps were set during the period lasting from the last week of March to the first week in June and were inspected for newts twice a day.

To provide a means of recognition of individuals, the pattern of black spots on the ventral surface of each newt was photocopied, modifying Hagström's (1973) technique of photographing newts. Newts were anaesthetized by immersion in a 0.1% solution of MS-222 (Sandoz) to facilitate the copying process. This allowed a reference series of uncontorted belly patterns to be created, which allowed easier recognition of recaptured animals than has been reported by Oldham & Nicholson (1986), who photocopied unanaesthetized animals. To minimize any possible detrimental effects of anaesthesia, efforts were made to anaesthetize newts only once during a breeding season. Prior to anaesthesia, newly-captured newts were compared with copies of belly patterns of all newts previously captured that year. However, newts recaptured in successive years were anaesthetized annually to allow changes in body measurements to be recorded (unpublished data).

### Population Size Estimates

The Petersen method described in Donnelly & Guyer (1994) was used to calculate adult population size each year. In the years when newts were captured both by drift fence/pitfall trap and by funnel trap, the drift fence/pitfall captures were used as the first sample and captures made in the pond, by use of funnel traps, as the second sample. Newts that were captured in the pond and identified by belly patterns as having also been captured during the first sample, at the drift fence, were regarded as 'marked' animals in the estimation of population size. In 1989 and 1990, some newts were

TABLE 1. Dates of trapping periods (day-month), numbers of adults captured (caps) and efficiency of capture (%), expressed as a percentage of the estimated adult population size, are given for two different sampling techniques (drift fence and funnel traps). The efficiency of both techniques combined is also presented.

| | Drift fence | | | | Funnel traps | | | | Fence and funnel traps |
|---|---|---|---|---|---|---|---|---|---|
| | From | To | caps | % | From | To | caps | % | % |
| 1988 | - | - | - | - | 12-4 | 28-5 | 37 | 35 | 35 |
| 1989 | 4-2 | 5-5 | 47 | 53 | 1-4 | 14-5 | 57 | 65 | 86 |
| 1990 | 30-1 | 22-4 | 56 | 64 | 12-4 | 26-4 | 42 | 48 | 79 |
| 1991 | 21-2 | 21-3 | 50 | 65 | 26-3 | 10-5 | 59 | 77 | 90 |
| 1992 | 15-2 | 2-3 | 16 | 22 | - | - | - | - | - |
| 1993 | - | - | - | - | 3-4 | 21-4 | 66 | 99 | 99 |
| 1994 | - | - | - | - | 29-3 | 3-5 | 95 | 78 | 78 |
| 1995 | - | - | - | - | 4-4 | 7-6 | 191 | 79 | 79 |

captured at the drift fence after the initiation of pond trapping. These captures were omitted from the estimation of population size. Funnel trapping was not attempted in 1992, so population size was not estimated.

From 1993 to 1995 the first and second sampling periods were designated by taking the date of the median capture each season as a watershed. Captures up to and including this point constituted the first sampling session, captures after this date were considered the second sampling session.

The use of different capture techniques between the first and second capture sessions within a year and different capture and sampling techniques between years may potentially bias the population estimates. Ideally, similar sampling techniques would be used each year. The present estimates rest on the assumption that any newt captured at the drift fence is no more or less likely to be captured in a funnel trap than newts that were not captured at the drift fence.

### ESTIMATION OF SURVIVAL

Survival was estimated as a function of recapture rate between years and sampling efficiency, as follows. A "recapture" between any two years was considered as the capture and identification of the same individual. Recapture rate represents the proportion of individuals recaptured between years. However, not all newts were captured in any year. A measure of sampling efficiency was calculated as the number of newts captured in any one year as a fraction of the estimated population size. When sampling efficiency is less than 100%, recapture rate between years will underestimate survival (some individuals surviving from one year to the next will not be recaptured). To correct for this, an estimate of annual survival was obtained by multiplying the number of recaptures by the reciprocal of sampling efficiency in any particular year.

During the last two years of the study, 1994-95, sufficient adult recruitment had occurred to allow a comparison of the survival of newly breeding adults with that of long-term members of the breeding population. All new captures in 1994 were regarded as breeding for the first time, since sampling efficiency in 1993 was almost 100%. The annual survival of these first-time breeders was compared with that of the other adults, all of which represented recaptures from previous years.

Recaptures of individuals originally captured as juveniles were used to estimate juvenile survival. Although the belly pattern changes as juveniles grow (Oldham & Nicholson, 1986; Arntzen & Teunis, 1993), the basic pattern is present at transformation. Immobilization of newts prior to photocopying facilitated the recognition of juveniles on recapture in succeeding years.

## RESULTS

The numbers of adult newts captured by the drift fence/pitfall system and the funnel traps are given in Table 1. It is estimated that 35-99% of the breeding population was captured and identified each year. Over the course of eight years estimated population size ranged from 67 to 242 adults (Fig. 1). Between 27% and 88% of the newts captured in any one year were recaptured the following year. The recapture interval tended to be one year (83% of male recaptures and 77% of female recaptures). In the cases when individuals were only recaptured at two-year intervals (16% of male recaptures and 22% of female recaptures), 70% of these occurred between 1991 and 1993, spanning the year when funnel trapping was not carried out. One male (1% of male recaptures) was recaptured four years after initial capture and one female (1% of female recaptures) was recaptured three years after initial capture.

The failure to capture all of the breeding population each year made precise assessment of recruitment impossible. Newts being recorded for the first time may have been new recruits to the breeding population, or longer-term members of the population that had evaded previous capture. In the latter case these "new cap-

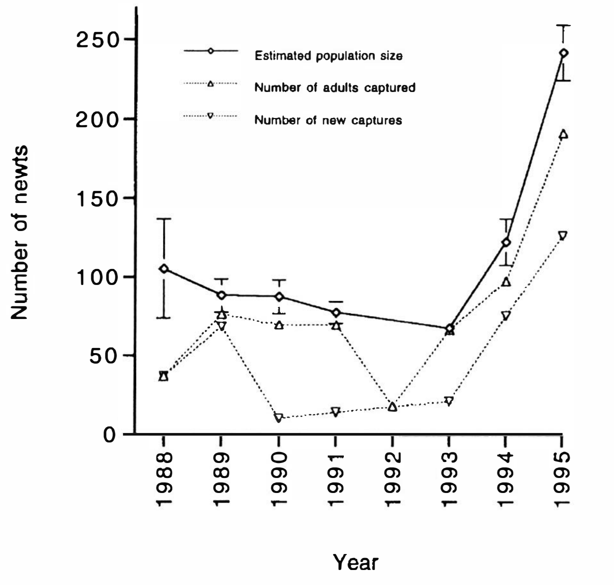


FIG. 1. Estimated population size (±1 SE) and numbers of adult *T. cristatus* captured at the Walton Hall Pond from 1988 to 1995. "New captures" refers to the number of newts captured in any year that were not identifiable from previous years' records.

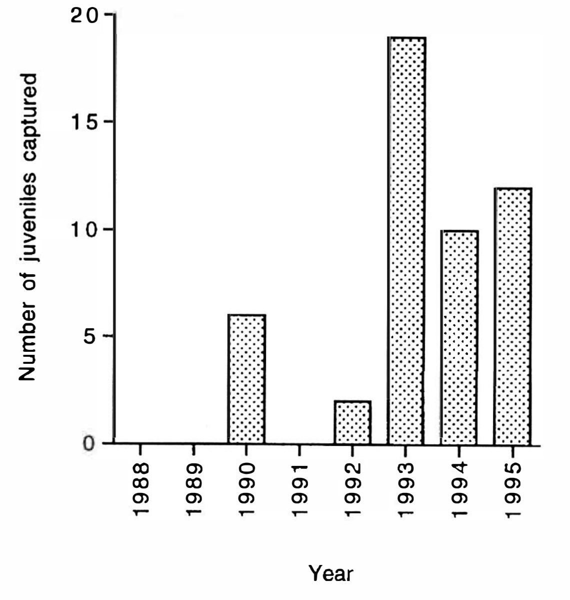


FIG. 2. Numbers of juvenile *T. cristatus* captured from 1988 to 1995.

tures" will give an overestimate of recruitment. The number of these new captures (10-126 per year, or 14-89% of all newts captured) is shown in Fig. 1.

### Adult Survival

Estimated adult survival varied between 31% and 100% (Table 2). There was little evidence of a consistent sex difference. Male survival was greater from 1992 to 1994, while females had higher estimated survival rates in the periods 1988 to 1991 and 1994 to 1995. Between 1994 and 1995, adults breeding for the first time were significantly less likely to be recaptured the following year than long-term members of the breeding population (recorded in the breeding population from two to eight years) $\chi^2 = 6.141$, $P < 0.025$ (Table 2).

The stickleback population was not systematically monitored, but its presence and disappearance was evident since the funnel traps were very effective in trapping these fish. Up to 50 sticklebacks could be captured in a single funnel trap, and from 1988 to 1990

TABLE 2. Annual recapture rates and estimated survival rates of adult *T. cristatus*. Recapture rates represent the number of recaptures as a fraction of the number of individuals captured in the previous year. Figures in brackets are percentages.

(1) *Recapture Rates*

| Year | 1988-89 | 1989-90 | 1990-91 | 1991-93 | 1993-94 | 1994-95 |
|---|---|---|---|---|---|---|
| Male | 5/23(22) | 31/36(86) | 22/33(67) | 24/33(73) | 10/32(31) | 35/59(59) |
| Female | 5/14(36) | 38/42(90) | 22/36(61) | 22/36(61) | 9/34(26) | 27/36(75) |
| Established breeders | - | - | - | - | - | 17/19(89) |
| First time breeders | - | - | - | - | - | 45/76(59) |
| All | 10/37(27) | 69/78(88) | 44/69(64) | 46/69(67) | 19/66(29) | 62/95 (65) |

(2) *Estimated annual survival(%)*

| Year | 1988-89 | 1989-90 | 1990-91 | 1991-92 | 1992-93 | 1993-94 | 1994-95 |
|---|---|---|---|---|---|---|---|
| Male | 25 | 100 | 74 | 85 | 85 | 40 | 75 |
| Female | 42 | 100 | 68 | 78 | 78 | 33 | 95 |
| All | 31 | 100 | 71 | 82 | 82 | 37 | 82 |

sticklebacks were the most abundant animals found in the traps. After 1990 no sticklebacks were trapped or otherwise observed during searches.

### JUVENILE SURVIVAL AND AGE AT MATURITY

During the eight-year study period 49 juveniles were captured and recorded (Fig. 2). Eighteen of the juveniles were recaptured over successive years. Since 12 of these juveniles were captured in 1995, juvenile recapture rate was determined to be equivalent to 18/37, or 49%. Juvenile survival, correcting recapture rate for capture efficiency as described for adults, produces an estimated survival rate of 22/37, or 59%.

In assigning an age to juveniles and in determining age at maturity, it was assumed that juveniles captured were one-year-olds. All captures were made during the spring breeding period, so any juveniles present must have originated from eggs oviposited during previous years. The possibility that these juveniles were any older than one year but still at a small body size due to slow growth was excluded because the recapture of juveniles the following year revealed that juveniles grew rapidly. Juveniles captured over two successive years grew by 19 mm SVL (49.5 to 68.5, $n$ = 16).

All of the juveniles recaptured, except for one, had reached sexual maturity by the following year, at a presumed age of two years. Even the smallest juvenile captured (SVL = 37 mm) grew to maturity by the succeeding year (SVL = 71.5 mm). A single male and single female were detected as adults two years after capture as juveniles. It is not possible to determine whether these individuals matured at three or at two years of age, but were not captured in their first year of sexual maturity. It can be assumed that the single newt that was captured as a juvenile in two successive years (SVL of 51 and 57.5) certainly did not mature until older than two years.

## DISCUSSION

The monitoring methods used during the course of this study demonstrated that funnel trapping was the most effective means of trapping a large proportion of the estimated population. The drift fence used from 1989 to 1991 was only effective in trapping 53-65% of the breeding population, which agrees closely with the 45-61% trap rates of *T. cristatus* achieved by Arntzen, Oldham & Latham (1995). The inability of the drift fence to trap all migrating amphibians is, in part, most likely due to the ability of amphibians to circumvent the fence (Dodd, 1991). There are additional factors which may contribute to the low capture rates of *T. cristatus* at drift fences. *T. cristatus* has a flexible life history. Individuals, particularly newly mature adults, may migrate to ponds in the autumn prior to breeding (Verrell & Halliday, 1985), and some juveniles and adults may remain aquatic all year (Smith, 1964; pers. obs.), thus avoiding drift fences set to capture the spring migration. Also, individuals may spend the terrestrial phase sufficiently close to a pond that they need not cross a drift fence in order to reach a breeding site. Vegetation prevented the construction of a drift fence immediately along the edge of the Walton Hall Pond, so that a band of 2-4 m of grass and scrub was left between the fence and the pond.

By comparison, funnel traps placed in the pond, even though they spanned only approximately 20% of the pond perimeter, were able to capture as much as 77-99% of the estimated population. Lower capture rates from 1988 to 1990 reflect time constraints on the investigator rather than limitations of the trapping technique itself.

Over the eight years of the study, the population dynamics changed from a stable but unproductive situation to one of rapid population increase (Fig 1). For the first six years the population showed a slow decline from 105 to 67 animals, with recruitment lower than 14-32% of the adult population (as indicated by newly captured newts between 1989 and 1993). However, over the next two years the population showed a dramatic increase in numbers, increasing more than threefold from 67 to 242. These changes in population size are smaller than the three orders of magnitude recorded for four temperate pond-breeders (Pechmann *et al*., 1991), and the sixty-fold fluctuations in visual counts recorded in *T. cristatus* at a different site in England (Cooke, 1995).

The present data also reiterate the need for studies that are long-term in nature, when examining amphibian population dynamics (Pechmann *et al*., 1991; Grossenbacher, 1995). For *T. cristatus* this may be of importance in assessing the success of translocation programmes (e.g. Gent & Bray, 1994) or other management practices (e.g. Cooke, 1997). The present population was able to persist for several years with little apparent recruitment. Hence, the presence of adults at a site for several years does not indicate successful breeding or the long-term survival of the population. Conversely, populations that appear to be non-productive over a short time-scale may not be so in the long-term. Breeding failures in *T. cristatus* populations, for up to three years, have been reported elsewhere (Verrell & Halliday, 1983; Oldham & Nicholson, 1986, Griffiths, 1996) and may be a common occurrence for this species.

Fish predation may have had some role in the regulation of the population of great crested newts in the Walton Hall Pond. While sticklebacks were present in the Walton Hall Pond there was very little recruitment to the adult population, but after the disappearance of the fish the newt population grew rapidly. Predatory fish can affect amphibian distribution (Bradford, 1989; Brönmark & Edenhamn, 1994; Fisher & Shaffer, 1996) and reduce the species richness of amphibian communities (Hecnar & M'Closkey, 1997). Great crested newts seem particularly sensitive to fish predation (Smith, 1964; Beebee, 1985; Oldham & Nicholson, 1986; Arntzen & Teunis, 1993; Swan & Oldham, 1993), probably due to the nektonic behaviour of the larvae (Dolmen, 1983*b*). In spite of a prolonged period of low reproductive success in the Walton Hall Pond, the adult newts continued to return to the pond to breed. The apparent failure of adult *T. cristatus* to detect and respond to the presence of predatory sticklebacks by altering breeding site selection, may be due to the inability of the newts to respond to a small, gape-limited predator which preys on newt larvae rather than on adult newts. Alternatively, the lack of other breeding sites nearby may have prevented movement away from Walton Hall Pond.

One curious aspect of the recovery of the study population from the surmised predatory effects of sticklebacks is a delay in the newt population size increase. No sticklebacks were found in the pond in 1991 or later years. Since it takes two years to attain maturity, the newt population might be expected to have increased in 1993. However, the population did not show signs of growth until 1994 (Fig. 1). The reason for this one-year delay in population size increase is not known. It is possible that the stickleback decline occurred in 1991, so that some fish survived long enough to prey on newt eggs and larvae. Alternatively, factors other than fish predation may have been involved.

Estimated adult survival ranged from 31%–100% per year. Between most years adult survival appears to have been very high, ranging from 76%–100%. However, in the periods 1988-89 and 1993-94, it was markedly lower, at 31% and 37%. The low adult survival between 1988 and 1989 may be attributable to some aspect of the handling and registration procedure. This conclusion is reached since the change in estimated population size, a drop of 17 from 105 to 88, is more than accounted for by the disappearance of those individuals that were captured, anaesthetized and photocopied in 1988 (only 10/37 individuals from 1988 were recaptured in 1989). Handling procedures were similar in 1988 and succeeding years, hence the detrimental aspect of the procedure has not been identified. The cause of low survival between 1993 and 1994 is also not known. However, the monitoring of individuals reveals that, during this period, an increase in population size occurred even though this was a period of relatively high adult mortality. The remaining years showed survival rates (76–100%) comparable to, or higher than, the upper ranges previously recorded for *T. cristatus* (70–80% [Hagström, 1979] and approximately 65% [Hedlund, 1990]).

The lower recapture rate of new recruits, compared to older individuals suggests that first-time breeders experienced lower survival (59%) than older newts (89%). This difference in survival between first-time breeders and older adults was also found by Hedlund (1990).

Juvenile productivity was not measured in the Walton Hall population. Moreover, the pitfall trapping and funnel trapping methods used to sample the adult population revealed very few juvenile captures, only 49 over the course of the study. The use of the aquatic environment by juvenile *T. cristatus* varies between populations (Bell, 1979), so the low capture rate of juveniles during the present study is not atypical. More striking was the complete failure to detect newt larvae over seven years of funnel trapping. It is possible that the design of funnel traps used in the present study is less effective in catching larvae than are the bottle traps (Griffiths, 1985) used in other studies (e.g. Cooke, 1995). Alternatively, the low capture rate of juveniles, and the lack of evidence of larvae may reflect the low productivity of this population. The low rate of recruitment to the breeding population from 1989 to 1993 indicates that this population underwent at least a five-year period with very low productivity of juveniles.

The annual recapture rate of juveniles (49%) and the estimated annual survival rates of juveniles at this site (59%) are relatively high compared to other temperate pond-breeding amphibians. This may be typical of newts in the genus *Triturus*, since *T. cristatus* and *T. vulgaris* have the highest juvenile survival rates of temperate pond-breeders reviewed by Beebee (1996). This high rate of juvenile survival in *T. cristatus* may compensate for periods of low productivity and the relatively low fecundity of this species. Fifty per cent of all eggs die at the tail bud developmental stage (Horner & MacGregor, 1985) leaving mean clutch sizes of approximately 100 viable eggs (Hedlund, 1990; Griffiths, 1996).

For those few newts that were identified as newly metamorphosed juveniles, and later as sexually mature adults, it appears that most individuals achieved sexual maturity at two years. This agrees with Beebee's (1980) observations made at a site in southern England, and also with the skeletochronological work on French populations (Francillon-Vieillot *et al*., 1990; Arntzen & Teunis, 1993) which suggests the attainment of sexual maturity at two to three years.

The current data also demonstrate the unreliability of counts as measures of population size. For example, in 1992 very few newts were captured at the drift fence. If drift fence captures had been used as a count to indicate population size then the population would have appeared to have crashed that year. However, monitoring the following year revealed that 68% of the newts captured in 1993 were recaptures from 1991, indicating that many of the individuals that evaded detection at the drift fence in 1992 were nevertheless still alive. A possible explanation for the lack of newts captured at the drift fence may be yearly variation in weather patterns, although the mechanism of the impact on the newts is not known (other local migrations were observed to occur as expected; pers. obs.). However, it is interesting to note that 1992 also resulted in Cooke's (1995) lowest mean count. In this latter study, as well, the increase in the numbers of newts counted in the following year seems unlikely to be due entirely to new recruits to the breeding population. Cooke's larval catches were minimal for the years 1990 to 1992, making it unlikely that the adults observed in 1993 were the resultant, newly breeding animals. These findings support the notion that newt counts do not necessarily reflect population size (Griffiths & Raper, 1994).

Monitoring individuals in the present study reveals information about population fluctuations. It demonstrates that a single population of *T. cristatus* can rapidly change in its demographic nature. Over the course of this study the population switched from a stable population, with low recruitment, to a rapidly increasing population. Rapid changes in *T. cristatus* population size have been noted elsewhere (Arntzen & Teunis, 1993; Cooke, 1995); however, the current data provide information on the population processes occurring during these fluctuations.

## ACKNOWLEDGEMENTS

I am grateful to Ken Hollinshead for allowing me to work at the Walton Hall Pond and to Chris Raxworthy and Verina Waights for assistance with field work. I am also grateful to Tim Halliday and the Open University for access to laboratory facilities. This work was not directly supported by any research funding, but was carried out whilst the author was in receipt of a Natural Environment Research Council funded studentship and a grant from the Agriculture and Food Research Council to Tim Halliday. I wish to thank Richard Griffiths, Tim Halliday, Jeff Houlahan, Robert Jehle and an anonymous referee for helpful comments on the manuscript. Handling of *T. cristatus* was carried out under licences from English Nature.

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*Accepted: 8.6.98*