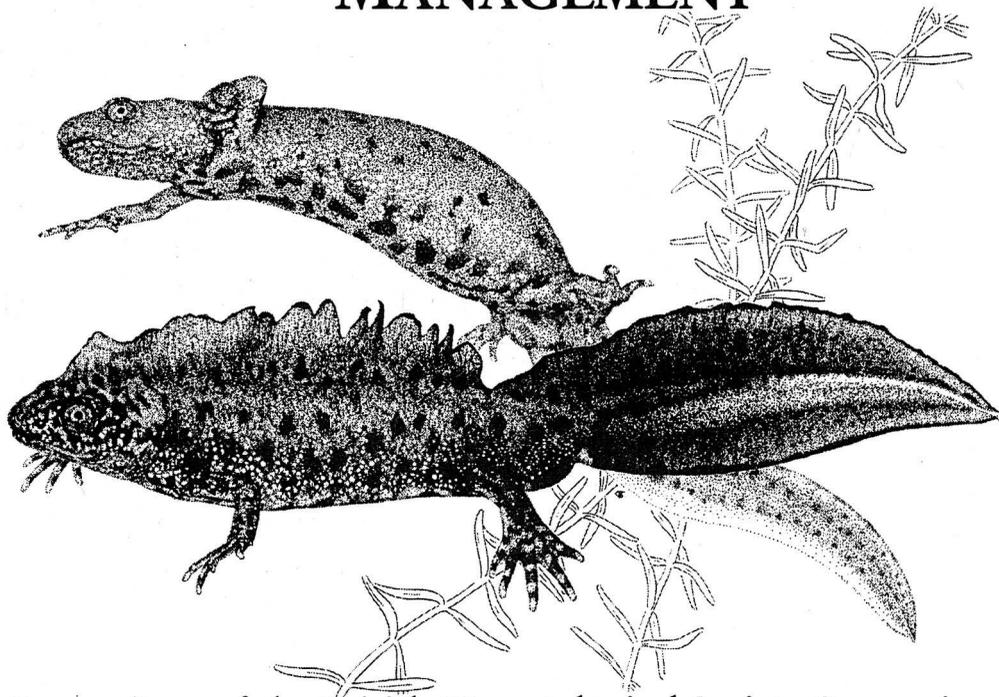


THE HERPETOLOGICAL JOURNAL

SCIENTIFIC STUDIES OF THE GREAT CRESTED NEWT: ITS ECOLOGY AND MANAGEMENT



Proceedings of the British Herpetological Society Symposium
held on 5 December 1998

A contribution to the Species Action Plan for the Great Crested Newt

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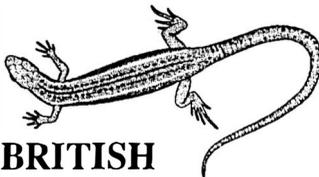
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FRONT COVER: Female and male great crested newts (Bas Teunis)

SCIENTIFIC STUDIES OF THE GREAT CRESTED NEWT: ITS ECOLOGY AND MANAGEMENT

PROCEEDINGS OF THE BRITISH HERPETOLOGICAL SOCIETY SYMPOSIUM HELD ON 5 DECEMBER 1998

EDITORIAL

The great crested newt (*Triturus cristatus*) is a priority species in the UK's Biodiversity Action Plan and has its own Species Action Plan (SAP), in which the British Herpetological Society is a lead partner. With the passage into law of the Wildlife and Countryside Act 1981, the great crested newt was propelled to the forefront of the herpetological conservation agenda in Britain. This initial impetus was reinforced by further protective legislation in 1994. The position in the UK today is that the species remains widespread yet declining in many parts of lowland England and Wales, though scarce in the south-west peninsula, the uplands and Scotland.

Because the great crested newt is both widespread and highly protected it is frequently the focus of conflicting interests between conservationists and developers. Therefore, the problems associated with the conservation of great crested newts may be considered under two broad categories. First, there are those conflicts that arise when a newt population is in the way of a proposed development, such as mineral extraction, or the building of houses or roads. Great crested newts and their habitat are protected by law, but when there are estimated to be thousands of populations in Great Britain, the authorities are often prepared to accept mitigation rather than insisting on total protection. In such situations, the economic pressure to resolve the conflict quickly often seems to take precedence over a more considered approach to the problem, and various questions can arise. For example, should the newts be moved to an existing pond elsewhere, or kept *in situ*? How much land should be set aside for terrestrial habitat? Could less land be set aside if the quality of habitat were increased?

Currently, decisions on such matters are often made more on the basis of experience and intuition than on the basis of scientific data. Without doubt, many environmental consultants aim to produce the best possible outcome in terms of conservation, but without firm evidence to support their position they may face an uphill struggle to convince their clients and the licensing authorities that their idea of what is best for the population is really necessary.

The second category of problems in the conservation of the great crested newt is primarily to do with long-term issues such as the fragmentation of habitat, habitat degradation and population genetics. Here, it is easier for scientists to devise relevant research projects that will not only address practical questions but will also meet the expectations of grant-awarding committees for "cutting-edge" science that addresses wider issues of general importance.

As a consequence of its role as a lead partner in the great crested newt Species Action Plan, and the broad base of its membership, the British Herpetological Society had been aware for some time of a lack of communication between those in the academic community who were conducting research on the great crested newt and a number of practitioners involved in mitigation schemes to offset the adverse impacts of development. To some extent, this might be portrayed as idealism versus pragmatism. However, there were feelings on one side that the results of research were being ignored, and on the other that researchers were not addressing the most important questions. In an attempt to improve the exchange of information and views between all parties interested in the great crested newt, the BHS Research Committee held a one-day symposium in London on 5 December, 1998. The meeting, entitled "*Scientific Studies of the Great Crested Newt: its Ecology and Management*", was attended by more than 100 delegates representing a wide range of organisations and interests. This special issue of the *Herpetological Journal* represents the proceedings of that meeting. Some of the papers presented here differ in some respects from those presented on the day, mainly as a result of peer review. We have also included two additional, relevant manuscripts that were submitted since the meeting.

We wish to acknowledge the financial support of English Nature, partly through the Species Recovery Programme. We thank the numerous referees, who gave freely of their time; Bas Teunis, for supplying the excellent cover illustration; and Tony Gent (then of English Nature), Jim Foster (then of Froglife) and Mary Swan, for helping to publicise the event. We are also indebted to the Council of the British Herpetological Society for supporting both the symposium and the publication of this special issue. Particular thanks must go to John and Mary Spence and Monica Green for their assistance with the logistics on the day. At the end of the symposium, we canvassed delegates for their views on what the future priorities in great crested newt research should be. It proved difficult to draw up a definitive wish-list, which perhaps underlines the diversity of views and approaches that exist within herpetological conservation in Britain. We hope that this special issue will stimulate further interest and debate between the various stakeholders in the conservation of great crested newts.

Clive P. Cummins
Richard A. Griffiths

DISPERSION PATTERNS OF YOUNG GREAT CRESTED NEWTS (*TRITURUS CRISTATUS*)

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Dispersion patterns of different life stages (egg, larva, metamorph and adult) of the great crested newt, *Triturus cristatus*, were recorded in two adjacent woodland ponds in Oxfordshire, UK. The places along the shores where adult females emerged were significantly different from those where eggs were laid, suggesting that the females do not choose egg sites that correspond with their routes of migration. In the northern pond the distribution patterns of eggs and larvae were very similar. In the southern pond the eggs and larvae were almost entirely restricted to two of the three shores, where they had very similar distribution patterns. Metamorphs emerged from both ponds along the same shores as adult males, suggesting that they were following directional cues. In laboratory tests, metamorphs showed a significant preference for their own, previously-used substrates over clean substrates, and over those used by other metamorphs. Metamorphs significantly preferred substrates previously used by an adult to clean substrates; the ability to use similar cues to orientate was further indicated by the significant tendency of metamorphs to follow a directional trail left on the substrate by an adult newt in a Y-maze, regardless of whether the adult was male or female. These results suggest that metamorphs can detect cues left by both metamorphs and adult newts and may be able to use them for orientation.

Key words: dispersion, great crested newts, metamorphs, cues, orientation

INTRODUCTION

The great crested newt, *Triturus cristatus*, has both aquatic and terrestrial phases during its life cycle. Courtship, breeding and larval development occur exclusively in the aquatic habitat. The terrestrial environment is used for feeding and over-wintering. Breeding adults must migrate between these two habitats. Site fidelity is common in many species of amphibian, with adults possessing strong, demonstrable homing abilities (e.g. Oldham, 1966, 1967; Dolmen, 1981; Sinsch, 1992). Such directed movements require mechanisms of orientation. Many sensory mechanisms, including olfaction, vision, hearing and magneto-perception, have been implicated in the perception by adults of orientation stimuli. Home pond odour (e.g. Oldham, 1967; Joly & Miaud, 1993), celestial compasses (e.g. Landreth & Ferguson, 1967*a,b*; Taylor & Ferguson, 1970; Taylor, 1972), polarized light (e.g. Adler, 1970; Adler & Taylor, 1973), vocalization of conspecifics (e.g. Ferguson, 1963; Oldham, 1966), the Earth's magnetic field (e.g. Phillips & Borland, 1994; Phillips, Adler & Borland, 1995) and use of landmarks (Adler, 1980) are all demonstrated orientation cues. Adults have the opportunity to use these cues in relation to known terrestrial and pond sites learned from previous years' migrations. This cannot

be said of newly-metamorphosed individuals (metamorphs) which disperse from the aquatic to the terrestrial habitat. Metamorphs possess no such previous knowledge of the direction of their goal, the terrestrial habitat, in relation to cues from their surroundings. Reaching suitable terrestrial sites is critical to their survival, so any mechanism by which they can improve their ability to locate favourable sites will be of survival value.

We can find no published reports on the dispersal behaviour of great crested newt metamorphs. They may disperse randomly and survive as best they can in whatever habitats they reach. Alternatively, directional mechanisms may be involved. There is some evidence to suggest that dispersal patterns of great crested newts are not random and that metamorph dispersal exhibits similar directional patterns to that of adults (Duff, 1989; Franklin, 1993). This may be a coincidental consequence of the effect of aquatic habitat characteristics on the larvae, or there may be some active recognition of adult presence, or long range orientational ability on the part of the metamorphs. If metamorphs do not disperse at random, they must use cues. This paper will address some of these issues. Specifically it will (1) assess the dispersal of great crested newt metamorphs from two ponds in Oxfordshire in relation to the adult, egg and larval distributions in the ponds; and (2) in laboratory experiments determine whether metamorphs have the ability to detect and follow paths used by other newts.

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MATERIALS AND METHODS

THE STUDY SITE

The breeding sites used for this study are two large, adjacent, spring-fed ponds at the centre of the 52 ha Little Wittenham Wood (National Grid Reference SU572928) in Oxfordshire, UK. The ponds (Fig. 1) lie in a generally NE – SW direction and are separated by a grassy land bridge about 10 m wide. The South Pond (c. 180 m perimeter) contains a large population of goldfish, *Carassius auratus*, thought to have been introduced about 20 years ago. The North Pond (c. 130 m perimeter) is fed from the South Pond but does not contain fish. Throughout the breeding season there is a 50-100% covering of duckweed (*Lemna trisulca* and *Lemna minor*). The extent of the duckweed cover is influenced by the wind. The woodland immediately surrounding both ponds is mixed deciduous. A small strip of grassland, about 5 m wide, borders both ponds on the western side.

DISTRIBUTION PATTERNS

The North Pond has four discernible shorelines. Shores 1, 2 and 3 of the North Pond (see Fig. 1) were sampled at each stage in the investigation but, owing to

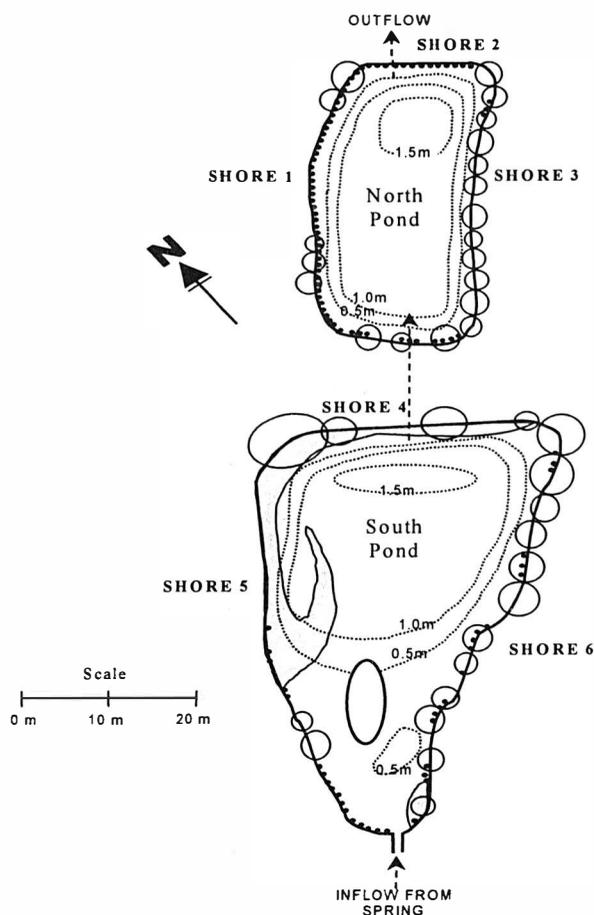


FIG 1. Map of the Little Wittenham study site. Thin dashed lines indicate water depth; thick dashed lines indicate water flow; circles and ellipses indicate overhanging trees; hatched areas indicate *Carex riparia* and black dots indicate *Carex distans*, the two major types of marginal vegetation.

the steep gradient and vegetational structure, it was not possible to sample along the fourth shore. The South Pond has three shorelines (shores 4, 5 and 6), all of which were sampled. Egg deposition was recorded from 3 April 1998 to 29 June 1998; larval distribution was sampled between 26 May 1998 and 22 September 1998; adult emigration from 3 June 1998 to 16 October 1998; and metamorph emigration from 12 August 1998 to 21 October 1998.

Egg deposition. Distribution of egg deposition sites around both of the ponds was monitored throughout the breeding season using egg sticks: sets of 20 strips of clear polythene, each 80 cm x 2.5 cm, were attached to garden canes and submerged, close to the water surface, at 8 m intervals around the perimeter of each pond. Thirteen egg sticks were used along the three shores sampled in the North Pond and fifteen sticks in the South Pond. The numbers of eggs deposited along the strips were counted every second day. The temporal patterns of egg deposition showed strong, positive correlations between shores. In the North Pond: shore 1 vs. shore 2, $r_s=0.80$, $P<0.01$; shore 2 vs. shore 3, $r_s=0.89$, $P<0.01$ and shore 3 vs. shore 1, $r_s=0.90$, $P<0.01$ (Spearman rank correlations). In the South Pond: shore 5 vs. shore 6, $r_s=0.92$, $P<0.01$ (Spearman rank correlation); no eggs were recorded along shore 4. This indicates that the pattern of egg deposition through time was similar across the sampled shores, so the peak egg counts for each individual stick (which occurred during the first two weeks of May) were used as data for the analysis of the spatial pattern of egg laying in the ponds.

Larval dispersion. The presence of larvae was monitored every week in each pond using anglers' keep nets; these are cylindrical nets, closed at the bottom and supported at intervals along their lengths by hoops. Ten nets (1 m diameter) were collapsed in the water and lay on the bottom of each pond, at depths of about 0.5 m, at 10 m intervals around the shores, with floats marking their positions. Once a week the nets were jerked upwards from the bottom of the pond and the numbers of larvae caught were recorded. Once counted, the larvae were returned to the pond and the nets were replaced. The temporal changes in larval dispersion showed significant, positive correlations between shores. In the North Pond shore 1 vs. shore 2, $r_s=0.67$, $P<0.01$; shore 2 vs. shore 3, $r_s=0.56$, $P<0.02$ and shore 3 vs. shore 1, $r_s=0.85$, $P<0.01$ (Spearman rank correlations). In the South Pond shore 5 vs. shore 6, $r_s=0.56$, $P<0.05$ (Spearman rank correlation); shore 4 was again excluded from the test for the South Pond, because of the very low number of larvae captured there. These correlations indicate that the temporal changes in larval distribution were similar across the sampled shores, so peak captures for individual nets (which occurred during August) were used as data for the analysis of larval distribution.

Dispersal of adults and metamorphs from the ponds. The movements out of the ponds by adults and

metamorphs were monitored using trough traps constructed from 1 m lengths of 15.3 cm-diameter plastic pipe. The ends of the pipes were closed using strong adhesive tape. A 5 cm slot was opened along the length of the pipe and 5 cm acetate strips were used as baffles along each edge to prevent the animals from escaping. The traps were buried in the soil, flush with the ground surface, and were positioned every 8 m around the perimeters of the two ponds, within 2 m of the shore. A number of newts caught within one week from each shore were kept for use in the laboratory experiments before being released. The rest were released at their point of capture. Total captures at each trough trap were used for the analysis of the patterns of adult and metamorph dispersal from the ponds.

Patterns of egg distribution, larval distribution and adult and metamorph dispersal in each pond were compared using chi-squared contingency tables. Adult influx was not monitored in this study, but it has been shown using mark-recapture methods that great crested newt adults usually leave the water within 10 m of the point at which they entered (Latham, *et al.*, 1996). The patterns of egg deposition were therefore compared with those of female dispersal under the assumption that influx and exodus patterns were similar. Comparisons between female dispersal and egg dispersion were made to determine whether the females actively moved around the pond to choose egg laying sites, or if they merely laid their eggs wherever they entered or left the water. Egg and larval distribution patterns were compared to determine whether the larvae associated with oviposition sites, or if they dispersed at random. Patterns of metamorph emergence were compared with larval distribution and adult male and female patterns of emergence to determine whether metamorph dispersal was random or influenced to any degree by their larval distribution or by adult dispersal.

LABORATORY EXPERIMENTS

Substrate preference. Great crested newt metamorphs were tested for their ability to detect – and to differentiate between – cues left by conspecifics on the substrate. Metamorphs were tested using one of the three following experiments. In experiment 1 (own vs. clean) the metamorphs were provided with a choice between a substrate previously occupied by themselves and a clean substrate. This experiment was performed to determine whether the metamorphs showed a preference for clean substrate (new habitat) or their own substrate (familiar habitat). In experiment 2 (adult vs. clean) the metamorphs were provided with a choice between a substrate previously occupied by an adult and a clean substrate. This was to determine whether metamorphs showed a preference for a substrate that an adult had used or a clean substrate, thus indicating whether metamorphs can detect the presence of adults or seek out new habitat. In experiment 3 (own vs. other metamorph) the metamorphs were provided with a

choice between substrates previously occupied by themselves or by a different metamorph. This experiment was performed to determine whether metamorphs are likely to orient towards other metamorphs or remain in familiar habitat. We refer to newts used to provide cues as source newts, while the metamorphs used to observe responses to the substrates are referred to as test metamorphs.

The newts used for laboratory tests were captured over a period of one week. They were kept under a LD 14:10 photoperiod, simulating the natural day length that the metamorphs would experience on emergence from the ponds.

Experimental procedures were similar to those described by Jaeger & Gergits (1979) and Dawley (1984). Twenty-four plastic dishes (9 cm diameter, 2 cm deep) were used as individual test chambers. For each experiment the bottoms of the dishes were divided in half, and each half was covered with two layers of filter paper. The filter papers were treated previously in one of three ways, according to the experiment: (a) with 1 ml of clean, one-week-old tap water, (b) as (a) and used as a substrate by a source adult for 24 hr; (c) as (a) and used as a substrate by a source metamorph for 24 h. In those experiments that provided a choice between the metamorph's own, previously-used substrate and another substrate, the source metamorph was later used as the test metamorph.

The dishes were orientated for observation so that the two halves of the dish could be classed as either left or right, as perceived by the observer. Lids, each with two air vents, were placed over the dishes to prevent the escape of the newts. The side (left or right) on which the different substrates were presented to the test metamorphs were randomized in each experiment. Throughout the experiments the dishes were screened from disturbance using 1 m high, light-proof screens. A single light source (60 W bulb) was placed directly over the test area.

A single test metamorph was placed into the centre of each dish, along the division between the two substrates. The lid was replaced and a five-minute settling period allowed before recording began. Each recording period lasted five hours. Preliminary observations of a small number of metamorphs indicated that activity tended to be more intense at the start of the trial. Accordingly, after the settling period of five minutes, the position of the metamorph was recorded every minute for the first hour and every ten minutes for the following four hours.

A total of 72 different test metamorphs were used in the three experiments. Each experiment used 24 test metamorphs and consisted of two trials, using the same 24 test metamorphs, with the positions of the substrates in the second trial reversed from their original random presentation in the first trial. The same test metamorphs were used for both trials of each experiment to determine whether the responses of the

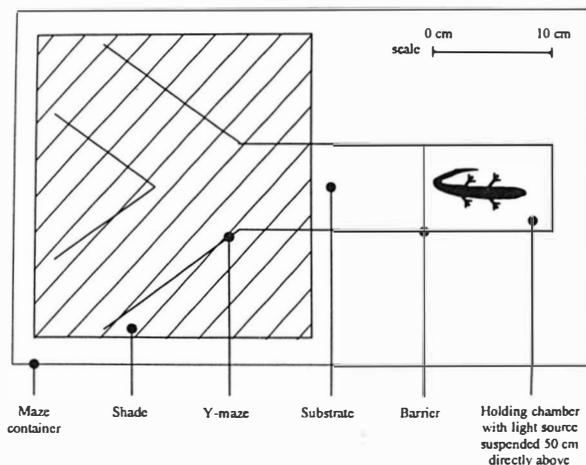


FIG 2. Y-maze used to test metamorph ability to follow cues left on substrate previously traversed by a foreign adult newt. The substrate was damp filter paper, changed for each test. The light gradient, created by the light source and the shading of the arms of the maze, provided the stimulus for the newts to move down the maze.

metamorphs to the substrates were consistent. Testing took place between 0900 and 1600 hrs from September to December 1998.

The numbers of responses the metamorphs made to each of the different substrates in the three experiments were compared using Wilcoxon signed-rank matched pairs tests for each time period (i.e. 1–30 mins, 31–60 mins and 61–300 mins) to determine whether the metamorphs were able to detect and show a preference for particular cues, and whether this changed with time.

Y-maze experiments. A Y-maze was used to determine whether metamorphs could follow cues left on the substrate by adult newts. As in the substrate preference tests, adult newts used to provide cues in the maze are referred to as source newts, while the metamorphs placed in the maze after the adults are referred to as test metamorphs. The Y-maze was constructed from corrugated plastic (Fig. 2). The stem was 15 cm long, 5 cm wide and 5 cm high, and each arm was 10 cm long. The floor of the maze was covered with clean, damp filter paper. A source adult newt was contained in a holding chamber at the end of the stem for five minutes to settle. One arm of the maze was blocked off from the source adult newt to control the adult's route. A light source (60 W bulb) was suspended over the holding chamber while both the arms of the maze were deeply shaded. The source adult newt was given unlimited time to move to the end of the unrestricted maze arm. This was normally accomplished within 15 mins, so this was the time limit set for each trial. The light gradient within the maze provided the stimulus for the newt to move. Once the source adult had completed the maze the restriction to the other arm was removed. A test metamorph was placed in the holding chamber for five minutes. The release procedure was the same as that for the source adult. Metamorphs that reached the end of the arm down which the source adult had travelled scored '+',

those that travelled the opposite arm scored '-' and those that did not finish within the time limit scored '0'.

The trial was replicated 100 times, using 100 different metamorphs and with 25 source adult males and 25 females which had each moved either to the left or the right arm of the maze. Direction and sex of the source adult were randomized in their order of presentation to the metamorphs. Source adults and test metamorphs were chosen at random. The test metamorphs were used only once while the source adults were not used more than once in every 20 tests. Between each replication the filter paper was removed, the maze was wiped clean, dried and the damp filter paper replaced. The maze was rotated 90° between each trial to avoid the possibility of a standard response to the starting direction (e.g. a response to magnetic cues). Numbers of metamorphs in each response category were compared using a chi-squared test to determine whether the metamorphs were able to detect and follow, or avoid, the path of an adult through the maze. Analyses both including and excluding the non-finishers were carried out. Metamorphs scoring '0' were not included in some analyses because, in their failure to produce a response to the source adults and the small numbers involved, their behaviour seemed atypical. Response times of the metamorphs were analysed using the *F*-test to check for equal variance. The mean response times were then compared using the two sample *t*-test, assuming equal variance, to determine whether response behaviour differed among the metamorphs according to the direction or sex of the adult.

RESULTS

DISTRIBUTION AND DISPERSION PATTERNS

The distribution patterns of great crested newt eggs, and larvae, and the points of departure of the metamorphs and adults from the North and South Ponds are shown in Figs. 3 and 4 respectively. Comparisons are indicated by double headed arrows and resulting probability levels.

North Pond. (Fig. 3) Female dispersal was significantly different from egg distribution around the pond ($\chi^2=28.58$, $df=2$, $P<0.01$). Egg and larval distribution patterns in the North Pond were not significantly different from each other ($\chi^2=4.66$, $df=2$, $P>0.05$). Metamorph dispersal followed a pattern significantly different from the distribution of the larvae ($\chi^2=6.643$, $df=2$, $P<0.05$). Metamorph dispersal was significantly different from that of adult female dispersal ($\chi^2=11.91$, $df=2$, $P<0.01$), but not significantly different from that of adult male dispersal ($\chi^2=3.369$, $df=2$, $P>0.05$).

South Pond. (Fig. 4) No eggs or adult females were recorded at Shore 4, but egg distribution and adult female dispersal were significantly different along the east and west shores ($\chi^2=25.14$, $df=1$, $P<0.01$, applying Yates' correction). The eggs and larvae, when comparing all three shores, had significantly different distribution patterns ($\chi^2=1.88$, $df=2$, $P<0.01$), though the patterns of dispersion of eggs and larvae along east

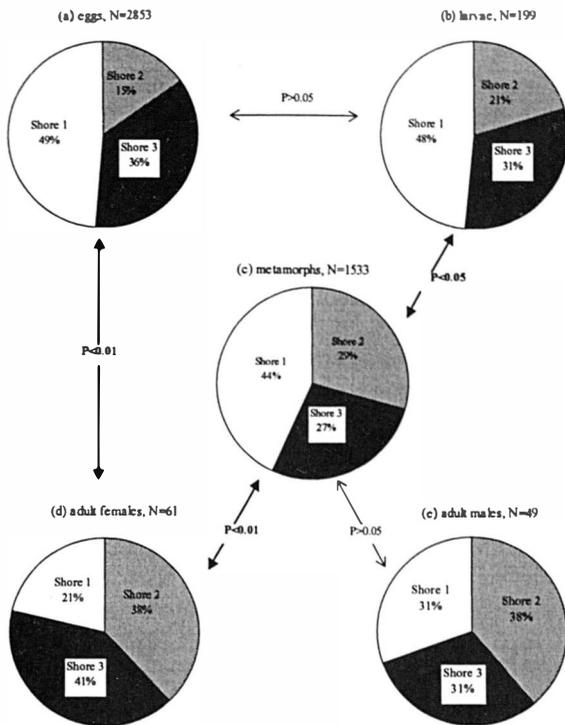


FIG 3. Dispersion patterns of the different life stages of the crested newt in the North Pond and a summary of their comparisons. Dispersion patterns were compared using chi-squared contingency tables. Bold arrows and probability levels indicate significant differences between the dispersion patterns of the life stages.

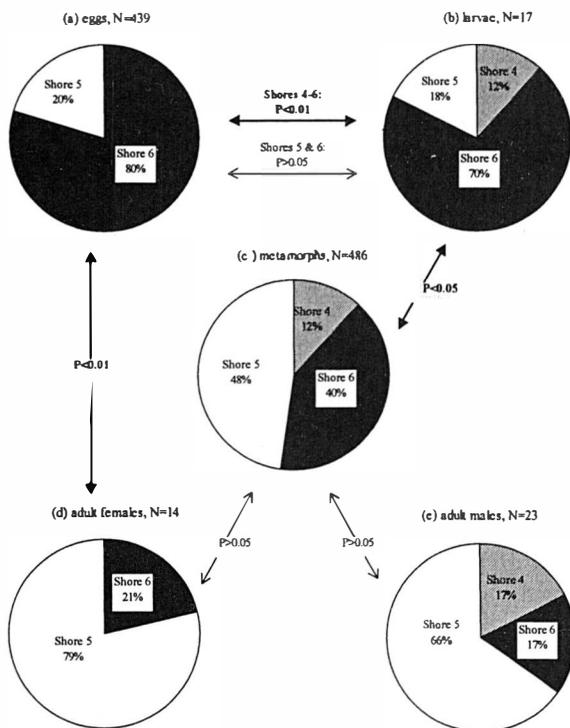


FIG 4. Dispersion patterns of the different life stages of the crested newt in the South Pond and a summary of their comparisons. Dispersion patterns were compared using chi-squared contingency tables. Bold arrows and probability levels indicate significant differences between the dispersion patterns of the life stages.

and west shores were almost identical ($\chi^2=0.117$, $df=1$, $P>0.05$, applying Yates' correction) and both eggs and larvae had very low peak counts (0 and 2 respectively) along Shore 4. Larval distribution and metamorph dispersal were significantly different ($\chi^2=6.918$, $df=2$, $P<0.05$). Metamorphs showed no significant difference in their dispersal patterns when compared to either female dispersal ($\chi^2=5.488$, $df=2$, $P>0.05$) or male dispersal ($\chi^2=4.785$, $df=2$, $P>0.05$).

LABORATORY EXPERIMENTS

Substrate preference. Responses of metamorphs to different substrates are summarized in Fig. 5. Test metamorphs showed a significant preference for the substrate previously used by themselves, over a clean substrate throughout the test period (1-30 mins: $N(N')=24(24)$, $T=59$, $P<0.02$; 31-60 mins: $N(N')=24(21)$ $T=36.5$, $P<0.02$; 61-300 mins: $N(N')=24(23)$ $T=39$, $P<0.002$; using Wilcoxon's signed rank matched pairs test - $N(N')$, number of metamorphs tested (statistical sample size); T , test statistic; P , two-tailed probability $\alpha=0.05$). The

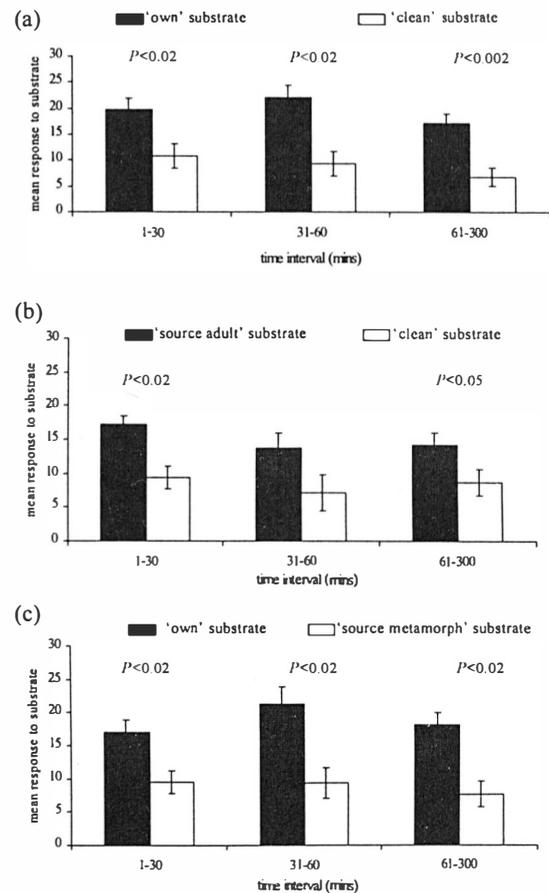


FIG 5. Responses of metamorphs in substrate preference tests, $N=24$: (a) own (i.e. previously used) substrate vs. clean substrate; (b) source adult substrate vs. clean substrate; (c) own (i.e. previously used) substrate vs. source metamorph substrate. Vertical lines show SE.

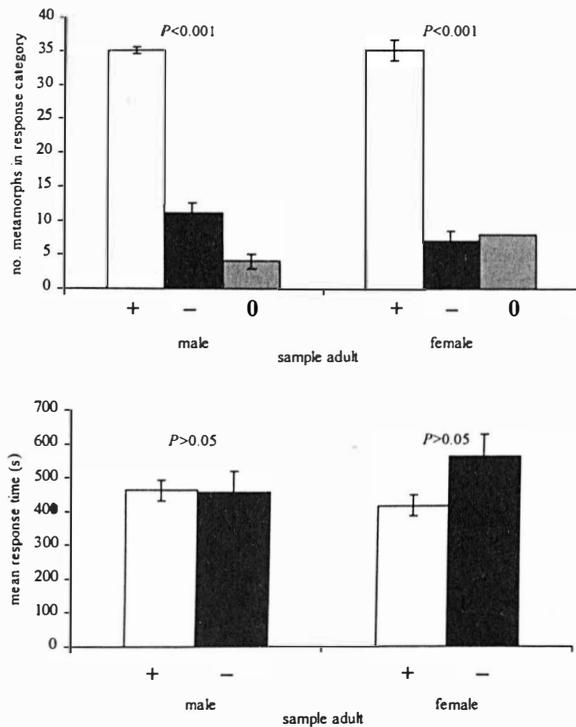


FIG 6. Responses of metamorphs in Y-maze tests: (a) numbers of test metamorphs in each response category ($N=100$) – metamorphs following the same path as source adults scored '+' (open bars), those taking the opposite path scored '-' (dark bars) and those not responding within the time limit scored '0' (grey bars); (b) response times of tests metamorphs following adult males or females (both $N=50$) – '+' (open bars) metamorphs following the same route as source adults, '-' following opposite route to source adults. Vertical lines show SE.

metamorphs also showed a significant preference for substrates previously used by a source adult, rather than clean substrates (1-30 mins: $N(N')=24(24)$ $T=59.5$, $P < 0.02$; 31-60 mins: $N(N')=24(20)$ $T=57.3$, $P < 0.1$ (not significant); 61-300 mins: $N(N')=24(20)$ $T=46.5$, $P < 0.05$). Although the 31 to 60 minute interval does not show a significant result, the metamorphs did continue to make more responses towards the adult substrate than the clean substrate (Fig. 5). Throughout the experiment the test metamorphs significantly preferred their own previously-used substrate to a substrate used by a different metamorph (1-30 mins: $N(N')=24(24)$ $T=52.5$, $P < 0.02$; 31-60 mins: $N(N')=24(23)$ $T=59.5$, $P < 0.02$; 61-300 mins: $N(N')=24(23)$ $T=58$, $P < 0.02$).

Y-Maze. The responses of metamorphs to adult trails in a Y-maze are summarized in Fig. 6. Significantly more metamorphs followed the same route as the adult source newt in the Y-maze ($\chi^2=30.73$, $df=1$, $P < 0.001$). Even if the non-finishers were added to those that chose the opposite path to the source adult, the metamorphs still showed a significant tendency to follow the adult newt ($\chi^2=16$, $df=1$, $P < 0.001$). There was no significant difference between the number of metamorphs following the same route as adult males and the number

following the same route as adult females ($\chi^2=0$, $df=1$, $P=1.0$). There were no significant differences between the response times of metamorphs following the same route as the source adult and those taking the opposite route (mean response times following males: same path=462.9 sec, opposite=456.7 sec, $t=0.09$, $df=44$, $P > 0.05$; mean response times following females: same path=416.6 sec, opposite=561 sec, $t=1.94$, $df=40$, $P > 0.05$).

DISCUSSION

The patterns of adult female exodus from the breeding ponds were significantly different to the distributions of eggs in both ponds. Previous work at this study site has shown that adult great crested newts leave the water within 10 m of their point of entry (Latham, *et al.*, 1996), suggesting either that individuals do not disperse widely once in the pond, or that they orientate towards their point of entry after a period of aquatic residence. There were no observations of adult influx to the pond in the present study. However, if exodus mirrors influx then the difference between egg distribution and pattern of female exodus at these ponds indicates that the females are actively seeking out suitable courtship/egg laying sites elsewhere in the ponds. Great crested newt courtship is based on a lek system (Hedlund & Robertson, 1989; Hedlund, 1990). Females are free to move between different male assemblages and may choose to mate with any male within an assemblage. Male aggregations form apparently at random, showing no association with any resources essential to females, nor with observable environmental factors (Hedlund & Robertson, 1989). Evidence of female selectivity in oviposition sites was found by Green (1984), who showed that females exhibit great care in choice of oviposition sites, generally preferring plants with broad leaves of good fibre. Therefore the females may have to move beyond their entry points to the pond in order to find suitable mates, and then travel further if suitable oviposition sites are not available at the mating sites. Ongoing work will determine possible correlations between egg distribution and vegetation structure.

The distribution of eggs was very similar to that of the larvae, indicating that the larvae associate with oviposition sites. Metamorphs, however, emerged from the ponds in patterns that differed from the distribution of the larvae. Similar observations were recorded by Pfenning (1990), who found that spadefoot tadpole density was greater at natal sites until just a few days before metamorphosis, when distribution of the tadpoles changed. Pfenning's results suggest that the tadpoles oriented towards cues associated with their natal habitat learned early in ontogeny. The disassociation from the natal site by metamorphs in the current study suggests that the metamorphs had begun to be influenced by some orienting mechanisms different from those influencing the larvae.

The pattern of metamorph dispersal from the North Pond was not different from that of the adult males. Metamorphs emerging from the South Pond did so in a pattern that was not different from either the adult males or females. The emigration routes of the adults may therefore have some influence upon those of the metamorphs. Previous work (Duff, 1989; Franklin, 1993) has found a relationship between the numbers of adults and the numbers of metamorphs leaving certain sectors of the ponds. In the current study, patterns of metamorph exodus showed greater affinity with those of emigrating males than females. This may reflect the tendency of males to leave the ponds later than the females (Duff, 1989; Franklin, 1993; pers. obs.) and so any cues left by the males would be more recent and more easily detected by the metamorphs.

Metamorph dispersion at this site may therefore initially be a result of the selection of oviposition sites by females (as the larvae show association with oviposition sites), later becoming influenced by the patterns of emigration of the adults, particularly the males.

The reactions of the test metamorphs to substrates previously exposed to different newts indicate their ability to detect cues left on the substrates by those newts. Their selection of a substrate appears to be influenced by whether newts have previously occupied the substrate. Metamorphs preferred to spend time on substrate that had been inhabited by a newt, rather than on clean substrate, indicating a tendency to go where other newts had been before – possibly an indication of a strategy adopted as an efficient means of finding suitable habitat. The Y-maze experiments indicate that metamorphs can detect and follow directional cues left on the substrate by adult newts. This study considers the ability of metamorphs to follow conspecifics rather than the motivation for them to do so. There may be a social attraction or implications for thermoregulation, osmoregulation and/or predator avoidance/defence. In the pond, it may simply be that some points of exit are superior for all and channel all the newts down the same corridors. Time and resource constraints meant that the examination of these possibilities was beyond the scope of this study.

No difference in behaviour was exhibited in the Y-maze whether the adult was male or female. This suggests that the metamorphs showed no bias in relation to the sex of the adult and seemed to follow males and females equally. Therefore, the greater affinity between metamorph exodus and adult males than females shown at the North Pond may depend on the age of the cue, rather than its origin. Ongoing work will investigate what effect the age of the cue has on the metamorphs' ability to detect it.

The cues being detected in this study are likely to be chemical in nature, in the form of skin or cloacal secretions, rather than visual – such as marks left by faecal pellets. The ability of amphibians to detect chemical cues has been studied extensively in the past. For example, amphibians have been found to use chemical cues

in prey detection (Risser, 1914), courtship and mate recognition and selection (e.g. Malacarne & Vellano, 1987; Cogalniceanu, 1994), homing and orientation (e.g. Grant, Anderson & Twitty, 1968; McGregor & Teska, 1989) and inter- and intraspecific communication (e.g. Jaeger & Gergits, 1979; Jacobs & Taylor, 1992). In all species studied so far, work has focused on adults.

This study proposes that the ability to detect cues left by conspecifics is present in the great crested newt at least as early as metamorphosis. Furthermore, it is possible that the cues, probably olfactory, can be used as an orientation mechanism by metamorphs on their first emigration for 'tracking' the paths of adults to suitable terrestrial sites. This is very likely an important mechanism in the young newts for finding suitable terrestrial habitat. Olfactory mechanisms do not require previous knowledge of both start and end point, but would simply enable the metamorphs to follow the paths of adult newts to suitable habitat for the first time. Once this first migration has occurred and they have obtained a 'reference point' for both the aquatic and terrestrial sites, they may then be able to expand the range of mechanisms used to move between the sites. Other mechanisms of orientation, such as magnetic navigation and celestial orientation have been documented in amphibians. This study does not discount these possibilities in great crested newt metamorphs; indeed, it is unlikely that one single orientation mechanism is responsible for the whole process of migration.

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THE TERRESTRIAL SUMMER HABITAT OF RADIO-TRACKED GREAT CRESTED NEWTS (*TRITURUS CRISTATUS*) AND MARBLED NEWTS (*T. MARMORATUS*)

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Thirty great crested newts (*Triturus cristatus*) and 25 marbled newts (*T. marmoratus*) were radio tracked for up to 31 days after leaving breeding ponds in western France. Around the pond where most newts were radio-tracked, 95% of all summer refuges fell within a radius from the pond of 63.0 m for *T. cristatus* and 59.5 m for *T. marmoratus*. The most frequently used habitats were directly adjacent to the pond shoreline. For the other two ponds, all summer refuges fell within radii of between 26.2 m and 32.3 m from the ponds respectively. No significant differences among species or ponds were observed in the mean distance that newts moved away from the breeding site. Five radio-tracked *T. cristatus* and two radio-tracked *T. marmoratus* that were moved back into their ponds migrated during the following night in almost identical directions to their initial emigrations, but did not return to the original refuges. In eight cases, several (up to ten) untracked newts were found in the refuges of radio-tracked individuals.

Key words: radio-tracking, terrestrial summer habitat, site fidelity, *Triturus cristatus*, *T. marmoratus*

INTRODUCTION

European newts (genus *Triturus*) exhibit the biphasic life history pattern typical of amphibians and require both aquatic and terrestrial habitats (Griffiths, 1996). In Britain, there is currently a special concern about the conservation status of the great crested newt *Triturus cristatus* (Gent & Bray, 1994; Beebee, 1997), which has become an important "umbrella species" whose protection serves to conserve a multitude of lesser-known, coexisting taxa. Nevertheless, protection measures for *T. cristatus* sites often concentrate on their breeding ponds only; this is mainly because empirical data on their terrestrial ecology and behaviour are scarce, owing to the difficulty of locating newts on land.

Lower fitness parameters for amphibians living in fragmented landscapes corroborate the prediction of the metapopulation concept that isolated populations are exposed to an increased risk of extinction (Hanski & Gilpin, 1997; Hitchings & Beebee, 1997; 1998), and demonstrate that studies on movement patterns are of vital importance for conservation issues. The recent application of radio-tracking to adult *T. cristatus* and *T. marmoratus* enabled Jehle & Arntzen (2000) to follow the movements of these newts over a period of approximately one month after leaving a shared breeding site in western France. In this paper, I extend the study and incorporate data from a second year and two additional ponds. The distance that radio-tracked adult *T. cristatus* and *T. marmoratus* move away from their ponds serves to determine a terrestrial zone around breeding sites which is used for summer refuges. Additionally, this

paper reports translocation experiments which tested the hypothesis that *T. cristatus* and *T. marmoratus* return to particular terrestrial shelters.

MATERIALS AND METHODS

The three study ponds are located in the Département de Mayenne, Western France. Pond 1 (approx. 50 m² area, at the edge of pastures with hedge-rows) and Pond 2 (approx. 20 m² area, an abandoned sand quarry) lie near the village of Jublains; Pond 3 (approx. 150 m² area) lies in a pasture near the village of Marcillé-la-Ville. In 1997 a radio-tracking study was conducted at Pond 1 only, focusing on a comparison of migration and habitat utilization patterns between adult *T. cristatus* and *T. marmoratus* (Jehle & Arntzen, 2000). In the present paper some data from 1997 are reanalysed alongside data collected in 1998 at all three ponds. At Pond 3 only *T. cristatus* were radio-tracked, despite the presence of a small population of *T. marmoratus*.

The radio-tracking was conducted between June 21 and July 30, 1997 and between July 1 and August 3, 1998. For a description of the radio-tracking procedure in 1997, see Jehle & Arntzen (2000). In 1998 newts were captured in the ponds between June 30 and July 2 with dip nets and kept in semi-terrestrial enclosures made from 220-litre metal barrels, cut lengthwise and covered with netting to prevent escape. Water in the enclosures was taken from the ponds where the newts were captured. Newts that had moved out of the water were assumed to have started their terrestrial phase, and were equipped with a transmitter and released at approximately 2100 hrs in the pond of their capture. In 1998, Holohil Systems transmitters BD-2A (mass: 0.69 g - 0.78 g; battery life: 25-35 days) were used exclusively, with the external antenna twisted around the

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TABLE 1. Summary of movement data of the radio-tracked adult newts at the three study sites. *T. c.*: crested newt (*Triturus cristatus*), *T. m.*: marbled newt (*Triturus marmoratus*).

	Pond 1		Pond 2		Pond 3
	<i>T. c.</i>	<i>T. m.</i>	<i>T. c.</i>	<i>T. m.</i>	<i>T. c.</i>
No. newts released	15	19	5	6	10
No. observed localisations	45	53	8	6	16
Tracking duration (days):					
minimum	3	3	4	4	5
maximum	28	31	13	6	10
median	16	15	5	6	8
Distance to pond (m):					
minimum	1.4	1.8	2.1	1.8	13
maximum	95.7	146.0	26.2	30.0	32.3
median	9.3	12.2	14.8	13.7	15.9

transmitter and fixed with "super glue". Prior to transmitter implantation, the newts were anaesthetised with MS 222 (Sandoz), until the muscular system was relaxed and the animals stopped moving (10-20 mins). The body cavity was opened at the ventro-lateral side for 8-10 mm with a scalpel, and the transmitter was inserted using forceps. The wound was closed with four sutures using an iris cutting needle (a C-shaped needle

7 mm long) and surgical silk supplied for human medicine. Bleeding rarely occurred, and no other complications were observed during the implantation procedure. All animals recovered from anaesthesia after approximately 30 mins with no apparent ill effects. At the end of the tracking period, newts had their transmitters removed and were then released in the pond, as recovering the newts would have damaged the

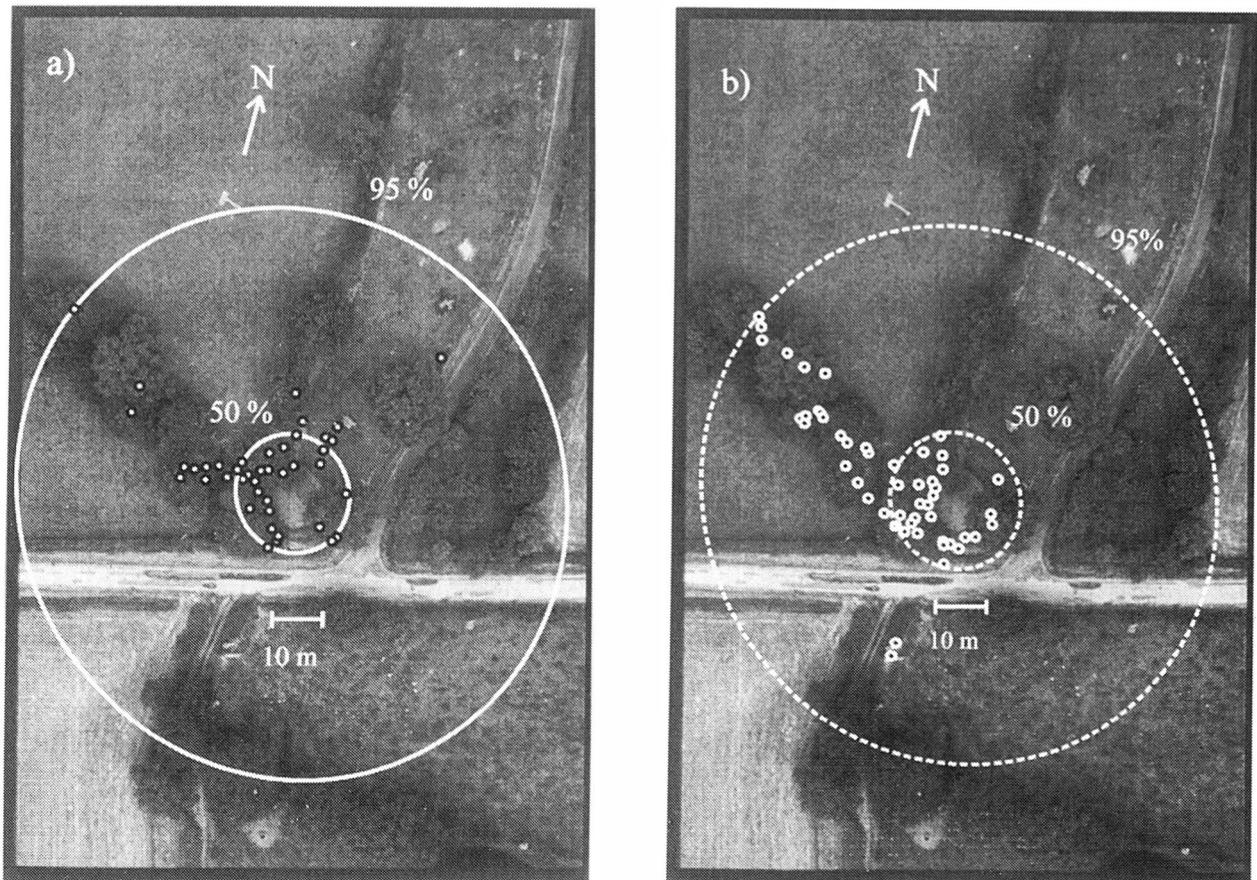


FIG. 1. Aerial photographs of Pond 1 and its surrounding area. The circles around the pond (corrected using ground reference points as the picture is not taken exactly above the pond) encompass the areas where 50% and 95% of the radio-tracked newts were observed. (a) *Triturus cristatus*, two localisations are outside the image; (b) *T. marmoratus*, three localisations are outside the image.

microhabitat in which they were found. Some transmitters were re-used.

The 1997 season showed that the vast majority of migratory activity took place during the first night after the newts were released (Jehle & Arntzen, 2000). The distance travelled from the pond edge after three days was not significantly different from that at the end of the tracking period, when the transmitter battery was due to expire (paired *t*-test with log-transformed data: $P > 0.05$). The collection of data in 1998 was therefore restricted to one record per day over a period of up to 13 days, in some cases including a translocation of the newt back to the pond. Localisations of newts are defined as refuges where they were resident for at least 24 hrs, and were marked with a numbered flag. For animals that were recovered dead, and for transmitters found without the animal, data were included up to the last recorded movement. Distance measures were taken to the nearest edge of the pond and to spatial reference points selected on the basis of good visibility and spacing (White & Garrott, 1990). Localisations were plotted on aerial photographs. For Pond 1, circles around the pond were drawn on the photograph to plot the area where 50% and 95% of all summer refuges were observed, as refuges were not expected to be evenly distributed in space. In line with the smaller sample sizes, only circles circumscribing 100% of refuges were plotted around Ponds 2 and 3. Ponds 1 and 2 were considered to be approximately circular and the circles were centred on the middle of the pond. For Pond 3 the circles were centred on the point of release of the newts. Because the aerial photographs were not taken exactly above each pond, the circles were corrected using the reference points and plotted as ellipses. Distances of refuges from the pond centre (Ponds 1 and 2) or point of release (Pond 3) were compared between ponds and between species (simple factorial ANOVA with all ponds) and between sexes within species (*t*-tests for Pond 1) using log-transformed data.

Translocation experiments were conducted with two *T. cristatus* and two *T. marmoratus* at Pond 2 and three *T. cristatus* at Pond 3. Newts that had already been radio-tracked to their terrestrial refuges were recovered during daytime and released back into their ponds at 2100 hrs on the same day. Their migrations were subsequently followed without changing the data collection procedure. The relationship between the direction (in azimuth) of initial emigration from the pond and emigration direction after translocation was determined using linear regression (after Batschelet, 1981). Owing to the limited sample size, data from both species were combined.

RESULTS

In 1997, 30 newts were radio-tracked at Pond 1. In 1998, four, eleven, and ten newts were radio-tracked at Ponds 1, 2, and 3, respectively (Table 1). Thirty-three (60%) newts were recovered alive; for seven newts

(13%) the transmitter was found without the study individual, six transmitters (11%) were detected but could not be recovered as they were inaccessible, three newts (6%) were found dead, three newts (6%) were eaten by snakes, and in three cases (6%) the signal was lost. All individuals but one left the pond on the night of release and moved between 2 m and 146 m away from the pond. Newts were tracked for periods ranging from three days to 31 days. Owing to a longer median tracking period in 1997, the number of localisations per individual was higher at Pond 1 than at Ponds 2 and 3 (Table 1).

Sixty-nine localisations of *T. cristatus* and 59 localisations of *T. marmoratus* were analysed (Table 1). The distance of the localisations from the pond/point of release did not vary significantly between *T. cristatus* and *T. marmoratus* ($F = 0.04$, $P > 0.05$), or between ponds ($F = 2.05$, $P > 0.05$). At Pond 1, no significant differences between the sexes were detected within species (*T. cristatus*: $t = 0.93$, *T. marmoratus*: $t = 1.73$, $P > 0.05$ in both cases). At Pond 1, the circles encompassing 50% of all *T. cristatus* and *T. marmoratus*

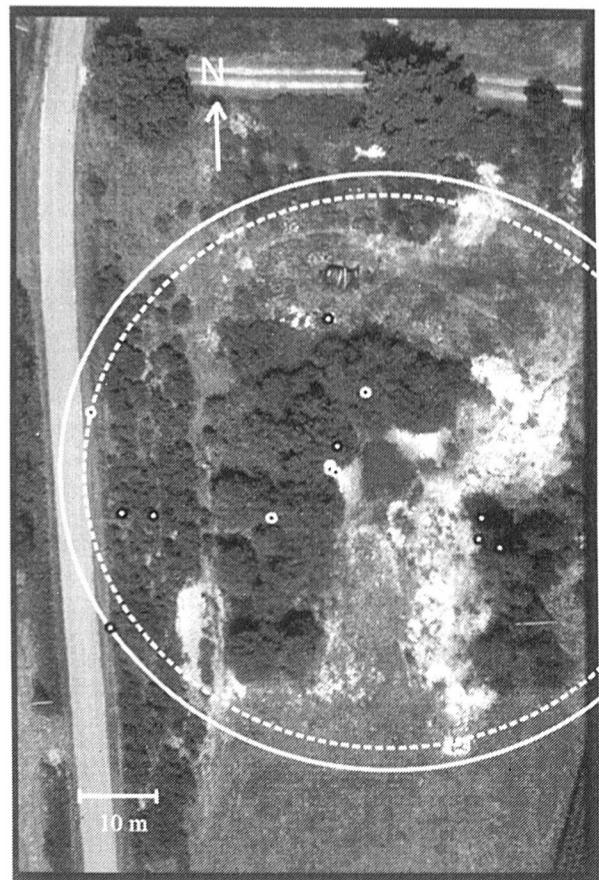


FIG. 2. Aerial photograph of Pond 2 and its surrounding area. The circles around the pond (corrected using ground reference points as the picture is not taken exactly above the pond) encompass the areas where 100% of the radio-tracked newts were observed. Solid line: *Triturus cristatus*; broken line: *T. marmoratus*.

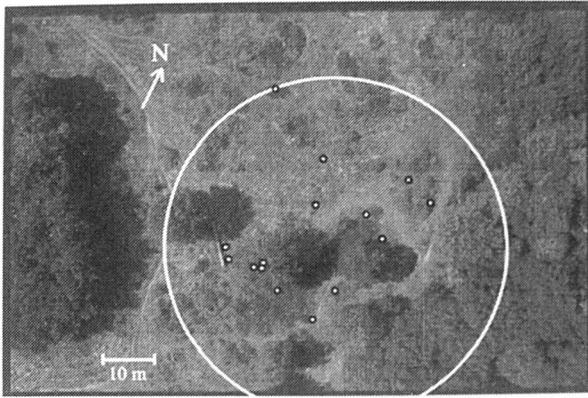


FIG. 3. Aerial photograph of Pond 3 and its surrounding area. The circle around the pond (corrected using ground reference points as the picture is not taken exactly above the pond) encompass the areas where 100% of the radio-tracked *Triturus cristatus* were observed.

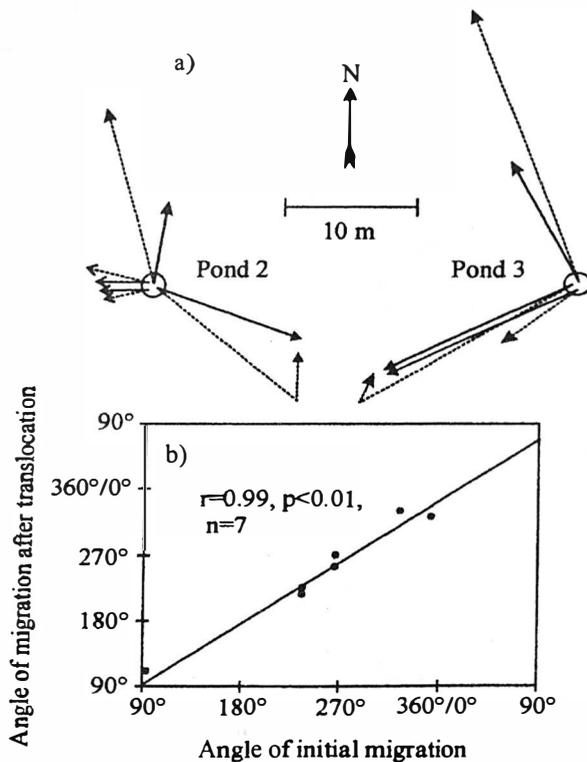


FIG. 4. Translocation experiments of radio-tracked newts. (a) Migrations of five *Triturus cristatus* (filled arrowhead) and two *T. marmoratus* (open arrowhead) which were released in Ponds 2 and 3, recovered, and put back into the ponds. Arrows with the same origin represent one individual. Solid line: initial emigration from the pond; broken line: emigration after translocation back into the pond. (b) Relationship between the initial direction of migration and the direction of migration after re-release in the ponds.

localisations had radii of 12.2 m and 14.8 m, respectively; the circles encompassing 95% of localisations had radii of 63.0 m (*T. cristatus*) and 59.5 m (*T. marmoratus*) (Fig. 1). The circles encompassing all localisations around Pond 2 had radii of 30.0 m (*T. cristatus*) and 26.2 m (*T. marmoratus*, Fig. 2). At Pond 3 a circle of radius 32.3 m encompassed all localisations of *T. cristatus* (Fig. 3).

Twenty-three untracked newts were found sharing the refuges of eight radio-tracked newts, with up to ten newts in one refuge. The five *T. cristatus* and the two *T. marmoratus* that were translocated back to their respective ponds left the pond on the day of translocation. They did not migrate to the refuge in which they were recovered the day before (Fig. 4a), but showed a significant tendency to depart in the same direction as before (Fig. 4b). Two *T. cristatus* spent four and seven days, respectively, in a transient refuge before moving closer to their initial site of recapture (Fig. 4a).

DISCUSSION

The radio-tracking methodology is a direct monitoring technique which is suitable for collecting data on the secretive terrestrial life of adult newts. The observed losses were within the range of other telemetric studies on urodeles (Madison, 1997; Madison & Farrand, 1998), and the frequent observations of radio-tracked newts sharing refuges with untracked newts is in line with the assumption that the migration behaviour of radio-tracked individuals was not abnormal. The time when the study individuals moved to the terrestrial part of their enclosures, prior to being implanted with transmitters, coincided with a decreasing number of newts in the ponds; this supports the view that the study animals were ready to leave the water. Nevertheless, the procedures of implanting and removing a transmitter are invasive and their full consequences are unknown; for example, no data are available on possible adverse consequences for the newts after the study period. One of the major limitations of radio-tracking newts is the short lifetime of transmitters, precluding the collection of data over entire seasons. The transmitters' mass was between 7.0% and 14.3% (median: 8.7%) of the newts' body mass, and more powerful batteries would raise the transmitter mass:body mass ratio to an unacceptable level. Future tracking studies, also with regards to juveniles, may be possible using remotely detectable tags without internal energy sources (Lovei, Stringer, Devine & Cartellieri, 1997).

Spatial movement patterns were very similar between breeding sites. During the period of study, 50% of all newts moved only a few metres away from the shore of Pond 1, which suggests that the most important area was directly adjacent to the breeding site. As only a few individuals performed the large-distance movements, the smaller apparent summer habitat range in Ponds 2 and 3 might be a consequence of the smaller sample size. For the purpose of defining a protected area of terrestrial habitat around a breeding site, a simple prescribed radius might not be satisfactory as a general guideline, as newts are likely to prefer certain directions and habitat types. However, quantifying habitat use is time-consuming, and radio-tracking data as well as drift fence studies have shown that, although movements are non-random in orientation, narrow migration corridors do not necessarily exist (Jehle,

Pauli-Thonke, Tamnig & Hödl, 1997; Dodd & Cade, 1998).

The radius encompassing 95% of all *T. cristatus* and *T. marmoratus* refuges in this study was considerably smaller than the 164.3 m buffer zone estimated for North American ambystomatid salamanders on the basis of 95% of recaptures (Semlitsch, 1998). Two factors might account for this difference. First, *T. cristatus* and *T. marmoratus* have an aquatic phase which lasts approximately 5 and 3 months, respectively (Bouton, 1986; Griffiths & Mylotte, 1987), whereas ambystomatids are more terrestrial, spending 86-99% of the year on land (Semlitsch, 1998). Second, ambystomatids exhibit bimodal migratory activity with peaks in April/May and October/November, and when radio-tracked over the entire year move up to 286.5 m away from their ponds (Madison, 1997; Madison & Farrand, 1998). Drift-fence studies on *T. cristatus* also suggested an increase of migration activity in autumn (Verrell & Halliday, 1985), and mark-recapture data showed that within about one year single *T. cristatus* can migrate over much larger distances than those observed in this study (Kupfer, 1998). With the present limitation of battery life, the task of collecting radio-tracking data of large-bodied newts after summer would require that animals be caught and tagged during their terrestrial phase. The data from the present study are not sufficient for the designation of a general terrestrial buffer zone encompassing the space required over all life stages (cf. Semlitsch, 1998).

Owing to successional processes and the relatively small size of typical amphibian ponds, many such ponds are short-lived on an ecological timescale. The colonisation of newly-formed breeding sites, in combination with abandonment of sites that become unsuitable, is a major component of amphibian population dynamics. The importance of hedgerows as corridors in the "bocage" landscape typical of western France is well documented (for example carabid beetles: Burel, 1989), and, being among the preferred habitat types (Jehle & Arntzen, 2000), it is very likely that they also serve as main corridors for dispersal of large-bodied newts. However, a study on *T. cristatus* in England revealed a preference for deciduous woodlands (Latham, Oldham, Stevenson, Duff, Franklin & Head, 1996), whereas in Mayenne a local expansion of the species' distribution was associated with the removal of shrubs and small woodlands (Arntzen & Wallis, 1991); this suggests that habitat preferences may vary across the species' range. The multiple functions and the varying quality of different types of hedgerow as lifelines between populations of mammals has been demonstrated (Bennett, Henein & Merriam, 1994), but the role of hedgerow quality for connecting newt breeding sites is not yet quantified.

That European newts return to their breeding ponds after being translocated has been documented before (Joly & Miaud, 1993), but according to the best of my knowledge this is the first study to show that they also

return to particular areas on land. Translocated newts moved away from their ponds in very similar directions to those of their initial emigration. Although none of the newts used exactly the same refuge again, that might have been due in part to disturbance associated with recovering the newt prior to translocation. Separate observations have indicated that when newts were translocated to different terrestrial habitats they subsequently moved only short distances (<5 m) and in no particular direction (unpublished data). Apparently, they were disorientated when translocated to an unknown site, as observed by Madison & Farrand (1998) with translocated, radio-tracked *Ambystoma tigrinum*. The question of whether newts become disorientated through massive alterations of the terrestrial area around established breeding ponds, for example due to urban development, is still open.

Personal observation suggested that ample refuges were available to the newts in my study area; this implies a social behavioural mechanism behind the frequent detection of several newts sharing a refuge. The basis of such behaviour in *T. cristatus* has been addressed by Hayward *et al.* (2000), but its implications have not been investigated in the context of alteration of habitat or translocation of animals to make way for roads or other developments.

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EVALUATING THE SUITABILITY OF HABITAT FOR THE GREAT CRESTED NEWT (*TRITURUS CRISTATUS*)

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A modification of the Habitat Evaluation Procedure (USFWS, 1976) applied to crested newt habitats is described, using ten key habitat criteria, based upon the assumption that habitat quality determines population size. Seven of these criteria (pond area, permanence, shading and density, macrophyte density, number of waterfowl and terrestrial habitat quality) are assessed using objective habitat measurements, the other three (site geography, water quality and fish occurrence) using qualitative rule-bases, to produce a Habitat Suitability Index for each site. Preliminary validation of the method for a set of 72 sites provides a significant rank correlation between indices of population size and of habitat. The procedure has the potential to provide a simple method of habitat assessment, for site surveying or selection of host sites for translocation, and can be upgraded easily as knowledge of crested newt habitat requirements improves. There was an incidental indication from the validation exercise that the number of newts caught by bottle trapping was affected negatively by the presence of macrophytes.

Key words: *Triturus cristatus*, crested newt, habitat suitability index, habitat evaluation, translocation, monitoring

INTRODUCTION

Crested newts as individuals and as populations depend upon habitats with a certain range of characteristics. The quality and quantity of these characteristics in part determines the presence and size of the populations. If we can measure the appropriate characteristics of a site, with the important proviso that there is a source of colonizers, then the occurrence of a population can be predicted. Our knowledge of habitat requirements in most species is adequate to make only crude predictions. Nevertheless, species occurrence and population size both depend upon habitat quality and there is a clear practical need to make predictions for conservation management, especially for rare or threatened species such as the crested newt.

Several efforts have been made to identify the determinants of distribution in amphibians. Pavignano *et al.* (1990) used multivariate analysis and, from a sample of 61 ponds, demonstrated the influences of macrophytes, pond age, terrestrial habitat characteristics and human interference on the presence of two anurans and two *Triturus* species (not *T. cristatus*). They were unable to relate habitat features to population densities. Beebee (1985) used discriminant analysis involving five British species and 203 ponds (17 with crested newts). He was able to separate ponds into two groups, those used and those not used for breeding, on the basis of the habitat characteristics. For the crested newt, geological features and terrestrial habitat were of greatest value in discriminating between sites. Swan & Oldham (1993, 1994) applied discriminant analysis to data from the breeding sites of two anuran species and *Triturus cristatus* with a sample of 1503 sites (1322 for the newts) and a wide range of habitat characteristics. For

the crested newt, relatively deep water, high macrophyte density and terrestrial habitat diversity were indicated as especially important. In Spain, in an analysis of 24 environmental variables, the populations of two toad species, *Bufo bufo* and *B. calamita* have been shown to vary in relation to the predictability of the climate (Romero & Real, 1996).

The approach used in the present paper is to identify readily observable habitat features and to assess to what extent they can be used to make worthwhile predictions. The objective is to produce a simple model for use by the non-specialist, which provides conservationists with an informed view of the value of a site and which can be upgraded readily as our knowledge of crested newt ecology improves.

HABITAT SUITABILITY

A large number of habitat features is associated with the crested newt. However, as described by Oldham (1994) and Swan & Oldham (1994), some features can be isolated as of particular diagnostic importance and used as a basis for determining the likelihood of crested newt occurrence. These are not necessarily the most obviously important ecological features. For example, food is clearly vital to newt survival; other factors being equal, the more food there is the more newts can be supported. Food can be assessed, but not easily. However, from experience we know that abundant newt prey occurs under conditions characterized by easily observed habitat features, such as the diversity and density of vegetation. Taking each of the presumed habitat requirements in turn in this way it is possible to produce a list of key diagnostic features for newt habitat. The same features are probably important as indicators of the level of population success at a site, reflected in population size, as distinct from mere species occurrence.

Key habitat variables were used during the construction of three separate computer-based expert systems at De Montfort University (Jeffcote, 1991; Cain, 1993), designed to predict the suitability of habitat for crested newt occurrence. These were subject to intensive evaluation. As judged against 100 known field sites, in blind comparisons the most developed of the systems (Cain, 1993) provided reasonable correlations. Newts were absent from only 3% of cases where the expert system predicted that they would be present. The error was larger for predictions of newt absence. Twenty percent of sites contained newts when the expert system predicted that they would not do so, possibly due to the longevity of the species. Individuals may persist at a site long after it has ceased to be suitable for breeding, for at least four years at one English site (Atkins, 1998) and perhaps for 16 years or more (Hagstrom, 1977, 1980).

Once installed on a computer, expert systems are easily used and they have the benefit of providing the user with the reasoning underpinning the determinations. On the other hand, they are based upon complex, costly, and ever-changing technology, so that they cannot easily be upgraded or amended by the non-expert. They are not readily available to many of the voluntary groups who may want to take advantage of them.

An alternative approach with a similar conceptual basis, more amenable to general use is the Habitat Evaluation Procedure (HEP; US Fish & Wildlife Service 1976, 1980, 1981), developed in response to the need to document the non-monetary value of wildlife resources. The original publications are not easily available, but the procedure is summarized by several authors (e.g. Usher, 1986, Spellerberg, 1992, Treweek, 1999). It is based upon a method devised by Daniel & Lammaire (1974) and assumes, for any given species, that habitat quality and quantity can be described numerically. HEP involves the determination of a Habitat Suitability Index (HSI) for each relevant species.

The HSI is a numerical index ranging from 0, representing unsuitable habitat, to 1.0, representing optimal habitat. It is assumed that there is a direct correlation, usually a linear relationship, between the index and the species carrying capacity of the habitat. Although the index is numerical, the model used to derive it, as with expert systems, may be expressed numerically or by verbal description (a qualitative rule-base or word model, Starfield & Bleloch, 1983). HSI's have been applied successfully to a wide range of species (e.g. mammals: Cook & Irwin, 1985; Thomasma *et al.*, 1991; birds: Conway & Martin, 1993; Prosser & Brooks, 1998; fishes: Pajak & Neves 1987; marine invertebrates: Soniat & Brody 1988) including at least four species of urodele amphibians (Sousa, 1985; Storm *et al.*, 1993). In the following account a method of deriving an HSI for the crested newt is proposed, based upon 10 key habitat variables.

KEY DIAGNOSTIC HABITAT VARIABLES

The 10 key variables are selected on the basis of two criteria: established or presumed importance to crested newt survival, and ease of field determination. Seven of them – pond area, pond permanence, pond shading, number of waterfowl, pond density, proportion of “newt friendly” habitat and macrophyte content – are expressed quantitatively; the other three – geographic location, water quality and occurrence of fish – are expressed qualitatively. The effect on crested newts of each variable is considered separately. For example, the presence of waterfowl at a newt breeding site has a damaging effect on newt populations, for reasons discussed below. The effect is probably negligible at low bird densities, but increases in proportion to the number of birds present. The effect is expressed as a Suitability Index (SI), on a scale from 1 (optimal suitability to the newts) to 0 (totally unsuitable), and plotted against bird densities (Fig. 1, SI₆). The procedure is repeated for the seven key habitat variables that are expressed quantitatively. The other three are related to the SI using a word rule base. The ten Suitability Indices are combined using a geometric mean, to derive the HSI.

The pattern of the relationship between waterfowl densities and habitat suitability, and the other patterns shown in Fig. 1, are essentially conjectural, based upon our long-term field experience, and informed by a number of sources, especially the results of National Crested Newt Survey and the National Amphibian Survey (Oldham & Nicholson, 1986; Swan & Oldham, 1993, respectively). These provide data on the aquatic and associated terrestrial characteristics of over 3000 potential crested newt breeding sites and are augmented by information in the literature (Beebee, 1981, 1983, 1985; Dolmen, 1980; Green, 1984; Strijbosch, 1979). In the account that follows the rationale for including each key variable is described. The actual assessment is detailed in Appendix 1 and Fig. 1.

1. GEOGRAPHIC LOCATION (SUITABILITY INDEX 1, SI₁; APPENDIX 1).

Fig. 2 is based upon existing maps of newt distribution (Arnold, 1995). This provides a shorthand method of accommodating all the large-scale habitat features which affect the newt, including climate, substrate and altitude. There are no sharp boundaries, however, between geographic regions of suitability, and this feature does not provide a linear relationship between suitability and location.

With this Suitability Index, as with some others, the lowest value is set at 0.01 rather than zero. A zero score for any one of the ten suitability indices would produce a Habitat Suitability Index for the site of zero. The very low SI value of 0.01 avoids this and in this instance reflects the possibility that unusual circumstances may favour the occurrence of a newt population, despite an apparently unfavourable geographic location – for ex-

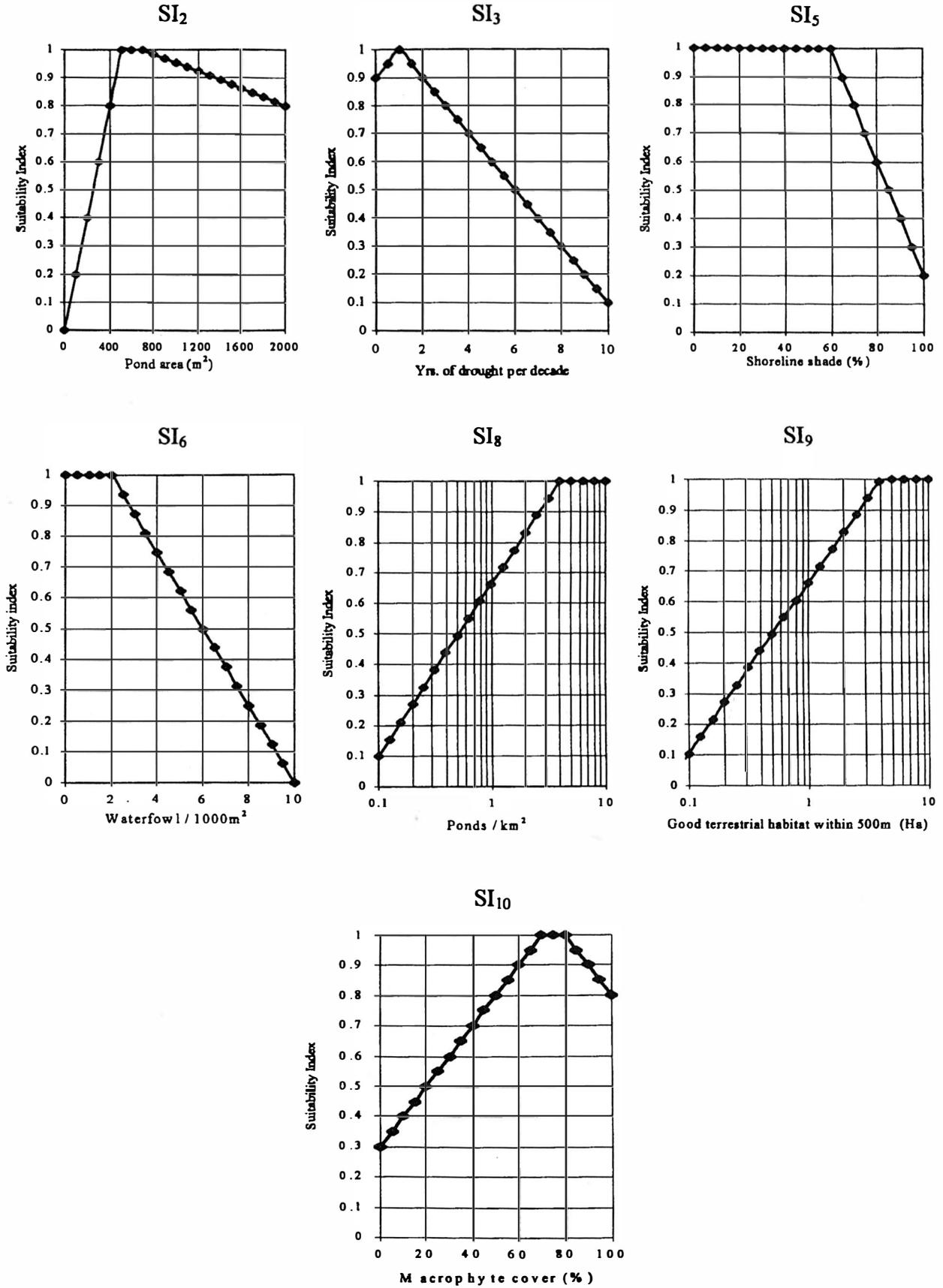


FIG 1. Suitability index derivation based upon seven separate habitat features.

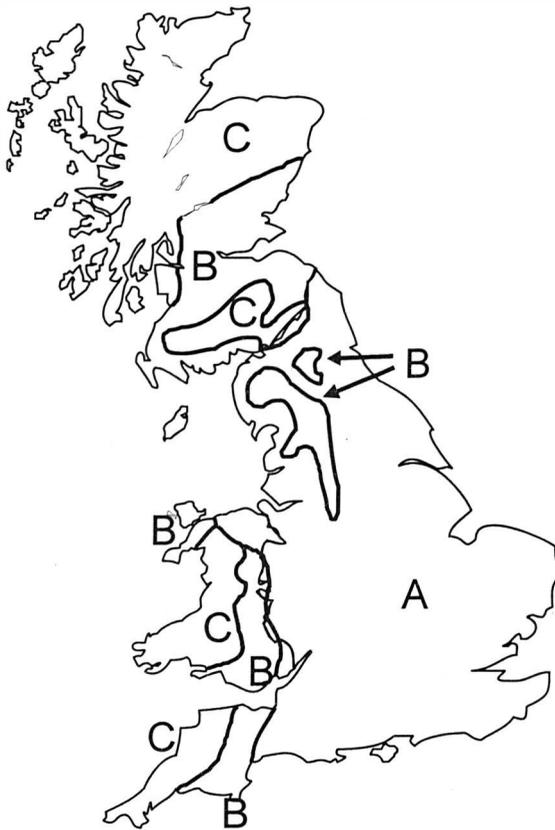


FIG. 2. Map used to determine the Suitability Index for location (SI_1), based upon the known distribution of the crested newt. Zone A (optimal) has a high probability of crested newt occurrence within each 10 km square; zone B (marginal) with patchy distribution and a low probability of occurrence; zone C (unsuitable) with a very low probability of occurrence, mainly outside the recorded range of the species.

ample, through human intervention. Again, since the distribution map is based upon observer records, there is a possibility that the species is marked as absent through observer error rather than species absence.

2. POND AREA (SI_2 : APPENDIX 1 AND FIG. 1)

Pond area is a determinant of the magnitude of biological productivity of the pond ecosystem upon which the newt population depends. In the Netherlands, Laan & Verboom (1990) demonstrated a positive relationship between species richness and pond size for ponds more than seven years old. In the National Amphibian Survey (Swan & Oldham, 1993) pond areas were categorized into 11 bands. The median area of 2987 surveyed ponds (1322, excluding garden ponds) was 175 m² (375 m² for non-garden ponds). The optimum size for crested newt occupancy in both cases was in a band between 500 and 750 m². Fig. 1 (SI_2) is constructed with this band as optimum (Suitability Index = 1), falling away for ponds with larger areas in line with the values seen in the National Survey. Ponds of zero area are clearly unsuitable for newts and SI values between 0 and 1.0 are interpolated linearly in Fig. 1. It must be admitted that very small ponds (<26 m²) sometimes contained newts and it might be argued that the

interpolation would be better on a transformed scale, such as logarithmic. However, we are attempting to reflect newt success, indicated by population size, rather than simple occurrence and it is unlikely that the smaller ponds support viable breeding populations. In fact, use of a logarithmic – rather than a linear – scale made virtually no difference to the performance of the model.

Theoretically, pond depth is less significant than area since productivity depends more upon the surface area receiving sunlight than upon water volume. Depth is also more difficult to measure than area and has been omitted as a key factor.

3. POND PERMANENCE (SI_3 : APPENDIX 1 AND FIG. 1)

Pond permanence is essential to permit the completion of metamorphosis in any given year. A succession of years in which the pond dries before metamorphosis is complete will lead to population extinction, in the absence of immigration. However, intermittent drying out may have an overall beneficial effect, preventing colonization by fish and other aquatic predators that are even more dependent upon permanent water than the newt. There is little quantitative information on the relative performance of ponds showing differing degrees of permanence. The National Amphibian Survey (Swan & Oldham, 1993) indicated that ponds that dried during drought years contained crested newts significantly more often than those which never dried and those which dried annually. The optimal frequency of drying is assumed to be one year per decade. Regression lines above and below this value are speculative. The value of SI_3 of 1.0, instead of zero, for 10 years of drying out is used to allow for the possibility of metamorphosis in some years before drying occurs.

4. WATER QUALITY (SI_4 : APPENDIX 1)

The adult crested newt is capable of using atmospheric oxygen – indeed, its respiration depends upon it – and is relatively tolerant of eutrophic conditions. The gill-breathing larva is more vulnerable and shares the need for reasonably well-aerated water with a number of aquatic invertebrates. Water quality can be measured precisely using chemical analysis, but this depends upon relatively sophisticated equipment, especially if temporal variation is included. Instead, the presence of indicator organisms can be used to assess water suitability, in much the same way as they are used to assess running water (e.g. Abel, 1996; Boon & Howell, 1997). They have the advantage over chemical methods of integrating temporal variability without repeated measurements. A qualitative rule base is used to derive SI_4 , using a four-point scale (Appendix 1). This is based upon the experience gained during development of an expert system (Cain, 1993; Jeffcote, 1991). The lowest SI value is set at 0.01, rather than zero, to guard against the possibility of mistaken identification of water quality and of changes in quality which can occur rapidly, with changing weather.

5. POND SHADING (SI₃; APPENDIX I AND FIG. 1)

Shade counteracts the growth of macrophytes and the benefits they provide. Additionally, excessive tree cover may increase the organic content through leaf fall and cause eutrophication. However, if not excessive, leaf fall may increase the nutrient level and enhance productivity. The National Amphibian Survey (Swan & Oldham, 1993) provided no evidence that a complete absence of shade reduces a pond's suitability for newts, but newt occurrence was significantly reduced above a threshold of 75% shade. The findings of Cooke *et al.* (1994), based upon crested newt larvae, suggest a somewhat lower threshold and a value of 60% is taken as the cut-off point (Fig. 1; SI₃). The low value of SI 0.2 in this figure is conjectural. A value of zero was thought to be inappropriate because in some cases central parts of the pond continue to receive sunlight even when the circumference is totally surrounded by trees. In Appendix 1 the emphasis is on the circumference, rather than the total area, because of the relatively greater importance of biological production in the shallow edges of ponds.

6. NO. OF WATERFOWL (SI₆; APPENDIX I AND FIG. 1)

Common waterfowl, such as moorhens and mallards, in naturally occurring numbers have little adverse effect upon newt populations. They are included in the list of factors because sometimes, when encouraged by supplementary feeding, they can seriously damage the habitat, partly by direct mechanical interference, but also by excessive nutrient enrichment, with resultant high BOD and reduced community diversity. The shape of the SI curve (Fig. 1, SI₆) is conjectural and is based upon a few instances with which the authors are familiar. Herpetofauna Conservation International (1991) quote a slightly lower threshold. They describe geese or duck densities of over 4 pairs per hectare of open water (approximately 1 bird per 1000 m²) as a negative indicator for crested newt translocation.

7. OCCURRENCE OF FISH (SI₇; APPENDIX I)

The effect of fish varies according to the species present and probably according to the pond habitat, although not in a manner that can be predicted readily. Some species, such as goldfish and carp, in some conditions, appear to be benign. Others, such as the stickleback, sometimes seem to have a serious impact – probably both predatory and competitive – and at other times to coexist with a healthy newt population. The larger predatory fish species such as perch and trout rarely coexist with crested newt populations. There are many records in the National Amphibian Survey (Swan & Oldham, 1993) of great crested newt populations surviving, probably in suppressed numbers, in the presence of fish. These may result from high adult newt longevity and immigration. The difficulty of assessing fish populations, coupled with uncertainty as to the impact of some species, makes this feature problematic. Nevertheless, the overall strength of the correlation ob-

served in the National Amphibian Survey and elsewhere means that it cannot be ignored. The qualitative rule base (Appendix 1, SI₇) reflects the above uncertainty.

8. POND DENSITY (SI₈; APPENDIX I AND FIG. 1)

In the National Amphibian Survey, Swan & Oldham (1993), using records of all ponds, not just those suitable for crested newts, suggested a minimum pond density threshold of about 0.7 ponds km⁻² for great crested newts to occur in an area. Only about 30% of study areas where pond densities were below this threshold supported the species, in comparison to 60% above it. Only at the much higher pond density of four ponds km⁻² did all the study areas contain crested newts. Grayson (1994) describes similar evidence. Pond densities above 4 km⁻² are therefore taken as optimal (Fig. 1, SI₈). At lower pond densities a logarithmic interpolation (in line with the original relationship in the National Amphibian Survey) provides more realistic SI values than a linear interpolation. The threshold density of 0.7 ponds km⁻² relates to an SI between 0.5 & 0.6.

The crested newt is generally accepted as exhibiting metapopulation dynamics (e.g. Griffiths & Williams, 2000) and population persistence depends, in part, upon the distance separating breeding sites (Halley *et al.*, 1996). If ponds are separated by more than the range of dispersal, or if there are barriers within the range (e.g. frogs: Reh & Seitz, 1990; toads: Hitchings and Beebee, 1998), genetic heterogeneity will diminish and colonization and recolonization will be inhibited, even if there is good terrestrial habitat. The situation may be complicated in ponds with especially large populations (e.g. Latham *et al.*, 1996). In this case metapopulation dynamics may be less significant and the population may be viable in the long-term, even if isolated (Halley *et al.* 1996). A low value of SI₈ at such isolated sites might result in unreasonably low HSI values. To allow for this possibility a correction is applied in the HSI calculation, as described below.

9. PROPORTION OF "NEWT FRIENDLY" HABITAT (SI₉; APPENDIX I AND FIG. 1)

The habitat occupied by crested newts is highly variable and we do not understand the species' detailed requirements at different phases of their life on land. However, we know from discriminant analysis based upon National Amphibian Survey data (Swan & Oldham, 1993, 1994) that newts occurred more frequently on land with low intensity use (crudely classified as scrub and woodland), than on pasture and arable and this is consistent with the findings of Arntzen *et al.* (in prep.) and Laan & Verboom (1990). Scrub, unimproved grassland, woodland (both deciduous and coniferous) and gardens are regarded as providing newt-friendly habitat, unlike improved pasture, arable and urban land. The greater the area of good habitat, the greater the confidence that the site was suitable.

Additionally, certain habitat features, notably hedges and ditches, enhance the suitability of a site. Swan & Oldham (1994) demonstrate that both these landscape features are significant positive determinants of crested newt occurrence in low diversity, – improved grassland and arable – habitats. Evidence of their value is also provided by Jehle (2000). They are probably important not only in enhancing habitat diversity and providing resources, but also in supplying stable refugia in a landscape subject to sudden, intermittent and massive change during normal agricultural practice. A hedge was considered good newt habitat when it was densely vegetated with good ground cover. Dry stone walls covered by dense, long vegetation from the ground upwards were also considered to be good habitat. Ditches were considered good habitat if they had good bank vegetation and imperceptibly moving water.

The presence of barriers to terrestrial dispersal of newts modifies the importance of newt-friendly habitat within range of the breeding site. Roads and rivers are perhaps the two most serious amongst the many man-made and natural barriers interfering with newt migration. Five hundred metres is selected as an appropriate distance for the ranging of crested newts on the basis of several studies (e.g. Baker & Halliday, 1999; Oldham & Humphries, 2000; Oldham & Nicholson, 1986). Arntzen & Wallis (1991) provide evidence of 1 km annual movement, but this is based upon range extension and probably applies mainly to juveniles which spend considerably longer on land between metamorphosis and adulthood than do the adults between one breeding season and the next. We used 4 ha as the lower critical limit of newt-friendly habitat within 500 m of the breeding site needed to sustain a thriving crested newt population (Oldham, unpublished). As in the previous section we consider that a logarithmic interpolation provides more realistic SI values when the areas of favourable habitat are low (Fig. 1, SI_q).

For each barrier a threshold of impact is needed, above which it has a serious effect on the likelihood of newt population occurrence. For example, at one extreme, motorways and dual carriageway roads in Britain almost certainly do seriously affect newt dispersal, whilst unpaved country lanes probably do not. In between, a judgement must be made in terms of the width of the carriageway and the density of night-time traffic. Anything less than about 20 vehicles per hour is probably not a serious threat. Rivers are less prevalent in the landscape, but there is evidence in two studies of their importance. In a regression analysis comparing the characteristics of 260 Leicestershire ponds, and their surroundings, with the occurrence of crested newts (Arntzen *et al.* in prep.) the proximity of the pond to a river proved to be the most important negative correlate. Similarly, discriminant analysis based upon the National Amphibian Survey data (Swan & Oldham, 1994) emphasized the importance of flowing water as a negative feature in the crested newt landscape. The prevalence of fish in water bodies in floodplains may

exacerbate the effect of the physical barrier. As with roads, a judgement must be reached on the likelihood of an impact; width is again important and rate of water flow replaces traffic volume as a key feature.

Barriers also influence metapopulation dynamics. Reh & Seitz (1990) and Hitchings & Beebee (1998) demonstrated reduced genetic heterogeneity in populations of *Rana temporaria* separated by roads, and in *Bufo bufo* by inimical habitat respectively. In the present state of our knowledge we have no way of incorporating this aspect into the habitat assessment.

Barriers: modification to "newt-friendly" habitat assessment. The impact of barriers is assessed in terms of the proportion of the available habitat within 500 m radius of the pond which is excluded from use, as a result of the barrier's presence. Subjective judgement is involved and a simple rule base is used as a guide to assessment (Appendix 1). The resulting values are used to modify the impact of SI_q , as described in Appendix 1.

10. MACROPHYTE CONTENT (SI_{10} : APPENDIX 1 AND FIG. 1)

Although not a direct food source for crested newts, macrophytes fulfil a number of roles. They provide a food source (direct or indirect) for prey organisms, cover from predators and a substrate for egg attachment. A paucity of plant life is normally associated with low pond productivity. Beyond a certain plant density, however, they restrict the space available for newt activity, including courtship, and a pond in a late stage of succession, especially when dominated by emergent vegetation, may provide limited aquatic space. Natural succession is the most commonly perceived threat to great crested newt populations (Oldham & Swan, 1991). Consequently, there is an optimum macrophyte content (Fig. 1, SI_{10}). National Amphibian Survey data (Swan & Oldham, 1993) showed the highest occurrence of great crested newts in ponds with emergent vegetation cover between 25 and 50% and submerged vegetation between 50 and 75%. For simplicity, in Fig. 1, the two are combined, giving an optimum of between 70% and 80% macrophyte cover. Although there was a clear optimum, in the National Survey newt occurrence was reported over the entire range of observed macrophyte-cover values. In Fig. 1 (SI_{10}), the SI values of 0.3 and 0.8 – chosen to represent, respectively, the upper and lower cover values – reflect the observed levels of occupancy in the National Survey.

Duckweed, especially *Lemna minor*, presents a special problem. It intercepts light, but occupies little space and can fluctuate markedly, both within and between seasons, and even within a day during strong winds. It is common knowledge that crested newts tolerate duckweed at breeding sites, and in the absence of information on its impact, we have elected to exclude it from the vegetation cover calculation in Appendix 1.

Whilst there are good reasons to believe the relationship shown in Fig. 1, SI_{10} , is a real one, it must be admitted that a direct relationship is likely between the

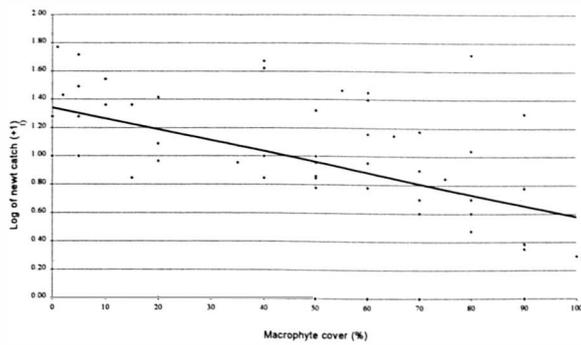


FIG. 3. The negative relationship between newts caught in bottle traps and the macrophyte cover (submerged, emergent and floating plants combined) in 53 ponds.

macrophyte biomass and the ability of the observer to detect newt presence. A population of newts in a plant-free pond is much more evident than the same population in a plant-dominated pond. This may have biased the results obtained in the National Amphibian Survey. Ponds with submerged vegetation cover values in excess of 75%, and emergent vegetation values in excess of 50%, might have contained newts more often than indicated by the survey. In the validation exercise described below, however, whilst there was a clear negative rank correlation between plant presence and newt catch in funnel traps ($r_s = -0.53$, $n=53$, $P<0.001$, Fig. 3), there was no such relationship between plants and newt count by torchlight ($r_s = 0.002$, $n=70$, $P>0.1$). This suggests that trapping by funnel traps is influenced by plant presence, whilst there is no evidence that this is the case for newt counts. The National Amphibian Survey data – based upon torchlight survey – may, after all, be meaningful. The solution to this problem lies in an independent method of population assessment, such as perimeter fencing, but these data are not available in sufficient quantity. In their absence, we have elected to provide the factor as an optional tenth Suitability Index, but to omit it from the validation exercise.

CALCULATION OF THE HABITAT SUITABILITY INDEX

The HSI for a site based upon a pond is determined as a geometric mean, the tenth root of the product of all the suitability indices, each relating to a key habitat variable, using the following equation¹:

$$HSI = (SI_1 * SI_2 * SI_3 * SI_4 * SI_5 * SI_6 * SI_7 * SI_8 * SI_9 * SI_{10})^{1/10}$$

where: HSI = Habitat Suitability Index; SI = Suitability indices (expressed as values between 0 and 1) in respect of each of the key habitat features, distinguished by subscripts as follows: 1, geographic location (evaluation of location relative to the map of national distribution, Fig. 2); 2, pond area (m²); 3, pond permanence (years of drying out per decade); 4, water quality

(via rule-base on extent of eutrophication); 5, shade (% of perimeter affected); 6, waterfowl (resident birds using the pond per 1000 m²); 7, fish (evaluation of impact using a rule-base); 8, pond density (pond density per km²); 9, terrestrial habitat (% “newt-friendly habitat” within 500 m); 10, macrophyte cover (% plant cover). Details of the derivation of each SI value appear in Appendix I.

Halley *et al.* (1996) suggest that large breeding populations of newts are much less prone to extinction than small ones and are less dependent on influx of animals from adjacent sites. In other words, populations living in very suitable habitats are likely to be less influenced by pond density than are those in relatively unsuitable sites. This was given expression by applying a correction to the HSI values such that pond density was incorporated into the calculation only if the preliminary HSI (calculated using all SIs except pond density) was less than 0.75.

The result of the above HSI calculation is a single number between 0 and 1. In our evaluations the lowest HSI obtained at a site known to support breeding crested newts was 0.43, the highest 0.96.

EVALUATION OF THE INDEX

The proof of the model is its ability to predict crested newt population status. Population status itself is difficult to define and a complete understanding would depend upon a knowledge of the proportions of each life stage as well as age structure and total numbers. However, if we accept adult population size as a measure of status, the model may be examined using a set of crested newt populations of known population size.

There are at least two difficulties in making such an examination. Firstly, crested newt populations exhibit well known annual fluctuations in population sizes and recruitment (e.g. Arntzen & Teunis, 1993, Cooke, 1994, 1995, 1997, Baker, 1999), meaning that either data from a large series of sites, or means from several years, are needed. Secondly, no easily applicable census method gives results which can be applied reliably and consistently to a set of sites with diverse habitat characteristics. Methods adopted by different workers include perimeter fencing (e.g. Arntzen *et al.*, 1995), trapping, dip netting and counting by torchlight (e.g. Cooke, 1995, Griffiths & Raper, 1994; Griffiths *et al.*, 1996), egg counts (e.g. Grayson, 1994), and mark, release and recapture (MRR) (e.g. Baker, 1999). Some of these – such as fencing and MRR – are too costly, in time, money and expertise, to be appropriate. Some are too disruptive of the habitat (e.g. netting). In some, such as egg counts, the relationship between the count and adult population size is not well understood. Furthermore, all the methods produce results which vary in relation to detailed habitat structure. For example, torchlight survey in a pond covered by duckweed, or bottle trapping in a pond with only 50% accessibility to observers, are both likely to produce unreasonably low counts.

¹ A Microsoft Excel spreadsheet is available (send senior author a blank 3 1/2" disk) to assist in the rapid calculation of HSI values based directly upon basic field measurements.

TABLE 1. Summary of data and Suitability Indices (SI) collected from 72 sites during validation of the Habitat Suitability Index (HSI). Details of the parameters are provided in Appendix 1.

Parameters	"Units"	Range of values recorded	Median value	Range of SI recorded	Median SI
Location	3 point scale (0.01, 0.5, 1.0) based upon map, Fig. 2	1-1	1	1	1.00
Area	m ²	1250-35	156	1-0.07	0.31
Permanence	Years of drought per decade	10-0	0	1-0.01	0.90
Water quality	Rule base on extent of eutrophication (4 point scale)	4-0	3	1-0.25	0.75
Shade	% of perimeter affected	100-0	35	1-0.20	1.00
Waterfowl	Resident pairs per 1000 m ² using the pond	5-0	1	1-0.60	1.00
Fish	Evaluation of impact using a rule-base (4 point scale)	4-0	0	1-0.01	1.00
Pond dispersion	Pond density per km ²	13-0	1	1-0.10	1.00
Terrestrial habitat	% "newt-friendly habitat" within 1 km ² sometimes modified by existence of barriers	75-0.3	4.9	1-0.01	0.70
Barriers	Significance of terrestrial barriers using a rule-base	1-0.25	0.75		
Macrophyte cover	% plants reaching water surface	100-0	57.5	1-0.31	0.71
HSI	Habitat suitability index	0.96-0.31	0.66		
Newt count	0-164	4			
Newt catch	0-58	8			

Our initial efforts to validate the model, reported below, suffer from both sets of problems. Site selection has involved a compromise. To enhance the reliability of the comparison we have included as many sites as possible, but excluded those sites for which appropriate readings could not be obtained (e.g. sites with very limited access). On the other hand, most of the sites were assessed for population status in only one season. Although this introduces limitations, the approach serves to illustrate the potential of the method, which can be enhanced as data accumulate.

Sites. The data derive from a set of 72 ponds (Table 1), mainly in Leicestershire and Gloucestershire. None of the sites was used in the original National Amphibian Survey upon which the model is based. The largest was a pond of 1250 m², the smallest 35 m². Four sites for which we have no evidence of crested newt presence were included. Both site habitat evaluations and population assessments were made during late spring and summer, between 1996 and 1999. The 34 Gloucestershire site determinations were all made in the same season (1999). At each site the habitat was assessed using the criteria listed in Appendix 1.

Population assessment. Population status at each pond was usually assessed by two methods, both conducted during the breeding season between the end of March and the beginning of June: counting at night by torchlight, and trapping in bottle traps. Torchlight surveys involved walking around the accessible perimeter of the pond after dusk, at a speed which depended on the conditions, but never more than 25 m per minute, and counting all the newts seen. Surveys were conducted only when there was negligible wind and rain and a temperature of at least 8°C.

Two-litre transparent bottles, set as described by Griffiths *et al.* (1996), were used for the bottle trap survey. Bottles were set, one to two hours before dusk, at 2 m intervals around the accessible shoreline of each pond at a depth of about 0.5 m. They were emptied between one and four hours after sunrise. The median number of inspections was two by torchlight and two by bottle trapping. The median interval between first and second surveys was approximately one month for both survey methods. Values of population size using both survey methods were corrected in proportion to the length of shore surveyed, to compensate for partly inaccessible sites.

Results. Population counts and catches were plotted against HSI for 66 and 55 sites, respectively. The respective Spearman rank correlation values were $r_s = 0.51$ and $r_s = 0.62$ ($P < 0.001$ in each case). The median count was four and the median catch eight, and there was a strong positive correlation between the two ($r_s = 0.63$, $P < 0.001$). For sites with both kinds of assessment, catch exceeded count in 47% of 49 cases, count exceeded catch in 37% and there was equality in the remaining 16%. At best, both methods reveal a fraction of the adult population. When the maximum value for each site, count or catch, is plotted against the HSI (Fig. 4) the correlation is correspondingly increased ($r_s = 0.73$, $n = 72$, $P < 0.001$).

In Fig. 4 there are a number of outliers, and an examination of them is instructive. The site labelled "A" in Fig. 4 was one of three crested newt sites remaining after the other two had been filled in. Previously the other two sites contained big populations and it seems likely that site "A" contained unusually high numbers through immigration. The group of 12 sites labelled

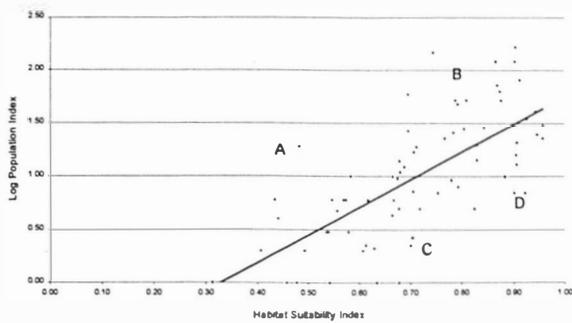


FIG. 4. Positive relationship between population index (maximum numbers of newts caught or counted on a single occasion) and Habitat Suitability Index in 72 ponds. A – D discussed in text.

“B” in Fig. 4 all contained more newts than expected on the basis of the HSI values. In each case the HSI values were the result of low individual SI scores, especially pond area, perhaps indicating that the negative impact of this feature was overstated in the formula. In one instance stone walls may have been undervalued as a habitat. The two sites labelled “C” were from a similar geographical location, in an area of poor terrestrial habitat, but with a number of ponds, and perhaps a thinly spread population. In both of the ponds labelled “D”, counting and catching were impeded in various ways. The sites with a zero score were all in areas close to crested newt populations. Hence the zero score is likely to reflect habitat conditions rather than an absence of immigration.

As discussed in Section 10 above, SI_{10} (macrophytes) was not included in the validation exercise. The addition of macrophytes altered the value of the above correlation value only marginally.

In an effort to establish whether any single index was predominantly responsible for the level of the correlation, each SI was tested in turn against the population indices. The model performed progressively better as the number of SI values was increased. The most useful indices in this sample were fish presence, water quality and terrestrial habitat; the least useful were waterfowl, macrophytes and shade. Although it is tempting to modify the index by enhancing the weight of the most useful parameters and reducing that of the least useful, this has been resisted, because the result may simply reflect the features of the relatively small sample of sites used in the validation exercise.

DISCUSSION

When an expert herpetologist assesses a series of sites for their suitability to support a crested newt population, he or she takes into account a range of features, weights their relative significance using knowledge of well studied sites and then integrates the information and comes to a judgement. As with an expert system, the method we have used attempts to formalize the knowledge possessed by an expert. However, the system cannot replace genuine expertise. A simple system of this nature does not cover all eventualities and pre-

dictions must be treated with caution, as indicated by the number of outliers in Fig. 4.

Use of the HSI is based upon the simple premise that the quality of the crested newt's habitat is reflected in the status of the population it supports. Whilst there are good reasons to believe that this is true, the practical step of relating the two parameters is beset by difficulties. The methods of habitat definition are crude, including, in several cases, the use of subjective criteria. The relationship between each Suitability Index and population status (Fig. 1 and Appendix 1), whilst based upon evidence, are essentially conjectural. Validation of the method depends upon the assessment of relative population size, which is itself problematic. In the face of these difficulties it is encouraging to arrive at a statistically significant correlation between HSI values and estimated newt status.

The range of values represented in our sample (Table 1) is reasonably wide for most of the key variables, although there is some tendency to emphasize sites with permanent ponds of relatively small size in agricultural areas. More seriously, because our sample was taken from the central part of the species range in England, the value of SI_1 , location, was 1.0 in all cases and we have not evaluated model performance in peripheral parts of the range. It is possible that the interaction of habitat characteristics may have different effects on populations in these areas. Furthermore, evaluation of the index would be difficult because a site with a perfect habitat score may not support a population simply because there are no colonizers. In the central parts of the range, even with the declining status of the species (Cooke & Scorgie, 1983, Hilton-Brown & Oldham, 1991), it is still sufficiently well distributed for most potential sites to be open to colonizers.

The model developed in this paper emphasizes the aquatic habitat. For some populations this may be appropriate, since crested newts have been found to concentrate their activity within a few hundred metres of the breeding site (Jehle, 2000). There is a paucity of information in this species on the terrestrial habitat, although in American species similar exercises have tended to emphasize the terrestrial habitat (Sousa, 1985, Storm *et al.*, 1993). It is possible that terrestrial landscape characteristics may be a better predictor of population persistence over long time scales.

The result of comparing macrophyte cover with newt catch (Fig. 3) was unexpected. It might suggest that newts caught by trapping are those involved in display in open water, rather than those in “normal” movement amongst the vegetation. The fall in trap catches following the peak of the crested newt breeding season (e.g. Oldham, 1994) may result from the same tendency.

The system proposed does not provide a definitive solution to habitat evaluation but we hope that it will provide a useful first step. At best it will help to rank a series of sites in order of merit as newt sites. It can also be used as a guide in conservation management by pro-

viding a checklist of factors to be taken into account during site evaluation. As demonstrated for translocation exercises by Oldham & Humphries (2000), there are many instances where the application of a system such as that now proposed, could have eliminated unsuccessful host sites from consideration.

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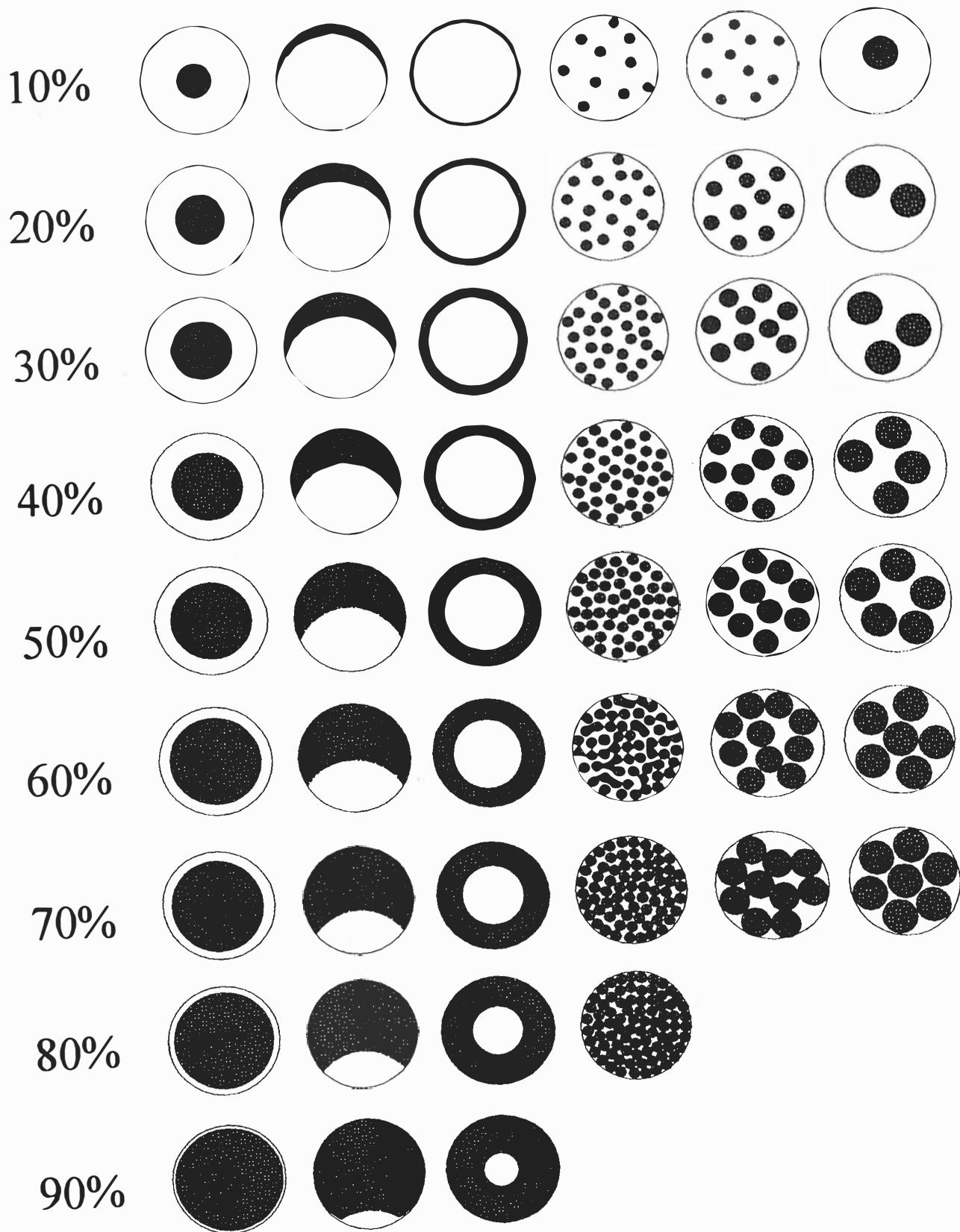
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APPENDIX 1. Suitability Index definitions.

SI	Factor	"Units"	Derivation of SI value
1	Location	Measured as map location	Refer to Fig. 2: If site occurs in zone A, location is optimal & SI = 1. If site occurs in zone B, location is marginal & SI = 0.5. If site occurs in zone C, location is unsuitable & SI = 0.01.
2	Pond area	m ²	Measure pond surface area. Measure axes in field for regularly shaped ponds or estimate from an OS map. Read off SI value from Fig. 1, chart SI ₂ .
3	Pond	years	Years out of ten that pond dries out during the spring or early summer. This depends upon access to long-term local knowledge of the site. Read off SI value from Fig. 1, chart SI ₃ .
4	Water quality	subjective scale	Water quality scored on a 4-point scale where: 4 = good quality; water normally clear and with an abundant and diverse invertebrate community including relatively sensitive groups such as mayfly larvae, water shrimps, amphibians (smooth newts and frog tadpoles) and fish (other than crucian carp); SI = 1. 3 = moderate quality, moderate invertebrate diversity; SI = 0.67. 2 = poor quality; low invertebrate diversity, with emphasis on species characteristic of low oxygen tension such as midge and mosquito larvae, and worms; few submerged plants; SI = 0.33. 1 = bad water quality; clearly polluted, only pollution-tolerant invertebrates such as rat-tailed maggots; usually turbid; no submerged plants; SI = 0.01.
5	Shade	%	Estimate of the % of perimeter shaded (usually by trees). Include only trees close enough to pond to shade water to at least 1 m from shore. Read off SI value from Fig. 1, chart SI ₅ .
6	Fowl	count	Number of waterfowl seen per pond or per 1000 m ² in large ponds. Read off SI value from Fig. 1, chart SI ₆ .
7	Fish	subjective scale	Subjective based on clues or local knowledge: 4 point scale: 4 = Absent; SI = 1. 3 = Possible; SI = 0.67. 2 = Minor (crucian carp and sticklebacks); SI = 0.33. 1 = Major (other species or carp/sticklebacks in dense populations); SI = 0.01.
8	Pond	count	Number of ponds occurring within 1 km of the target site (excluding the target site and ponds on the distal side of important barriers). Use an OS map of at least 1:25 000 scale or field survey an area previously marked on the map. Divide the number of ponds by π (=3.14). Read off SI value from Fig. 1, chart SI ₈ .
9	Terrestrial	map	OS map with 500 m radius around pond shaded to indicate "newt-friendly" habitat, viz.: habitat judged as woodland, scrub, long grass, meadow, or gardens. Calculate the area shaded (Ha). Also mark good hedges and ditches on the map and estimate length. Calculate total area of shaded and linear features (using 2.5 m as hedge and ditch width, unless determined otherwise). The resulting value (A, in Ha.) is multiplied by the barrier factor (B), described below. The value AB is read off as an SI value from Fig. 1, chart SI ₉ . Barriers subjective. Barriers scored on a 5-point scale, where: 5 = no serious barrier within 500 m; effectively none of habitat unavailable to population; factor B = 1. 4 = minor barrier (such as minor road with light night traffic); up to approx. 25% of habitat, within 500 m of pond, difficult of access by newts; B = 0.8 3 = moderate barrier (road, river, buildings) with up to 50% of available habitat difficult of access; B = 0.6. 2 = major barriers with up to 75% of habitat difficult of access; B = 0.4. 1 = almost total barrier to newt movement in vicinity of pond, so that newts are virtually confined to the pond and its immediate surroundings; B = 0.2.
10	Macrophyte	%	Estimate of the % of the pond surface-area occupied by macrophyte cover (sum of emergents, floating plants and submerged plants reaching the surface, except duckweed). Estimate with help of chart (Appendix 2) between May and the end of September. Read off SI value from Fig. 1, chart SI ₁₀ .

APPENDIX 2. Guide for use in assessment of the proportions of vegetation cover in a pond. The percentage of each circle shaded in the figures is indicated. The circles simulate a variety of vegetation dispersion patterns.



MODELLING POPULATION DYNAMICS OF GREAT CRESTED NEWTS (*TRITURUS CRISTATUS*): A POPULATION VIABILITY ANALYSIS

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The effects of pond isolation, drought, habitat fragmentation and dispersal on populations of crested newts (*Triturus cristatus*) were investigated using stochastic models constructed from existing life history data. The models predict that small isolated populations have a higher risk of extinction than large isolated populations. However, even large populations had a relatively high extinction risk over a fifty year period if they remained isolated. Pond desiccation affects metamorphic success and recruitment, and the risk of extinction decreased with decreasing frequency of regional droughts. In a subdivided population, increasing dispersal between subpopulations decreased the extinction risk of the metapopulation as a whole. However, even in the absence of dispersal, a subdivided population had a lower overall extinction risk than a single isolated population of the same size. Environmental stochasticity may therefore result in asynchronous dynamics within subpopulations, which leads to the risk of extinction being spread across the subpopulations. Although population viability analysis has the potential to provide an objective assessment of population management decisions, it has not yet been a component of conservation planning for the crested newt in Britain.

Key words: *Triturus cristatus*, population viability analysis, metapopulation, modelling

INTRODUCTION

In a thought-provoking review of species conservation programmes, Caughley (1994) argued that there are two fundamental approaches to addressing species conservation problems. These two approaches are enshrined within what he termed the 'Declining Population Paradigm' (DPP) and 'Small Population Paradigm' (SPP). In sum, the DPP is concerned with identifying those factors that have led to population declines, and the attempts to neutralize them. This approach to addressing conservation problems is firmly rooted in empirical field biology, and there are many case-studies of the application of this approach to amphibian conservation problems (e.g. Richards, *et al.* 1993; Kuzmin, 1994; Pounds & Crump, 1994; Fisher & Shaffer, 1996; Denton *et al.*, 1997). In contrast, the SPP is concerned with risk of extinction as a result of genetic and demographic stochasticity within populations that are already small. The main tools used in this approach to conservation problems are predictive models, which aim to utilize genetic, demographic and environmental information on the species concerned to make predictions about the long-term viability of the population. 'Population Viability Analysis' (or 'PVA') is a modelling process concerned with assessing the risk of extinction of a population (Boyce, 1992), and can be employed using the principles of the SPP. Caughley (1994) concluded that the DPP is short of theory, and the SPP is short of practice, and neither can therefore be totally effective if used to address conservation problems on their own.

In recent years there have been major advances in the sophistication of predictive modelling. Although widely used to assess extinction risks in mammal and bird conservation programmes (e.g. Soulé, 1987), population modelling has rarely been applied to herpetological conservation problems, or to species conservation programmes in Britain in general. As far as British amphibians are concerned, the only previous modelling study is that by Halley *et al.* (1996) on the common toad (*Bufo bufo*) and crested newt (*Triturus cristatus*). These authors predicted that crested newt populations will persist even in small ponds, providing they are close to a source of immigrants. Whether or not an initially unoccupied pond was used at all after 20 generations depended upon immigration rates. On the other hand, there are now several studies that have assembled data on the population biology of crested newts (e.g. Bell, 1979; Hagström, 1979; Verrell & Halliday, 1985; Arntzen & Teunis, 1993; Miaud, 1991; Miaud *et al.*, 1993; Cooke, 1995; Baker, 1999). In general, these studies have shown that the population dynamics of the crested newt are characterized by year-to-year fluctuations in adult population sizes, due to variable recruitment as a result of environmental variability. In addition, dispersal between ponds may play an important role in buffering extinction in local populations, and a metapopulation structure may therefore be important in maintaining crested newts within a wider landscape (Miaud *et al.*, 1993; Griffiths, 1997).

In this paper we construct a simple model of crested newt population dynamics utilizing demographic data obtained from the literature and from a metapopulation in Kent. We then use the model to predict the effects of progressive population subdivision, and newt dispersal between ponds, on population persistence.

MATERIALS AND METHODS

THE MODELS

We used RAMAS Metapop version 3.0 (Akçakaya, 1998) to carry out several population viability analyses. The analyses used available data on population size, demography, spatial structure and environmental variability to calculate population trajectories over a 50 yr period. The analyses used a stochastic simulation, calculating 1000 estimates of projected population size for each year. From these 1000 estimates the number of populations going extinct within 50 yrs was used to derive the risk of extinction over this period.

AGE STRUCTURE, SURVIVAL AND FECUNDITY

The basis of the models is a Leslie matrix of age-specific survival and fecundity schedules. The models used an age-structure based on those derived from skeletochronological analyses of two *T. cristatus* populations in France (Francillon-Vieillot *et al.*, 1990; Miaud *et al.*, 1993). We also incorporated further skeletochronological data from three populations in Kent (Williams, 1999). The percentage of individuals in each age class was calculated for each population, and then averaged across the five populations (i.e. two populations from France, three populations from England) to give an aggregated age structure. There were very few individuals in any of these populations over 12 years old, so these were pooled into the final age class (i.e. >12 yrs).

Oldham (1994) constructed a survivorship curve for crested newts by combining data from the study by Arntzen & Teunis (1993) with new information from Leicestershire. This assumed that crested newts breed for the first time at 2 or 3 years, and then breed every year until death. From this survivorship curve, annual adult survival was estimated at around 0.68, and juvenile survival at 0.2. However, published estimates of adult annual survival vary from around 0.31 to 1.0 (Baker, 1999), and juvenile survival is more variable than adult survival (Arntzen & Teunis, 1993). Standard deviations of 0.3 were therefore attached to the survival estimates for each age class (as juvenile survival is lower than adults, the SD of 0.3 provides a higher coefficient of variation for juveniles than for adults, and allows survival to fall to zero in some years).

As the model included post-metamorphic age classes only, 'fecundity' was modelled as the number of new individuals produced per individual within each age class (i.e. 'recruitment'). Published estimates of fecundity range from 189-220 (see citations by Arntzen & Teunis, 1993). Assuming a 1:1 sex ratio, and taking account of the 50% egg abortion, 95% egg/larval mortality and 80% juvenile mortality – based on data provided by Arntzen & Teunis (1993) and Oldham (1994) – this translates to about five new recruits per adult, with an estimated standard deviation of 0.2.

The life-table produced from these data yields a net reproductive rate (R_0) of close to 1.0 (Arntzen &

Teunis, 1993). This means that in the absence of catastrophes or environmental, demographic and genetic stochasticity, the population will be stable over time. Demographic stochasticity was modelled by drawing the number of survivors each year from a binomial distribution described by survival rate and population size; and by drawing the number of recruits from a Poisson distribution described by the mean of fecundity \times population size. Environmental stochasticity was modelled by drawing values randomly from lognormal distributions described by the fecundity and survival values and their associated standard deviations detailed above. The effects of stochasticity on fecundity, survival and carrying capacity were assumed to be correlated, and the extinction threshold for each population was set to one remaining newt. Density-dependent population growth was simulated using a ceiling model (Akçakaya, 1998).

MODEL PARAMETERS

All of the models used the same age structure and Leslie matrix described above. The effects of pond isolation, catastrophe (drought), and population subdivision on extinction risk were modelled as follows:

Isolated populations. Models were constructed for isolated populations with starting population sizes (N_0) of 10, 50, 100 and 200 newts. The carrying capacities for crested newt populations are unknown, but as populations have been observed to fluctuate by an order of 15 or more (e.g. Arntzen & Teunis, 1993; Cooke, 1995), carrying capacities (K) were set at $K=20 N_0$.

Drought. Pond desiccation in the summer will result in few – if any – crested newt larvae surviving to metamorphosis. Drought was therefore modelled as causing total mortality of eggs and larvae in all ponds during drought years, which subsequently led to zero recruitment of first-time breeders 2-3 years later. The impact of a drought occurring every 1, 2, 3 or 4 years on population viability was compared using isolated ponds with $N_0=10, 50, 100$ and 200 newts, and $K=20 N_0$.

Fragmentation and dispersal. The effects of habitat fragmentation were modelled by comparing the persistence of a metapopulation under increasing degrees of

TABLE 1. Predicted extinction risks of isolated crested newt populations that differ in population size. K , carrying capacity; N_0 , starting population size; N_{50} , mean population size \pm SD of extant populations ($n=1000$ simulations) after 50 years; $K=20 N_0$.

	Population parameters		Extinction risk	
	K	N_0		N_{50}
	200	10	100 \pm 86.3	0.275
	1000	50	607 \pm 395.6	0.087
	2000	100	1207 \pm 778.6	0.049
	4000	200	2496 \pm 1542.0	0.025

subdivision (i.e. 1, 2, 5 and 10 ponds). The total number of newts was therefore kept constant but was divided among different numbers of smaller patches. In each of the models, the metapopulation carrying capacity ($K=1000$) and starting population size ($N_0=500$) was the same, with both parameters divided equally between the patches (e.g. a metapopulation of two ponds each had $K=500$ and $N_0=250$). Dispersal of amphibians between ponds can 'rescue' declining or extinct populations (e.g. Gill, 1978; Sjögren, 1991), and may therefore be important for metapopulation persistence in crested newts. Although adult newts sometimes move between ponds (e.g. Miaud *et al.* 1993; Williams, 2000), most dispersal probably occurs during the immature stages. We therefore modelled dispersal as the movement of 1-2 year-olds between ponds. Dispersal rates were modelled as 0%, 1% or 10% of 1-2 year-olds, and dispersal was assumed to occur between all ponds within the metapopulation. Fragmentation and dispersal models all incorporated the effects of a drought that eliminated recruitment on average once every three years.

RESULTS

ISOLATED POND MODEL

In isolated populations, the risk of extinction steadily declined as population size and carrying capacity increased. However, even in the absence of catastrophes or other major environmental changes, populations that can sometimes reach sizes of 100-200 individuals still have a 27% chance of disappearing over a 50 yr period, as a result of demographic and environmental stochasticity (Table 1). Predicted population sizes varied between 0 and K , resulting in

large standard deviations in estimated population size, which is consistent with real populations. According to the model, an isolated population needs to be able to support at least 1000 newts if the extinction risk is to fall below 10%.

TABLE 2. Predicted extinction risks of isolated crested newt populations that differ in population size and suffer different frequencies of drought. Interpretation as Table 1; $K=20 N_0$. Drought is assumed to eliminate recruitment in the year in which it occurs.

Population parameters		Frequency of drought	Extinction risk
N_0	N_{50}		
10	0	Every year	1.000
10	5±24.5	Every 2 yrs	0.911
10	19±47.5	Every 3 yrs	0.745
10	34±64.2	Every 4 yrs	0.654
50	0	Every year	1.000
50	27±120.9	Every 2 yrs	0.811
50	133±272.1	Every 3 yrs	0.533
50	231±351.5	Every 4 yrs	0.402
100	0	Every year	1.000
100	68±286.6	Every 2 yrs	0.746
100	278±554.4	Every 3 yrs	0.453
100	484±707.9	Every 4 yrs	0.335
200	0	Every year	1.000
200	134±558.9	Every 2 yrs	0.714
200	572±1140.0	Every 3 yrs	0.453
200	1052±1469.0	Every 4 yrs	0.305

TABLE 3. Predicted extinction risks of crested newt populations that are subdivided into 1, 2, 5 or 10 subpopulations, with different rates of juvenile dispersal (0, 1% or 10%) between subpopulations. N_0 , starting population size of *each* subpopulation; N_{50} , average overall metapopulation size (±SD) after 50 yrs ($n=1000$ simulations); drought occurs in all ponds on average once every three years and eliminates recruitment to the metapopulation in that year. See Table 4 for a comparison with single (i.e. isolated) populations with the same values of K and N_0 .

No. subpopulations	Population parameters		N_{50}	Dispersal rate	Extinction risk of metapopulation
	K of each subpopulation	N_0			
1	1000	500	157±289.1	0	0.461
2	500	250	143±203.3	0	0.298
5	200	100	123±136.6	0	0.155
10	100	50	94±94.6	0	0.124
2	500	250	194±250.8	0.01	0.237
5	200	100	258±218.7	0.01	0.035
10	100	50	317±223.6	0.01	0.007
2	500	250	294±321.7	0.1	0.136
5	200	100	485±304.1	0.1	0.004
10	100	50	588±312.7	0.1	0.001

TABLE 4. Predicted extinction risks in single populations, with other population parameters as in Table 3.

Population parameters				Extinction risk
No. subpops.	K of each subpop.	N_0	N_{50}	
1	1000	500	157±289.1	0.461
1	500	250	69±139.0	0.566
1	200	100	24±53.1	0.672
1	100	50	10±25.1	0.780

DROUGHT MODEL

Recruitment increases with decreasing frequency of drought, and this was reflected in a decreased risk of extinction as drought frequency declined (Table 2). As expected, no population is viable with recruitment failure every year, and under this scenario the probability of extinction is therefore $P=1.0$. However, even when drought occurred only once every four years, the risk of extinction was still at least 30% even in the very largest populations modelled. In this scenario, around half of all the populations with $K=200$ went extinct within 25 years. As in the isolated pond model, predicted population sizes over the 50 year period varied widely between 0 and K .

FRAGMENTATION AND DISPERSAL MODEL

Isolated populations with no dispersal have a relatively high risk of extinction. Although larger isolated populations will persist for longer than small isolated populations (Table 1), the risk of extinction is reduced when individuals are distributed across several patches, even in the absence of dispersal (Table 3). Although the risk of extinction of a small population is therefore high, collectively the risk of extinction of a group of small populations is lower than an equivalent sized population occupying a single patch (Tables 3, 4). As the rate of dispersal of 1-2 year-old newts between ponds increases, the extinction risk of the newt metapopulation as a whole decreases. Indeed, with a metapopulation spread across 10 or more patches and a dispersal rate of 10% of immatures between all ponds, the risk of extinction over 50 yrs is less than 0.1% (Table 3).

DISCUSSION

MODEL JUSTIFICATION

How well do the models presented reflect reality? This question can only be answered by using the models to generate hypotheses that can be tested with field data over fifty years. The age-structure and survival-fecundity schedule used were certainly realistic as they were based on well-founded field data sets. Although these parameters may therefore be regarded as fairly

'typical' of crested newt populations, it is unlikely that real populations will have identical initial age-structures and survival-fecundity schedules as assumed here. However, incorporating environmental and demographic stochasticity into the models ensured that population structures did not remain identical for the duration of the simulations. What is certain is that the models were simplistic, and did not incorporate the full range of environmental parameters that may influence crested newt population dynamics. In a real metapopulation, for example, there are many other catastrophes (e.g. fish introduction, disease outbreaks, pollution incidents etc.) that may impact upon the population. Equally, there may be more subtle environmental changes that result in progressive fragmentation and increasing isolation of ponds that were once connected. The models also did not take into account genetic stochasticity; this can result in detrimental affects within small populations, leading to increased risk of extinctions (e.g. Hedrick, 1996). As well as being simplistic then, the models presented here may be over-optimistic.

METAPOPULATION DYNAMICS

The models predict that even relatively large crested newt populations may not be viable in the long term if they are completely isolated. Indeed, the likelihood of extinction within a 50 yr period may actually be rather higher than predicted, as the isolated pond model assumed recruitment every year and no catastrophes or environmental degradation – something that would appear to be rare in real populations. Although a long life-span, repeated breeding, and high fecundity may be adaptations to catastrophic loss of reproductive effort in some years (Griffiths, 1997), even relatively infrequent droughts that eliminate recruitment one year in four result in a marked increase in extinction risk compared to models with recruitment every year. However, pond desiccation can have positive effects on crested newt populations by eliminating predators, such as fish and aquatic invertebrates. The interaction between the positive and negative affects of pond desiccation is therefore worthy of further theoretical exploration and empirical testing.

Halley *et al.* (1996) modelled extinction risk in crested newts in terms of carrying capacities and distances between ponds. They predicted that relatively small populations could persist providing that they are close to (i.e. <0.75 km) sources of immigrants, while large populations could persist at greater distances (i.e. <1.5 km from a source). In the current study, inter-pond distances were implicitly reflected by the dispersal rates, although there are other factors, such as the landscape structure between ponds, that will also affect these parameters. Halley *et al.* (1996) tested different hypotheses to those tested here, and used different input and output parameters. However, their finding that even large populations (i.e. ponds with >100 females

located at >3 km from a source) have a less than 5% chance of surviving 20 generations is broadly in line with our prediction that large isolated ponds have low viability in the long-term.

The classical Levins (1970) model of metapopulation dynamics assumes that there is no variation in habitat quality between patches that support different subpopulations. This was simulated in the dispersal models used here; however, in nature habitat patches – including crested newt ponds – vary in quality. Likewise, in nature dispersal rate between ponds will not be the same for all populations. Dispersal rate will depend on the distances between subpopulations, the habitat structure in between, and perhaps the density of the donor and recipient populations (e.g. Hansson, 1991; Fahrig & Merriam, 1994). The models presented here suggest that a threshold dispersal rate of around 1% of first time breeders needs to be reached if the system is to act as a functional metapopulation. However, dispersal rates higher than this may be required if the populations are small and/or the habitat varies in quality. Equally, large subpopulations that suffer fewer catastrophes may function as a metapopulation with a lower dispersal rate. In the latter case, the subpopulations may behave functionally as isolated populations, with dispersal playing no significant role in influencing population persistence.

In nature, habitat fragmentation invariably leads to (1) decreased habitat, and (2) increased isolation of the remaining patches. Both of these effects can lead to extinction independently of each other, but in practice, are difficult to distinguish. The fragmentation and dispersal models presented here illustrate the effects of isolation without an overall decrease in habitat. In that increasing fragmentation leads to a decreased risk of extinction, the results contradict traditional island biogeography theory (MacArthur & Wilson, 1967). Indeed, in terms of whether newts are best conserved in 'single large' rather than 'several small' habitat patches (e.g. see Simberloff & Abele, 1976, 1982; Wilcox & Murphy, 1985), the models tend to support the latter theory. Providing that the dynamics of individual subpopulations are asynchronous and regulated by environmental factors that are not correlated, it is quite possible for a subdivided population to persist for longer than a single population of equivalent size, due to the spreading of risk between patches (e.g. Den Boer, 1981; Verboom *et al.*, 1993). Factors such as drought are likely to be regional rather than local in their effects, and in the models used here drought was modelled as affecting all ponds every three years in a correlated fashion. In nature, a combination of regional factors that will affect all subpopulations (e.g. drought, severe winters) and local factors that will affect individual subpopulations asynchronously (e.g. fish introductions, egg infections) are both likely to impact on crested newt metapopulation dynamics. The likelihood of a subdivided population persisting for longer than an isolated

population depends upon the relative importance of synchronous and asynchronous impacts. The current models therefore suggest that environmental stochasticity will generate sufficient asynchronicity in subpopulation dynamics to allow longer persistence of a subdivided population.

Interestingly, a similar analysis on the brushtail possum by Lindenmayer & Lacy (1995) reached the opposite conclusion. The models produced by these authors predicted that increasing subdivision of populations invariably had negative effects, irrespective of dispersal rates between populations. However, above a certain population threshold, dispersal of possums resulted in reduced extinction risk.

As Boyce (1992) points out, one of the major strengths of population viability analysis lies in its potential to provide an objective assessment of management options for species and habitats. For example, translocations can also be conveniently modelled, as it is possible to simulate the effects of both removals and introductions. Likewise, modelling can be used to explore the implications of creating a new pond within an existing metapopulation. However, the reliability of any population viability analysis depends very much on the demographic and environmental parameters upon which it is constructed. For many threatened species, there is insufficient population data to make population viability analysis a worthwhile exercise, and Halley *et al.* (1996) point out that it is currently not easy to obtain all the parameters needed to construct models of amphibian population dynamics. However, if research data on the population biology of the crested newt continues to accumulate, it will be possible to construct more reliable models. The simulations described here are therefore a useful starting point for the development of more complex models, that through progressive testing and refinement, should become a central part of great crested newt conservation planning. When that stage is reached, herpetological conservation in Britain will have gone some way towards achieving Caughley's (1994) goal of an integrated conservation strategy, in which theory and practice complement each other, rather than operating independently in parallel universes.

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POPULATION ECOLOGY OF THE GREAT CRESTED NEWT (*TRITURUS CRISTATUS*) IN AN AGRICULTURAL LANDSCAPE: DYNAMICS, POND FIDELITY AND DISPERSAL

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Aspects of the population ecology of the great crested newt (*Triturus cristatus*) were studied over a period of seven years (1989-1995) in an agricultural landscape of the Drachenfelder Ländchen, south-west of Bonn, Germany. Seven ponds – three natural and four man-made – were monitored by drift fences and pitfall traps. The numbers of adults increased from 1992. The number of juvenile emigrants showed marked fluctuations between years at all ponds and in some years juvenile production failed completely at the temporary ponds. A total of 63% of the adult newts identified in 1994 at four sites were recaptured in the subsequent year. Ninety-nine percent of the newts recaptured returned to the place of the first capture. In contrast to the adults, a number of juvenile great crested newts moved to neighbouring ponds, migrating a maximum distance of 860 m within the year of metamorphosis. Two out of four artificially constructed ponds were colonized naturally.

Keywords: population ecology, pond fidelity, dispersal, colonization, *Triturus cristatus*

INTRODUCTION

The great crested newt can be found in most parts of central Europe (Arntzen & Borkin, 1997). Throughout its wide distribution it is regarded as an endangered species and it is legally protected in Germany and across Europe (Corbett, 1994; Beutler *et al.*, 1998). The decline of the great crested newt is mainly a result of the loss of suitable ponds for breeding, the destruction of the terrestrial habitat, the fragmentation of landscape and the introduction of modern farming methods in agricultural areas (Beebee, 1975; Feldmann, 1981, Grosse & Günther, 1996).

Other studies available on the population ecology of great crested newts or other members of the *cristatus* super-species have covered periods ranging from one season up to ten years (e.g. Hagström, 1979; Blab & Blab, 1981; Glandt, 1982; Verrell & Halliday, 1985; Arntzen & Teunis, 1993; Cooke, 1995; Ellinger & Jehle, 1997, Baker, 1999). However, most studies have been carried out only at a single breeding site, and in most cases the emigration of juvenile newts after metamorphosis has not been reported. The aim of the present paper is to give an overview of the dynamics of neighbouring local populations of the great crested newt over a period of seven years. Capture-mark-recapture methods have been used to investigate possible movements of adult individuals between the ponds. Further aspects of the study were the dispersal behaviour of juveniles and the colonization of newly-created ponds.

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MATERIAL AND METHODS

SITE DESCRIPTION

Research was carried out continuously from 1988 to 1995 within a 4 km² area south-west of Bonn (North Rhine-Westfalia, Germany, Central Europe), located within a mosaic of farmland, urban areas and patches of forest (Schäfer & Kneitz, 1993, Kneitz, 1998). The climatic conditions of the study area are sub-Atlantic, with an average air temperature of 7.8 ° to 8.5 ° C and an annual precipitation between 600 mm and 650 mm. Usually, the winters are mild and humid. Most of the summers are hot and dry.

During the research, seven ponds were studied (Fig. 1); three ponds were natural (ponds 1 to 3) and four were created artificially in 1988 (ponds A to D). The older sites had maximum areas between 200 m² and 1200 m² and their water levels fluctuated greatly. The areas of newly created sites ranged from 64 m² to 80 m² and their water levels were more stable, owing to the plastic liners that were used in their construction. The distances between neighbouring ponds ranged from 430 m to 1940 m (Table 1).

Great crested newts shared their breeding sites with smooth newts (*Triturus vulgaris*), alpine newts (*T. alpestris*), agile frogs (*Rana dalmatina*), common frogs (*R. temporaria*), common toads (*Bufo bufo*) and pool frogs (*Rana lessonae* / *R. kl. esculenta*).

Great crested newts were present in all of the older sites at the beginning of the study, in 1989; however, the population at pond 2 consisted of only a few individuals (Schäfer, 1993). To augment this population at site 2, ten adult specimens were released in spring 1992. At site C, six adults were introduced in spring

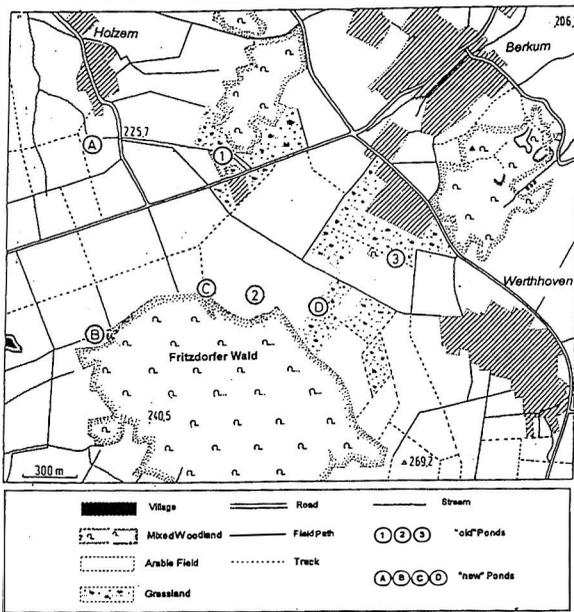


FIG. 1. Map illustrating the structure of the study area and the locations of the ponds.

1991 to establish a population. The donor-site for both these introductions was a clay pit 3.5 km distant (for further details see Schäfer, 1993).

POPULATION MONITORING

All migrating amphibians at the seven study ponds were monitored by a drift fence and pitfall system. The ponds were encircled by drift fences, 70 cm in height, consisting of plastic-covered metal gauze (Fig. 2). About 30 cm of the fence was buried in the ground and a plastic gutter was placed on its top to prevent newts from climbing over the fence undetected. On both sides of the fence, 35 cm deep plastic buckets (80 l capacity) were sunk into the ground at five-metre intervals. The edge of every bucket was taped with a plastic strip to prevent the newts from escaping (for further details see Kneitz 1998). The fence efficiency (FE) for great crested newts was estimated in 1995, both for immigra-

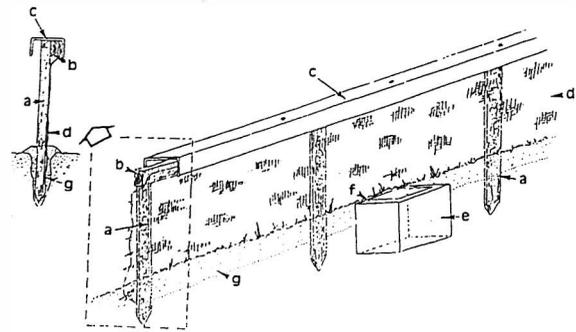


FIG. 2. Schematic representation of the drift fence/pitfall system at the ponds: a, post; b, gutter; c, plastic gutter; d, drift fence; e, pitfall trap; f, plastic tape; g, buried drift fence.

tion (FE_i) and emigration (FE_o), using the Lincoln Index (Table 2). Fence efficiency was defined as the percentage of the population approaching the fence which was caught in the pitfalls (for methodology see Arntzen, Oldham & Latham, 1995). For adults the FE_i varied between 67 % (pond 2) and 100 % (pond C), while FE_o varied between 32 % (pond 1) and 83 % (pond C).

To investigate the emigration of juvenile amphibians at pond 2, a different type of terrestrial trap was used in the summers of 1994 and 1995. The trap consisted of two flower boxes (98 x 14 x 16 cm each) with a fence, 50 cm high, fixed at the back of the boxes in the direction of emigration. The edge of every box was taped with a plastic strip to prevent animals from escaping. The terrestrial traps were sunk into the ground of the surrounding fields at distances of 10 m to 110 m from the edge of pond 2 (Fig. 3). Terrestrial traps were also placed at the edge of the forest. These traps consisted of two buckets, as described above, at the centre of a radial array of four 5 m-long drift fences (Hartung & Glandt, 1988, see Kneitz, 1998 for further details).

All pitfalltraps were checked for animals daily in the morning hours (Kneitz, 1998). The trapping systems at the ponds and in the forest were erected in summer

TABLE 1. Description of pond parameters. Terrestrial habitat types found within 100m of the pond were identified: 1, arable farm land; 2, pasture farm land; 3, mixed wood; 4, deciduous wood; 5, scrub; 6, garden.

Pond	Maximum area (m ²)	Maximum depth (m)	Scrub cover	Open water	Terrestrial habitat	Inter-pond distance, mean and range (m)
1	1200	1.5	high	80%	2, 3, 6	995 (700-1220)
2	450	1.2	low	30%	1, 5	773 (300-1200)
3	200	0.9	moderate	30%	1, 2, 5	1242 (530-1850)
A	80	0.9	low	25%	1, 5	1315 (730-1940)
B	64	1	moderate	40%	4, 5	1215 (710-1340)
C	64	1	moderate	40%	1, 3	795 (300-1140)
D	64	1.2	low	40%	1, 2	1007 (430-1940)

TABLE 2. Estimated fence efficiencies for drift fences used at four study ponds in 1995, with 95% confidence intervals.

Pond	Estimated fence efficiency (%)	
	immigration	emigration
1	81 (71-91)	32 (19-44)
2	67 (53-80)	46 (26-67)
3	94 (88-100)	76 (71-82)
C	100 (100)	83 (100)

1988 and were removed in December 1995 (Schäfer, 1993; Kneitz, 1998). The terrestrial traps used near pond 2 were set up on 1 June 1994 and dismantled on 24 October 1994. In 1995 the traps were used from 15 June to 3 August and from 1 October to 30 November.

To monitor movements of newts between the ponds, adult newts at sites 1, 2, 3 and C were identified by their individual belly patterns in 1994 and 1995 (e.g. Hagström, 1973). The pattern was recorded photographically (Minolta X 700, Metz CT-4 flashlight). The juveniles at sites 1 and 2 were marked by toe clipping during the emergence of newly-metamorphosed newts in 1994 and 1995 (August and September). Two toes were clipped in each animal and the code used identified the pond and the direction of emergence. We were able to identify marked animals up to the spring immi-

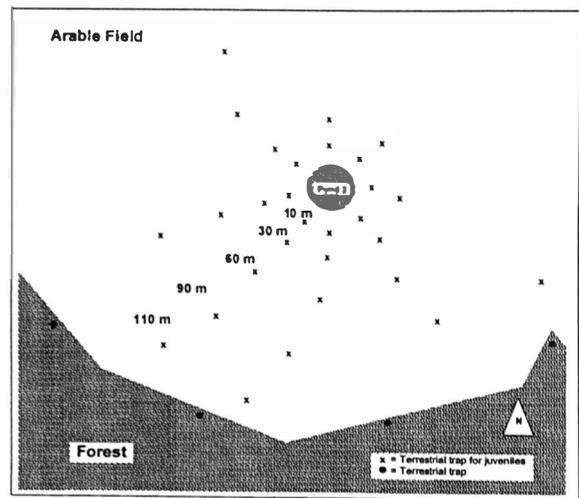


FIG. 3. Map of the pitfall system applied to monitor emigrating juveniles at pond 2 in 1994 and 1995.

gration of the following year. In some cases the regenerated toes were still recognizable in the summer. The captured animals were released subsequently to the marking procedures on the opposite side of the fence to that on which they were captured.

To check for the presence and breeding activity of great crested newts in the years following the removal of the drift fences, the seven ponds were searched for eggs from April to June in 1996 and 1997.

TABLE 3. Population sizes of *Triturus cristatus* at four neighbouring breeding sites from 1989 to 1995 (data from January 1989 to June 1992 obtained from Schäfer, 1993). The sizes are presented as the numbers of immigrating adults and sub-adults and the numbers of emerging juveniles. The mean juvenile production per female is defined as the number of emigrating juveniles divided by the number of reproductive females.

Year	Pond 1						Pond 2					
	Males	Females	Total	Subadults	Juvs	Juv/Fem	Males	Females	Total	Subadults	Juvs	Juv/Fem
1989	11	15	26	1	133	8.9	-	-	-	-	-	-
1990	13	20	33	4	55	2.75	-	-	-	-	-	-
1991	14	20	34	6	164	8.2	-	-	-	-	-	-
1992	23	43	66	21	26	0.6	6	4	10	-	112	28
1993	43	32	75	5	3	0.1	1	2	3	1	32	16
1994	44	53	97	-	106	2	13	15	28	-	176	11.7
1995	36	55	91	12	13	0.4	15	11	26	3	43	4.7

Year	Pond 3						Pond C					
	Males	Females	Total	Subadults	Juvs	Juv/Fem	Males	Females	Total	Subadults	Juvs	Juv/Fem
1989	1	2	3	-	17	8.5	-	-	-	-	-	-
1990	2	3	5	-	-	-	-	-	-	-	-	-
1991	3	4	7	-	-	-	3	3	6	-	23	7.6
1992	1	1	2	-	53	53	2	3	5	-	40	13.3
1993	1	1	2	3	-	-	3	1	4	-	-	-
1994	6	2	8	1	1	0.5	1	1	2	2	-	-
1995	6	10	16	-	-	-	2	4	6	-	-	-

TABLE 4. Capture and recapture data for adult *Triturus cristatus* in 1994 and 1995. The belly patterns of 132 out of 135 newts immigrating in spring were recorded photographically. Only one adult female was recorded at a different site in the second year (at pond C instead of pond 3).

	Pond 1			Pond 2		
	captures (1994)	recaptures (1995)	%	captures (1994)	recaptures (1995)	%
males	35	23	66	11	9	82
females	49	32	65	12	5	42
total	84	55	66	23	14	61

	Pond 3			Pond C		
	captures (1994)	recaptures (1995)	%	captures (1994)	recaptures (1995)	%
males	10	5	50	-	-	-
females	13	7	54	2	2	100
total	23	12	52	2	2	100

RESULTS

POPULATION STRUCTURES AND DYNAMICS

The largest number of adult great crested newts was found at site 1 (Table 3). Adult numbers increased from 26 at the beginning of the study to 97 individuals in 1994 (mean=60±11). Numbers of newly-metamorphosed juveniles fluctuated from year to year (Table 3): the greatest number was observed in 1991, followed by a sharp decrease in 1993. An increase in the number of new juveniles emerging was always followed by an increased number of adult newts two years later. Sub-adult newts were encountered almost every year when a large number of juveniles had left the pond the previous year.

Since the introduction of great crested newts in 1992 a moderate number of adult crested newts was found at site 2 (mean=17±6). From 1992 to 1995 the adult part of the population increased from 10 to 28 individuals. As in pond 1, juvenile newts showed marked fluctuations in numbers, with peaks in 1992 and 1994 and lower numbers in 1993 and 1995.

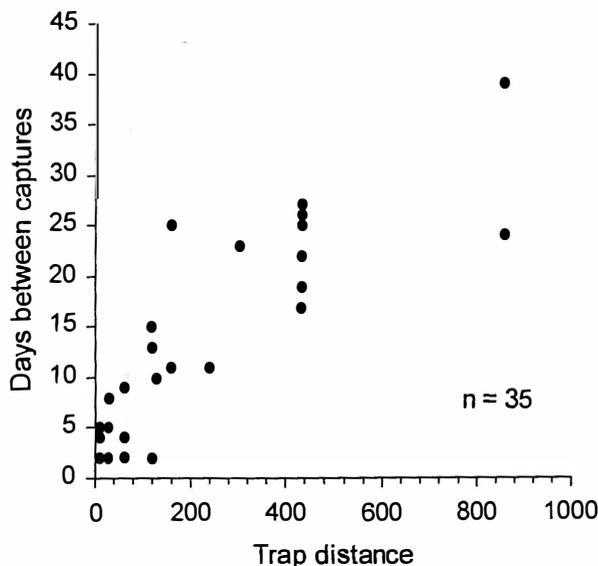


FIG. 4. The relationship between the distance between traps (m) and the number of days between captures.

Small numbers of adults were observed at pond 3 and in the seven years of study juveniles emerged only in 1989 ($n=17$), 1992 ($n=53$) and 1994 ($n=1$); in other years juvenile recruitment failed completely. At pond C we found no adults before six were introduced, in 1991. Twenty-three juveniles were produced in 1991 and 40 the following year, but no juveniles were produced in the years 1993-1995.

The yearly mean number of juveniles per female ranged from zero to about nine juveniles per female at pond 1 (Table 2). The highest values observed at ponds 2, 3 and C all occurred in 1992 (> 10 juveniles per female); this was the most successful year in terms of juvenile recruitment at ponds 3 and C, in the run of seven years. We found no significant correlation between the numbers of immigrating females and emigrating juveniles.

CAPTURE AND RECAPTURE OF ADULT NEWTS

Of 132 adults individually identified by their belly patterns in 1994, 83 (i.e. 63 %) were identified in the subsequent year (Table 4). Eighty-two newts returned

TABLE 5. Presence of *Triturus cristatus* at two newly-created ponds, B and D, from 1989 to 1997; ad, adult; sub, sub-adult; juv, juvenile; -, great crested newts not present.

year	Pond B	Pond D
1989	-	-
1990	-	-
1991	-	-
1992	-	1 juv
1993	-	-
1994	-	8 juv
1995	1 ad., 1 sub.	1 ad., 8 sub.
1996	eggs	eggs
1997	eggs	eggs

to the pond of their first capture, while only one adult female was recorded at a different site (pond C instead of pond 3). A total of 70 newts were recaptured entering the pond during the spring immigration. Thirteen newts were recaptured elsewhere and at different times of year. Of the latter, four animals were captured near the ponds, but did not enter them; three animals were not recorded at the breeding site in spring, but entered the ponds in autumn; six animals were found only in the inner traps of the drift fence in summer 1994 and may have hibernated in the ponds or passed the drift fence undetected.

DISPERSAL OF JUVENILES AND COLONIZATION

Of 176 juveniles marked at pond 2 in 1994, a total of 35 were recaptured in traps at distances ranging from 10 m to 860 m. Seventeen newts were caught in terrestrial traps in the surrounding field between 10 m and 60 m from the pond after an average of four days. Seven juveniles were captured in traps at the edge of the forest at distances from 120 m to 240 m after an average of 11 days. Thirteen juveniles were captured in the outer traps of the neighbouring ponds (ponds C, D and 3) at distances of 300 m to 860 m after an average of 23 days. The maximum distance travelled away from the natal pond was 860 m (to pond 3). There was a significant positive correlation between the trap distance (second capture of a juvenile newt in a terrestrial trap after moving away from the pond) and the days between captures ($r=0.872$, $P<0.0001$; Fig. 4).

At pond D, one juvenile great crested newt was caught in 1992 and eight juveniles were caught in 1994; subsequently, between 8 August and 9 September 1995, nine animals were captured by drift fences (Table 5). Of the latter, one newt was an adult male (SVL=73 mm), five animals were identified as sub-adult males (SVL=65.4 ± 5 mm) and three as sub-adult females (SVL=66.7 ± 2 mm). In 1996 and 1997 breeding activity was confirmed by the presence of eggs at the pond (Table 5).

In 1995, one female great crested newt was captured at Site B during the spring immigration (4 April) and again during the emigration (14 September). A subadult male (SVL=60 mm) was captured on 27 October. In 1996 and 1997 eggs were found at pond B, indicating breeding activity at this site.

Site A was monitored together with the other ponds from 1989 to 1997. Throughout this period there was no record of great crested newts at all. This site was not colonized by this species.

DISCUSSION

In accordance with previous work by several authors (e.g. Gill, 1978; Blab & Blab, 1981; von Lindeiner, 1992; Schäfer, 1993; Griffiths, 1996), the population sizes are presented in terms of estimated numbers of immigrating adults and subadults and emigrating juve-

niles. The drift fence system used at the ponds during the course of the study captured immigrating *Triturus cristatus* quite effectively. It was estimated that 67-100% of the breeding population was trapped during the immigration. This relatively high value may be compared with the data on the Danube crested newt at Donauinsel near Vienna (see the comparison of fence efficiencies in Arntzen, Oldham & Latham, 1995). However, the fence efficiency during the emigration was much lower (32-83%). The possibility cannot be excluded that newts either circumvented the fences or hibernated within the fenced area. Another explanation for a lower apparent fence efficiency might be a higher mortality of adult animals in the course of the breeding season. The actual mortality was not analysed in the present study.

The neighbouring populations revealed fluctuations in the numbers of adults and juveniles. In general the trend was towards an increase in numbers of adults. The largest population of great crested newts, at pond 1, increased from 26 individuals in 1989 to 97 in 1994. The increase might indicate the successful recruitment of newly-matured newts, following a series of years of sustained production of juveniles. Similar dynamic processes within the adult component of a population had been observed at other long term studies on *Triturus cristatus* around Europe (Hagström, 1979; Blab & Blab, 1981; Glandt, 1982; Arntzen & Teunis, 1993; Baker, 1999). In Westfalia, for example, the adult population size remained fairly stable during the course of four years, at between 89 and 108 individuals (Glandt, 1982). In other cases the adult population size underwent heavy fluctuations: in north-west France the population size ranged from 16 to 346 individuals (Arntzen & Teunis, 1993) and in England the population size varied between 67 and 242 individuals (Baker, 1999).

Massive fluctuations in juvenile recruitment were observed at all four ponds where breeding occurred. The two larger ponds produced juveniles almost every year, the smaller ponds 3 and C frequently had no juvenile recruitment. Although they might have suffered from the failure to produce metamorphosed juveniles, neither of the smaller populations became extinct during the study period. A possible cause for the lack of juveniles at pond 3 was the lowering of the water level in the summer months, and the consequent failure of newt larvae to complete metamorphosis. The pond drying process is not uncommon, leading to a loss of a juvenile production in many amphibian species that breed in ponds (Berven, 1990; Pechmann *et al.*, 1989). The failure in juvenile recruitment at pond C following the introduction in 1992 may have been associated with high predation by numerous dragonfly larvae (*Aeshna cyanea*) and diving beetles (*Dytiscus marginalis*). Declines in juveniles of other syntopic amphibian species at the pond were observed prior to the introduction (Kneitz, 1998).

Eighty-three adults (63%) of 132 adults captured in 1994 were recaptured in 1995 and identified by their belly patterns. All adults except one female were recaptured at the same ponds in which they had first been captured. This suggests strongly that the movement of adult individuals between the ponds was rare between 1994 and 1995. The failure to move to other ponds may have been a function of the distance between ponds and the structure of the area. The ponds were located within an agricultural landscape at distances of not less than 300 m apart and pond 1, which held the largest local population of *Triturus cristatus*, was potentially isolated by a frequently-used road. Nevertheless, homing experiments by Blab (1978) and Müllner (1991) on adults of *Triturus cristatus* indicated an ability to move up to 800 m to a breeding site after being displaced during the breeding season. Other studies on breeding populations of great crested newts in France (Miaud, Joly & Castanet, 1993) and Germany (Wenzel, Jagla & Henle, 1995) indicated an exchange of adult individuals within the breeding season. However, these sites were located within 100 m of each other and the habitat between the ponds was suitable for newts. In contrast to the latter studies, the adult newts in our study expressed a high fidelity for their breeding pond.

In contrast to the adults, recently-metamorphosed great crested newts moved to neighbouring ponds up to 860 m away within a year of metamorphosis. The dispersal distance fits well with the presumed genetic dispersal rate of 1 km per year in a moving hybrid zone of *Triturus cristatus* and *T. marmoratus* in western France published by Arntzen & Wallis (1991). Pond D was probably first colonized effectively by juvenile newts in 1994. Given the pattern of production of juveniles in 1994 (Table 3), it is likely that the colonizers came from pond 2, 430 m away (Fig. 1). Sub-adult newts were recorded at pond D in 1995, and in 1996 and 1997 breeding activity was evidenced through egg counts. However, it was not possible to prove that the newts captured as juveniles in 1992 and 1994 were the breeders of 1996.

Although there are studies available on the colonization of newly-created ponds by great crested newts, it is not clear whether juveniles are the first animals to enter new ponds. For example, in a long-term study on the Danube crested newt, individuals entered two ponds at distances of 200 m and 700 m from the pond of emergence (Greßler, 1997). In Vienna, newly created ponds were colonized after at least two years. In another case study, in Britain, farm ponds were colonized at distances of up to 400 m from existing ponds (Baker & Halliday, 1999). Lenders (1996) recorded adult great crested newts colonizing ponds in the Netherlands in the first year after construction, within distances of 100 m.

In the present study the creation of new breeding habitats seemed a success for great crested newts. Two of the four newly-created habitats were used as breeding sites. However, the first immigrating great crested

newts were found after three years (pond D) and six years (pond B). The relative success of colonization was confirmed by means of egg counts after seven years at both sites. A more precise method of measuring successful recruitment should be obtained by quantifying metamorphosing juveniles.

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VARIATION IN DORSAL CREST MORPHOLOGY AND TAIL HEIGHT WITH AGE IN GREAT CRESTED NEWTS (*TRITURUS CRISTATUS*)

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Variation in dorsal crest morphology and tail height in males of a population of great crested newts (*Triturus cristatus*) was examined in relation to putative age. Newts were divided into three age classes according to the number of years that they had been recorded in the breeding population: first-year breeders, second-year breeders and long-term breeders. Crest morphology differed between the age classes, with a tendency for the crest's teeth to be more irregular in older males. We believe this is the first recorded evidence of age-dependent variation in a sexually selected, morphological character in an amphibian. However, it remains to be tested whether females distinguish between males on the basis of crest morphology. Body size (snout-vent length) and tail height, which is strongly correlated with crest size, also differed between the age groups: body size increased with age and males breeding for the first time had tails that were less tall than those of older animals.

Key words: great crested newt; *Triturus cristatus*; crest; sexual selection; age; courtship; behaviour

INTRODUCTION

Among urodeles, newts of the genus *Triturus* exhibit an unusually high degree of sexual dimorphism, and are unusual in lacking amplexus (Halliday, 1977; Duellman & Trueb, 1986). During the breeding season, males develop bold coloration, toe flaps, tail filaments, deep tail fins and, in most species, dorsal crests. The role of the crest of *Triturus* newts has a long history of attention (Darwin, 1871; Halliday, 1977; Green, 1989).

The dorsal and caudal crests of *Triturus cristatus* were noted by Darwin (1871) as examples of male ornamentation that have been sexually selected. The lack of amplexus in *Triturus* provides conditions under which such selection may occur through female choice (Halliday, 1977). Halliday's (1977) supposition that females select mates on the basis of crest size has been supported by experimental evidence: larger crests are associated with greater mating success in *T. cristatus* (Hedlund, 1990), *T. carnifex* (Malacarne & Cortassa, 1983) and *T. vulgaris* (Green, 1991; Gabor & Halliday, 1996). However, as Malacarne & Cortassa (1983) point out, such results can be ambiguous, as crest development is controlled by hormones that may also influence other, potentially confounding, factors such as courtship behaviour. For example, prolactin is involved in the development of the dorsal crest (Vellano, Mazzi & Sacerdote, 1970) and also in inducing courtship behaviour (Grant, 1966; Malacarne *et al.*, 1982). Males with better-developed secondary sexual characters also spend longer displaying to females, which in turn increases sexual attractiveness (Malacarne & Cortassa, 1983). Although methodological problems exist in separating the role of crests from other aspects of newt courtship, the positive association between tail height

(a measure of the caudal crest) and body condition in *T. cristatus* suggests that crest height potentially provides a reliable, fitness-related, cue (Baker, 1992).

The present study further investigates the crest of *T. cristatus* as an indicator of male quality by examining the relationship between crest traits and male age. Female preference for older males may be adaptive (Trivers, 1972; Halliday, 1978, 1983; Manning, 1985) and has been demonstrated in numerous species (Andersson, 1994; Kokko & Lindström, 1996; Kokko, 1998). In newts, males contribute only sperm to reproduction, so female choice can relate only to the acquisition of "good genes", as opposed to age-related male parental skills (e.g. Searcy, 1982). The argument that older males must have superior genotypes has been disputed by Hansen & Price (1995). They argue, for example, that genetic benefits associated with proven longevity will tend to be offset by deleterious age-related effects such as decreased male fertility and the accumulation of mutations in the male germ-line. Models developed by Kokko (1997, 1998), however, suggest that female preference for older males can be favoured by selection on the basis of a "good genes" effect. The present study examines the relationship between age and tail height, and between age and crest morphology, in *T. cristatus*, age being estimated from the number of years that individuals had been recorded in a breeding population.

MATERIALS AND METHODS

Great crested newts were captured at a pond on the campus of the Open University, Milton Keynes, England, during the course of an eight-year monitoring programme, from 1988 to 1995 (Baker, 1999). This programme entailed the annual registration of breeding adults to yield data on population dynamics. During the last year of the programme, 1995, the crest morphology of males captured between 4 April and 23 May was also recorded.

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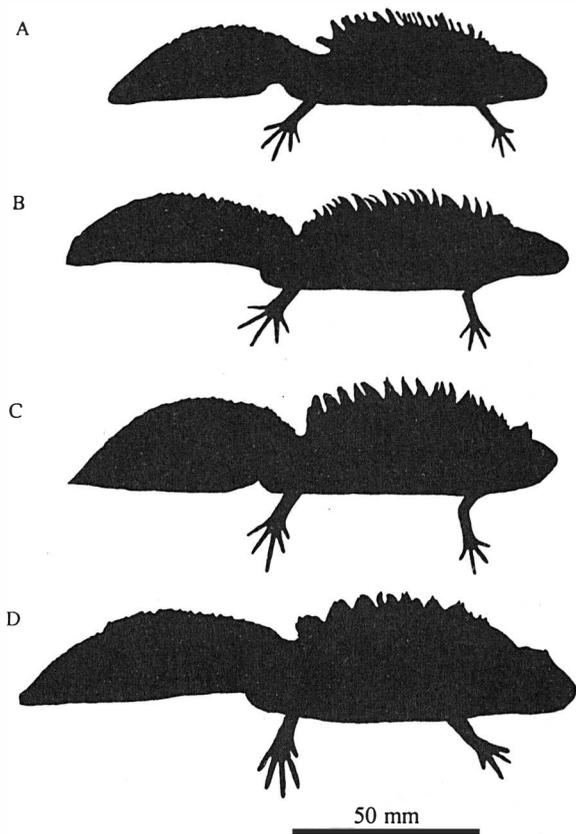


FIG. 1. Silhouettes of male *Triturus cristatus* showing variation in crest morphology. These illustrations were made by tracing the outlines of photocopied newts selected as representative of four different categories of crest shape. A, digitate; B, serrate; C, dentate; D, irregular. These males had been recorded in the breeding population for one, two, two and seven years, respectively.

Upon capture, each male was anaesthetized by immersion in a 1:1000 solution of MS222, placed on its side on a sheet of transparent plastic, and photocopied. The dorsal and caudal crests were laid flat with the aid of a small paintbrush. The lateral profiles of 112 males were recorded. The dorsal crest profiles were assigned to one of six categories on the basis of shape. The categories were defined as follows – (1) digitate: the projections of the crest form relatively regular, finger-like projections; (2) dentate: the projections of the crest form pointed, triangular-shaped projections; (3) serrate: the projections of the crest form relatively regular, sharp-pointed, backward-sloping teeth; (4) intermediate between digitate and dentate; (5) intermediate between serrate and either digitate or dentate; and (6) irregular: the crest profile consists of irregularly shaped projections. Fig. 1 illustrates some of the variation in crest morphology.

Snout-vent length (SVL) and the maximum tail height (TH) of anaesthetized newts were measured to the nearest 0.5 mm using a ruler with 1 mm graduations. SVL provided a measure of body size and TH was used as a measure of crest size. In *T. cristatus*, tail height, or the size of the caudal crest, is a more discrete character than that of the dorsal crest and hence more

accurately measured. The sizes of the two crests are highly correlated (Baker, 1992).

Male great crested newts were assigned to one of three age classes as follows: (1) newts recorded in the breeding population for the first time, referred to as first-year breeders; (2) newts recorded in the breeding population for the second year in succession, referred to as second-year breeders; and (3) newts recorded in the breeding population for more than two years (3-8 years), referred to as long-term breeders. Males in the study population bred for the first time at two years of age (Baker, 1999); hence, first-year breeders were assumed to be two years old, second-year breeders three years old and the long-term breeders more than three years old.

Ageing newts on the basis of the number of years for which they were recorded in the breeding population makes the assumption that all males were captured each year. Although this was not always achieved, the numbers of newts captured as percentages of the estimated population size were high: 100%, 77% and 86% in 1993, 1994 and 1995, respectively. So, although the number of years for which some individuals had been in the breeding population may have been underestimated, the number of newts concerned was small and unlikely to have affected the overall pattern that emerged.

RESULTS

The distribution of the six categories of crest morphology across age groups (Table 1) was examined using a contingency table and χ^2 analysis. Data from the second-year and long-term breeders were combined to achieve sample sizes large enough for statistical analysis. There was a statistically significant difference in the distributions of the crest shapes between first-year breeders and second year- and long-term breeders (χ^2 with Yates' correction = 36.65, $df=5$, $P<0.001$). In the first-year breeders, 54% had digitate crests and the remainder were spread fairly evenly across the other five categories of crest morphology. Among the second-year breeders, there was no large group of newts with digitate crests; instead, all males were spread evenly over the remaining five crest morphology categories. Among the long-term breeders, there were no digitate

TABLE 1. The distribution of six categories of dorsal crest shape across three different age classes (1, first-year breeders; 2, second-year breeders; 3, long-term breeders). Crest morphology categories are: 1, digitate; 2, dentate; 3, serrate; 4, intermediate digitate/dentate; 5, intermediate serrate and either digitate or dentate; 6, irregular.

Age class	Category of crest morphology						n
	1	2	3	4	5	6	
1	41	10	9	6	8	2	76
2	1	4	3	5	8	6	27
3	0	0	1	0	1	7	9

TABLE 2. The snout-vent lengths and tail heights of male newts from three age classes. Note that the *n* value for the second-year breeders differs from Table 1 because a body size measurement was not made for one of the males photocopied.

Age class	Snout-vent length			Tail height			<i>n</i>
	Mean	SD	Range	Mean	SD	Range	
1	71.1	4.86	60.0-82.5	17.5	2.78	10-23.5	76
2	77.7	3.20	71.0-84.0	19.2	3.11	13.0-25.0	26
3	84.5	5.63	75.0-90.0	20.0	3.41	14.5-24.0	9

crests, but instead a preponderance of irregular crest profiles (category 6).

Snout-vent length and tail height were measured for 111 of the males (Table 2). One-way ANOVAs indicated that both SVL and TH varied between age classes ($F_{2,108}=46.61$, $P<0.05$ and $F_{2,108}=5.073$, $P<0.05$, respectively). Tukey multiple comparison tests indicate that there were significant differences ($P<0.05$) in SVL between all three age groups: the long-term breeders were larger than first-year breeders ($q_{108,3}=11.66$) and second-year breeders ($q_{108,3}=5.39$), and second-year breeders were larger than first-year breeders ($q_{108,3}=8.92$). Long-term breeders and second-year breeders tended to have taller tails than the first-year breeders ($q_{108,3}=3.390$ and 3.485 , respectively), but there was no significant difference between the heights of tails of long-term breeders and second-year breeders ($q_{108,3}=1.042$). There was no evidence that relative tail height differed between the age classes. A one-way ANOVA of tail height as a fraction of snout-vent length was not statistically significant ($F_{2,108}=0.244$, $P>0.05$).

DISCUSSION

The data on crest morphology suggest that crest shape in this population of *T. cristatus* changed with the age of males. As age increased there was a progression from regularly shaped teeth to an irregular crest profile. If this is so, we believe it is the first reported case of age-dependent variation in a sexually selected, morphological character in amphibians. Older males were also larger than young males and had higher tails, although there was no evidence that tail height increased disproportionately to body size.

The observed differences in crest morphology may have been due to damage incurred as males aged. Longer-lived animals are likely to have sustained greater damage to their crests. In spite of the considerable regenerative abilities of newts (Smith, 1964), our observations on captive *T. cristatus* are that damaged dorsal or caudal crests do not regenerate completely, except in circumstances when the whole distal portion of the tail is lost. In *T. cristatus* in southern Britain, the dorsal crest is not completely resorbed outside of the breeding season, but persists in a much reduced form. Damage to the crest may thus persist between breeding seasons. Alternatively, the shape of the crest may change with age, irrespective of damage incurred. In either case, the shape of the dorsal crest in *T. cristatus* may provide a cue for discriminating between males of different ages.

Although crest morphology may provide cues pertaining to male age, it should be noted that the courtship of this species occurs in conditions under which subtle visual cues may be redundant: namely, at night (Zuiderwijk & Sparreboom, 1986; Green, 1989), and in ponds where water may be turbid. Under such conditions female discrimination between males may be based on more salient visual cues such as overall body size, or crest size, which would be consistent with data from a Swedish population (Hedlund, 1990). The present data indicate that such cues could allow age-related discrimination, as older males tend to be larger and have taller tails.

It is also possible that female *T. cristatus* do not rely on visual cues at all to discriminate between males. The courtship of *T. cristatus* also provides olfactory and mechanical stimulation (Green, 1989). Tail-fanning and lashing motions observed in this species may be detected by the female's lateral line organs (Green, 1989) or may deliver courtship pheromones (*sensu* Arnold & Houck, 1982) from the abdominal gland (Belvedere *et al.*, 1988). Green (1989) has suggested that the dorsal crest of *T. cristatus* serves no visual function during courtship, but instead aids the direction of pheromone towards the female.

A further consideration is that newts' crests may have evolved in response to selection agents other than within-species female mate choice. Crests may be significant in species recognition (Smith, 1964; Halliday, 1977) or they may function as auxiliary respiratory surfaces (Czopek, 1959), increasing the length of time that displaying males can remain submerged (Halliday, 1977). Finally, crests may play a role in intrasexual signalling. Male *T. cristatus* have been observed to display to other males, possibly in defence of courtship sites within a pond (Zuiderwijk & Sparreboom, 1986; Hedlund & Robertson, 1989).

The precise role of the newt crest has not been fully established, and the possible functions listed above may not be mutually exclusive. However, Baker (1992) has shown that in *T. cristatus*, the caudal and, by inference, dorsal crests are condition-dependent characters. The present data suggest that crest morphology in this species provides information on the age of a male. Information concerning both age and condition is potentially useful to females choosing mates. Whether *T. cristatus* uses this information as the basis for mate choice remains to be determined.

Although crest morphology changed with age in the population studied, variation within each age class was

too great to allow this cue to be used by a researcher wishing to precisely determine the ages of individuals. Nevertheless, it may be possible to gauge recent recruitment to a population by noting the proportion of males that have digitate crests.

An alternative explanation for the observed differences in crest morphology between age classes is that phenotypic differences between age cohorts reflected genotypic differences. For example, a newt with genes for a digitate crest may have contributed strongly to the cohort of first-year breeders. Although we cannot rule out such an explanation, on the basis of our observations we believe there is substantial evidence that crest shape in *T. cristatus* changes with age.

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LONG-TERM SURVIVAL AND GROWTH OF FREE-LIVING GREAT CRESTED NEWTS (*TRITURUS CRISTATUS*) PIT-TAGGED AT METAMORPHOSIS

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Twenty-one late-larval or newly-metamorphosed great crested newts (*Triturus cristatus*) were implanted with passive transponders (PIT tags) and released into the wild at their natal pond, in England, in 1996. Body mass at the time of release ranged from 0.69 g to 1.57 g, excluding the tag. Eight of the tagged newts were recaptured as breeding adults in 1999 (5 males, 3 females). Seven of the eight were recaptured again in 2000 (5 males, 2 females), along with four more tagged animals (3 males, 1 female). The mean annual survival over the four years from tagging and release in 1996 to the breeding season in 2000 was at least 85%. The tagged newts recaptured in 1999 were among the smallest in the breeding population that year, which was consistent with their being the youngest; this interpretation was supported by the appearance of a new group of similar-sized newts the following year. The growth of tagged newts between 1999 and 2000 was consistent with that of the population at large. Overall, we found high mean annual survival and normal rates of growth among great crested newts PIT-tagged at metamorphosis, indicating that the tagging procedure we used was benign. This use of PIT tags, which allow long-term and instant identification of individual animals, provides a means for investigating dispersal, colonization and metapopulation dynamics during the hitherto little-studied juvenile phase of the life cycle of this protected species.

Key words: PIT tags, newt larvae, marking methods, survival, growth

INTRODUCTION

There have been numerous studies of the survival, growth and reproduction of adult great crested newts, *Triturus cristatus* (e.g. Hagström, 1979; Verrell & Halliday, 1985; Francillon-Vieillot *et al.*, 1990; Miaud, 1991; Arntzen & Teunis, 1993; Baker, 1999). Such studies have been facilitated by the annual movement of adults into breeding ponds, which makes them susceptible to trapping by various methods, and by the fact that each adult can be identified by its unique, black-and-yellow belly pattern (Hagström, 1973). Although such studies have contributed much to our knowledge of the population dynamics of great crested newts, the juvenile period – between the times when newly-metamorphosed newts leave their natal pond and first appear as adults in breeding condition – remains very largely unstudied. This is because no satisfactory, long-term means of marking juveniles individually has been developed.

Practical considerations in choosing methods for marking newts and salamanders have been discussed recently by Henle *et al.* (1997) and Ott & Scott (1999), including the time taken to mark each animal, the cost of equipment, reliability and specificity of marks and the objectives of the study. Toe-clipping may be effective in the short term, but it is not reliable in the medium- to long term because of newts' capacity to regenerate lost digits, and because digits or limbs may be lost in other ways. Attempts to identify individuals or

particular groups of animals (e.g. size-classes) by clipping combinations of toes are particularly prone to uncertainty, owing to the greater probability that at least one of the clipped digits will re-grow to the extent that it is no longer recognizable.

The unique belly pattern of a great crested newt provides a potentially harmless means of "marking", requiring only that the animal be captured and photographed to record its identity. However, two limitations on the use of this method are (1) the instability of the pattern in juveniles (Arntzen & Teunis, 1993); and (2) the ever-growing magnitude of the task of comparing new records with previous ones, and the associated probability of making mistakes (Jehle & Hödl, 1998; Oldham & Humphries, 2000).

The use of passive integrated transponders (PIT tags) offers a tractable and increasingly affordable means of identifying individual newts quickly and reliably (Fasola *et al.*, 1993; Faber, 1997; Jehle & Hödl, 1998; Ott & Scott, 1999), and is particularly attractive for long-term studies. PIT tags are also particularly suitable for studies of dispersal, because tagged immigrants can be recognized without the need to catalogue members of any resident population. As with any means of marking wild animals, however, the potential long-term and sub-lethal consequences of implanting PIT tags in newts must be considered, both from an ethical standpoint and as a possible source of bias. Fasola *et al.* (1993) injected PIT tags into larval and post-metamorphic alpine newts (*T. alpestris*) and adult Italian crested newts (*T. carnifex*), using the metal cannula supplied for routine use with larger animals.

Although the smallest larva (1.3 g body mass) died, Fasola *et al.* (1993) found no adverse effects on growth or survival of the remaining tagged animals kept in captivity over the following six months; they recommended a minimum body mass of 2 g for newts to be PIT-tagged. Faber (1997) tagged and released juvenile and adult *T. alpestris* weighing 1.5–6.7 g, using the injection technique. He recaptured many tagged newts during the same season but did not test for adverse effects. Jehle & Hödl (1998) tagged juvenile and adult *Triturus dobrogicus* weighing more than 2 g, also by injection. They compared the recapture rate of tagged newts with the recapture rate of newts recognized using photographs of belly patterns, but recapture rates in all cases were too low and erratic to discount the possibility of adverse effects of tagging. Ott & Scott (1999) implanted PIT tags surgically in recently-metamorphosed marbled salamanders (*Ambystoma opacum*) weighing 1.7–4.1 g, and found no significant effect of tagging on subsequent growth or survival over a five month period in outdoor enclosures. Here, we describe PIT-tagging of late-larval and newly-metamorphosed great crested newts (*T. cristatus*), their release into the wild, and their survival and growth up to four years later.

METHODS

The study was carried out at a pond in Cambridgeshire, UK (national grid reference TL1878). The pond measures approximately 12 m x 3 m x 1 m deep when full and was created in 1994, within 100 m of a breeding pond that was subsequently destroyed during the widening of the A1 highway. Since 1995 an area of rabbit-grazed turf and scrub around the pond, maximum dimensions approximately 70 m x 40 m, has been largely enclosed by a fence of polythene sheeting about 1 m high. The fence was intended to confine the newt population to a safe area around the pond while construction work was under way, and until surrounding vegetation had re-grown, especially along a ditch which connects the site to nearby gardens and arable land. The fence has not presented a complete barrier to newts, but the site is now almost completely surrounded by roads and there is no other known breeding site within 1 km, so the population was effectively isolated during the period of study. The management plan for the site provides for the removal of the perimeter fence in 2001, when newts will be free to disperse. The fenced area includes two man-made refugia comprising heaps of rubble, capped with soil, within 5 m of the pond.

In the summer of 1996, 21 larval *T. cristatus* were rescued from the pond as it dried out (temporarily). Subsequently, as late-larval or newly-metamorphosed newts, they were tagged by one of us (CPC) using passive integrated transponders (PIT tags). The PIT tags used consist of a transponder encased in a glass capsule 11 mm long x 2.1 mm in diameter, total mass approximately 100 mg (Trovan system, AEG, supplied by

UKID Systems Ltd, Preston, UK). Each tag was supplied in a sterile, metal cannula which was not suitable for use with such small animals. Therefore, the tag was removed from the cannula and washed, then manipulated using forceps. Each newt was anaesthetized in a buffered solution of MS-222, a small incision was made in the side of the abdominal wall, behind a fore-leg, and the tag was inserted gently into the peritoneal cavity. The wound was then closed with a single suture. No antiseptic was used. Tagged newts were placed in a tank of shallow water (larvae) or a box lined with damp paper tissue (metamorphs) and were kept under observation for 2–3 days, during which time the wound healed over. The suture was removed without anaesthesia on the third day if it had not already dropped out. In larval newts, metamorphosis began immediately after tagging. Experience has shown that both larval and post-metamorphic newts will usually accept food as soon as the effect of the anaesthetic has worn off. However, to reduce the risk of disturbing the tag or the wound, food was not offered until the day after tagging. It was considered important to establish that each newt was able to feed and pass faeces before release. Immediately prior to release, each newt was weighed and its belly pattern was recorded. The tagged newts were released at the edge of their natal pond, shortly after dusk on three occasions when the weather was mild and wet: 20 August ($n=7$), 28 August ($n=2$) and 25 September ($n=12$), in 1996. By the time of their release, all the newts had completed metamorphosis.

We sampled the pond on four occasions between March and July in 1997, on five occasions between April and June in 1999, and on six occasions between February and June in 2000; we did not sample the pond in 1998. In 1997 we used bottle traps, but subsequent sampling was carried out by searching the pond margins after dusk and catching newts by hand or with a small, hand-held net. All newts encountered were photographed alongside a ruler and scanned for the presence of a PIT tag, and most were weighed to 0.01 g precision. We measured the lengths of the newts from photographs, using the ruler in the photograph for calibration (1 mm precision). We measured from the tip of the snout to the posterior end of the cloaca, which we found to be the most easily definable point in the cloacal region in males. We termed this measurement snout-vent length (SVL), although others may have used the same term differently (e.g. Arntzen & Teunis, 1993). We made allowances as best we could for curvature of the body and when more than one photograph was available in a breeding season (e.g. multiple recaptures), we used whichever showed the newt in the straightest posture, i.e. we assumed no growth during the breeding season.

In 2000, we estimated the proportion of adult newts we had encountered, and hence the number of tagged animals that we might have missed. To do this, we estimated the numbers of adult males and adult females in

the pond at the height of the breeding season, in mid-April, using belly patterns as individual marks. We were dealing with a closed population in which the proportion of animals susceptible to sampling (i.e. in the pond) increased during the early part of the breeding season, as animals arrived from their winter refuges on land; therefore, we did not use a mean estimate of population size derived from multiple-recapture data. Instead, we calculated simple Petersen estimates (Begon 1979) from our mid-April sample, assuming that all newts encountered previously in 2000 were still present in the pond at that time; this seems to be a reasonable assumption, given that courtship and egg-laying were still going on and that mean annual survival of adults was high. We based confidence intervals on the estimate of standard error given by Begon (1979), after Bailey (1951). As in many mark-recapture exercises, we do not know what proportion of the adult population was actually at risk of being captured.

RESULTS

TAGGING

All the newts accepted food readily on the day after they were tagged, and no adverse effect of tagging was apparent. Upon release, the mass of the newts, excluding the tag, ranged from 0.69 g to 1.57 g (mean \pm SD = 1.05 \pm 0.23 g).

SURVIVAL

None of the tagged animals described above was encountered in 1997. The first recaptures of tagged newts were made in 1999, when five males and three females were encountered among the breeding population. Seven of the eight tagged newts encountered in 1999 (five males, two females) were recaptured during the 2000 breeding season, along with another four of the tagged animals (three males, one female). Thus, at least 12 of the 21 animals tagged in 1996 were still alive three years later, in 1999 – a mean annual survival of at least 83%. Furthermore, at least 11 of the 12 tagged newts known to be alive in 1999 were still alive and breeding in 2000 – a mean annual survival of at least 85% over the four years. These are minimum values for survival, based on the numbers known to be alive. It is possible that other survivors went undetected.

We estimated the number of adult males in the pond in mid-April 2000 to be 104; the upper boundary on the 95% confidence interval was 116. After the mid-April sampling exercise we had encountered 96 different males, and by the final sampling exercise, on 21 June 2000, the total had risen to 98 males. Assuming that the great majority of breeding newts were in the pond in mid-April, it is likely that we missed about six males over the season (104-98=6), but unlikely that we missed more than 18 ($P\approx 0.025$, assuming 95% confidence intervals symmetrical about the mean estimate). Eight of the 98 males encountered were tagged, so if tagged newts were neither more nor less likely to be

TABLE 1. Initial body mass (excluding tag) and snout-vent length (SVL) at recapture of great crested newts implanted with PIT tags at metamorphosis and released into the wild in 1996, then recaptured in 1999 and/or 2000. n.c., not caught.

Ref. no.	Sex	1996 Body mass (g)	1999 SVL (mm)	2000 SVL (mm)
A1F4	F	1.00	68	73
D246	F	1.00	66	n.c.
D66E	F	0.88	64	69
DBA5	F	1.56	n.c.	76
6179	M	1.01	n.c.	71
9812	M	1.31	64	69
BF1E	M	0.81	65	72
C3D7	M	1.03	62	68
E450	M	0.85	64	72
E40B	M	1.27	n.c.	69
EBC6	M	0.92	65	72
F5B4	M	1.19	n.c.	71

captured than non-tagged newts, it is not unlikely that we missed one tagged male.

We estimated the number of adult females in the pond in mid-April to be 72, with an upper 95% confidence limit of 88. By 21 June we had encountered no females that had not already been encountered by mid-April, the total remaining at 61. Thus, we are likely to have missed about 11 females, but unlikely to have missed more than 27. Three of the 61 adult females encountered (i.e. 5%) were tagged. Extrapolating from that percentage, which is based on a sample of about 85% of adult females, and a best estimate of 11 females missed, it is not unlikely that one tagged female was missed over the season.

There was no significant difference between the means of initial mass of the tagged newts recaptured as adults and those of newts not recaptured: 1.07 (SD \pm 0.22 g) and 1.02 (SD \pm 0.25) g respectively, excluding the mass of the tag. The body mass at release in 1996 and snout-vent length (SVL) at recapture in 1999 and/or 2000 are listed for recaptured newts in Table 1. The body mass of recaptured newts at the time of their release was not correlated significantly with body length at recapture in either 1999 ($r=0.09$, $P>0.10$) or 2000 ($r=0.24$, $P>0.10$).

GROWTH

Without evacuating the gut contents of newts, we found that short-term fluctuations in body mass were too large for body mass to be a useful indicator of individual growth. Therefore, our analyses of growth are based on snout-vent length (SVL). To investigate the possibility that tags had an adverse effect on adults' growth, we used SVL data from all newts captured in both 1999 and 2000. We calculated separately for males and females a linear regression of SVL in 2000

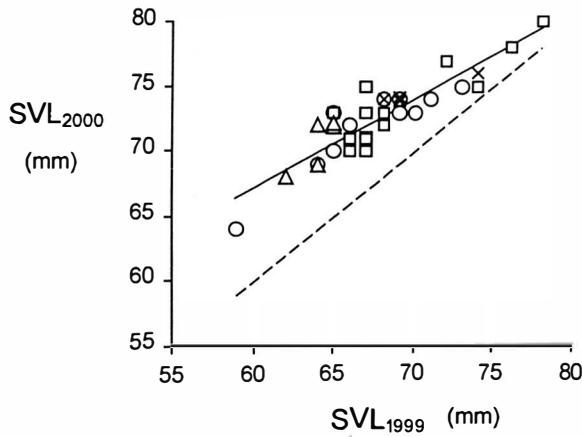


FIG. 1. The snout-vent length (SVL) of adult male great crested newts (*Triturus cristatus*) captured in 1999 and 2000 at a pond in Cambridgeshire, UK. Open triangles represent newts of the 1996 cohort, which were implanted with PIT tags at the time of metamorphosis. Other newts were recognized by their unique belly patterns and are labelled according to the year in which they were first encountered at the site: circles, 1999; crosses, 1997; squares, 1996. The solid line shows a least-squares regression of SVL_{2000} on SVL_{1999} for non-tagged newts; the broken line indicates $SVL_{2000} = SVL_{1999}$, i.e. no growth.

on SVL in 1999, excluding data from newts tagged as metamorphs in 1996. Figures 1 and 2 show that the increase in SVL of tagged newts between 1999 and 2000 was entirely consistent with the trends among other adult males and females during the same period. Because the tagged newts were at the (lower) end of the range of sizes of adults, it is important to note that the regressions shown in Figs 1 and 2 are not influenced by

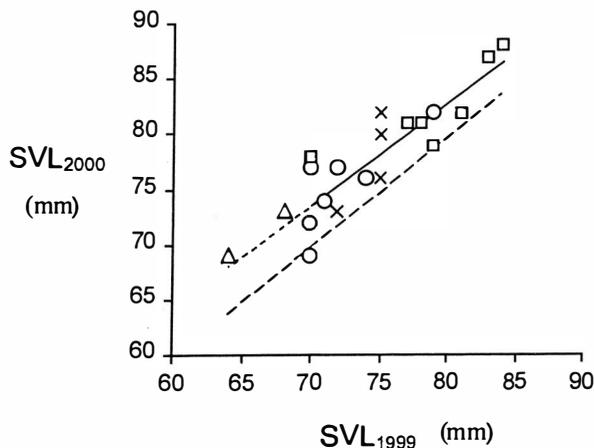


FIG. 2. The snout-vent length (SVL) of adult female great crested newts (*Triturus cristatus*) captured in 1999 and 2000 at a pond in Cambridgeshire, UK. Open triangles represent newts of the 1996 cohort, which were implanted with PIT tags at the time of metamorphosis. Other newts were recognized by their unique belly patterns and are labelled according to the year in which they were first encountered at the site: circles, 1999; crosses, 1997; squares, 1996. The solid line shows a least-squares regression of SVL_{2000} on SVL_{1999} for non-tagged newts and is extrapolated as a dashed line; the broken line indicates $SVL_{2000} = SVL_{1999}$, i.e. no growth.

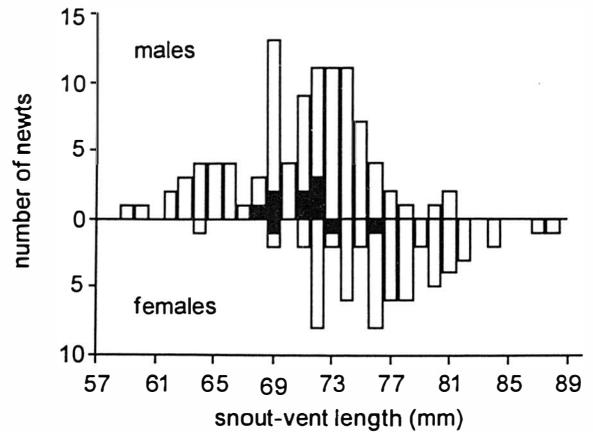


FIG. 3. The length-frequency distribution of great crested newts (*Triturus cristatus*) captured at a pond in Cambridgeshire, UK, in the year 2000. Filled bars represent newts of the 1996 cohort, which were implanted with PIT tags at the time of metamorphosis. Open bars represent newts of other cohorts, not tagged as metamorphs.

data from the tagged newts. The single instance of a newt's measured length decreasing between 1999 and 2000 may be attributed to the "error" inherent in measuring newts that are not at maximum extension. Other data points may be assumed to be subject to such errors, but we have no reason to suspect any bias.

The lengths of tagged males when captured in 1999 (62–65 mm, Table 1), aged three, corresponded well with the modal length of a group of males that were captured for the first time in 2000 and which were smaller than the tagged newts recaptured in that year (Fig. 3). In fact, 21 of the 22 non-tagged newts of $SVL < 69$ mm in 2000 were encountered for the first time that year; the other one was first seen in 1999 ($SVL_{1999} = 59$ mm, $SVL_{2000} = 64$ mm; Fig. 1). Because the pond dried out before any newt larvae had reached metamorphosis in 1996, albeit temporarily, we know that the tagged newts were the sole representatives of the 1996 cohort. Our current interpretation of the data is that the males of SVL 62–66 mm in 2000 were from the 1997 cohort and that the smaller males were probably from the 1998 cohort. Accordingly, we think that most males in this population matured at three years of age, with a minority maturing after two years (e.g. the male first encountered in 1999 with $SVL = 59$ mm). In that case, our observations would suggest that tagged males were not unusually small by the age of three. There are fewer data from which to make a similar comparison for females. In 2000, some of the females first encountered in 1999 were similar in SVL to the tagged females (Fig. 2) and it is pertinent to ask whether they were younger or older than the latter. We know that the former were already at least 69 mm long in 1999 (Fig. 2) and it seems unlikely that they could have reached that size in two years; accordingly, we think it more likely that those newts were from the 1995 cohort or earlier and that the 64-mm female encountered in 2000

(Fig. 3) was probably the first representative of the 1997 cohort. An alternative interpretation of the data is that the 1997 cohort was poorly represented in the adult population and that the smaller newts seen for the first time in 2000 were mostly from the 1998 cohort. Although we cannot refute that interpretation, we think it unlikely for the reasons given above.

DISCUSSION

The mean annual survival of the tagged newts in our study was higher than values reported elsewhere for free-living, non-tagged *T. cristatus* (e.g. Hagström, 1979; Dolmen, 1982; Francillon-Vieillot *et al.*, 1990; Miaud, 1991; Arntzen & Teunis, 1993; Baker, 1999). Even if the 12 recaptured newts were the only survivors in 1998, their mean annual survival in the first two years of terrestrial life would have been 75%, whereas other estimates of juvenile survival, from six- and eight-year studies, respectively, have been 17% (Arntzen & Teunis, 1993) and 59% (Baker, 1999). It may be that our study site was inherently less hazardous than those studied by others, though it was certainly visited by avian predators and grass snakes (*Natrix natrix*) and was disturbed by a variety of people erecting and removing fences, digging pitfall traps and removing vegetation from the pond. Also, if the urge to disperse is relatively short-lived, that may have contributed to the high rate of recovery of tagged animals in our study, as several days elapsed between tagging and release. The important point is not so much that annual survival was higher in our study than in others, but that it was as high as 85% over a four-year period – which is strong evidence that our tagging had little, if any, adverse effect on the newts' survival.

We cannot quantify any effect that tagging may have had on the newts' growth as juveniles. The tagged newts were among the smallest in the breeding population in 1999, but that was consistent with their being the youngest, aged three years, apart from one small male that may have been a two-year-old. We found no evidence that tags affected adult growth.

Arntzen & Teunis (1993) were able to recognize individual, juvenile *T. cristatus* in subsequent years from their belly patterns, as long as they were recaptured each year. However, the changes in belly pattern in the first few years of life make this method of recognition unreliable without such a complete record. In our study, tagged newts were first recaptured at three years of age and we could not have identified members of a free-living, unmarked, control group unequivocally. Therefore, we could not have made a direct comparison of survival or growth between tagged and non-tagged newts in the same cohort. In these circumstances, we believe that our results demonstrate as clearly as is practicable that judicious use of PIT tags in late-larval or newly-metamorphosed great crested newts is essentially benign.

Perhaps the most useful application of PIT-tagging great crested newts at metamorphosis is in the study of

dispersal, colonization and metapopulation dynamics. Little is known of the dispersal behaviour of great crested newts when they first leave their natal pond (cf. Kupfer & Kneitz, 2000; Hayward *et al.*, 2000), but in studying this behaviour it may be prudent to tag and release newts prior to, or soon after, the completion of metamorphosis. Although the range of detection of PIT tags is limited to about 15 cm or less, the tags can be used to locate and identify animals in dense vegetation or other inaccessible refuges (Faber, 1997). The ability to identify an individual quickly and unequivocally allows its displacement from previous, known locations to be determined reliably and with minimal disturbance. Furthermore, tagged animals that have dispersed from their natal pond and joined other populations can be identified as such simply by scanning members of the receiving population. PIT-tagging at metamorphosis also provides a means of ageing newts unequivocally, and is therefore an improvement on skeletochronology (Francillon-Vieillot *et al.*, 1990) and inference based on body size or fluctuations in recruitment (Arntzen & Teunis, 1993; Baker, 1999), particularly during the early years of life.

In theory, PIT-tagging should be permanent, but several authors have reported loss of tags (Faber, 1997; Jehle & Hödl, 1998; Ott & Scott, 1999). Usually, loss occurred shortly after implantation and may have resulted from incomplete closure of the wound or subsequent infection, allowing the tag to drop out. In this study, all the tagged newts were intact at the time of release. Another possible source of error is a failure of a tag to respond to the signal from the scanner. All the tags in our newts were working at the time of release, but of 40 unused tags from the same batch, two did not work when scanned in 2000. We do not know why those tags failed to respond, but it appears to cast some doubt on their reliability over the potential lifespan of a great crested newt.

Overall, we have demonstrated that PIT tags can be used to mark great crested newts individually at the time of metamorphosis, with little or no adverse effect on growth or survival. This methodology provides a means of investigating aspects of the hitherto little-studied, juvenile phase of the life cycle, particularly dispersal and metapopulation dynamics. In the UK a Home Office licence is needed to carry out the tagging procedure and this methodology is not available for routine monitoring.

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EVALUATING THE SUCCESS OF GREAT CRESTED NEWT (*TRITURUS CRISTATUS*) TRANSLOCATION

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Published evidence from 178 great crested newt population translocations in the UK carried out between 1985 and 1994 emphasizes the need for continued monitoring following translocation. In more than half the cases, there was insufficient evidence for judging success, mainly due to lack of monitoring. Using the liberal criterion of the presence of a population one-year following translocation, 37% of all cases were successful and 10% unsuccessful. Most of the failures were predictable from existing knowledge of great crested newt requirements. Conflict between development objectives and great crested newt conservation at a site in northern England prompted a large-scale translocation of over 1000 individually photographed adults to a conservation area immediately adjacent to the development site. During the first year following translocation, adult newts showed a strong tendency to move towards their previous breeding site, some travelling 500 m in doing so, but none reaching home ponds 900 m away. At least 60% of the translocated newt population either escaped from – or attempted to leave – the conservation area. The remainder accepted the ponds in the conservation area, some of which were less than one year old, and bred successfully. Population sizes were extrapolated from the results of trapping both outside and within the conservation area. The estimated density of adults in the conservation area, at 150 ha⁻¹, was high compared to that in the proposed development site (about 5 ha⁻¹). Nevertheless, in the first year the population in the conservation area showed good production of metamorphs, and mortality consistent with that found in previous studies. Furthermore, most recaptured adults had grown (median of 18% gain in mass) during the season. This was probably the result of the increased habitat diversity in the conservation area, especially the aquatic habitat. It must be recognised that this translocation procedure can be applied only to the adult component of the population.

Key words: *Triturus cristatus*, great crested newt, translocation, conservation, population size, survival, site fidelity

INTRODUCTION

The protected status of the great crested newt in the UK commonly leads to difficulties in land-use planning. Translocation, referring to the intentional transfer of populations from one location to another, presents an attractive solution. Seemingly, at a stroke, it frees the land for development and preserves the newt population. In consequence, the strategy is widely adopted in the UK and commonly accepted as a solution to land-use conflicts by the statutory conservation authorities. However, difficulties with the strategy are serious.

Firstly, in the UK there is no published evidence that the procedure actually works. A recent summary of amphibian and reptile translocation procedures (Clemons & Langton, 1998) is replete with prescriptions for translocation, but contains no evidence that the process is successful and few references to relevant research. Cooke & Oldham (1995) provide a case study of the translocation of UK populations of the common toad and common frog. However, for the toad there was heavy mortality of adults in the first year following introduction to the new site.

Secondly, even if it can be shown to work, there are often difficulties in selecting a suitable receptor site. Such a site must provide appropriate aquatic and terrestrial habitat and it may be difficult to establish that this is the case. An existing resident population at the receptor site provides good evidence, but in this case, the addition of new animals could result in the population size exceeding the carrying capacity of the habitat. In turn, this could increase the level of mortality of the combined populations, so defeating the objective of preserving the newts. A possible solution is to create new habitat or to enhance the habitat occupied by the existing population, but this presumes clear knowledge of the newt's requirements and the relationship between the environmental carrying capacity and the size of the introduced population. This is difficult to demonstrate, is usually taken on trust and – as will be seen below – is sometimes misinterpreted.

Thirdly, most – if not all – methods used to collect newts from doomed sites depend upon the collection of animals converging on, or leaving, breeding sites and so concentrate heavily on the adult component of the population. The limited evidence on newt life tables (Arntzen & Teunis, 1993, Halley *et al.* 1996) suggests that in a productive population about 70% of the population is comprised of non-breeding animals. Unless the

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process of interception is continued for several years, this non-breeding element is not included in the translocation.

The current paper addresses the first of these three issues. Two surveys of translocations conducted in the UK – the results of neither of which are widely available – will be reviewed, in search of evidence that the procedure is successful. The second part of the paper is concerned with an individual case study of translocation in northern England. This investigates whether a self-sustaining population of newts can be established in a “conservation area” following translocation. It reaches a reasonably encouraging conclusion, but with important provisos.

TEN YEARS OF TRANSLOCATIONS IN THE UK

Statutory protection was given to the great crested newt in the UK in 1982, following enactment of the Wildlife & Countryside Act 1981. In consequence, the Nature Conservancy Council (now English Nature) established a system of licensing to allow actions, including translocation, which would otherwise be prohibited under the Act (Gent & Howarth, 1998). Each successful applicant is permitted to undertake previously agreed actions, during a prescribed period, under a series of conditions. These include the requirement to provide details of the work carried out during the period covered by the licence. Since, in 1982 (or indeed today), there was no established method of ensuring successful translocation, the first licences were, in effect, granted for experimental translocations, based upon the best practice at the time. The accounts of translocations undertaken under licence thus, theoretically, provide an ideal opportunity to determine the factors militating for or against the progress of translocation efforts.

All the records held by English Nature up to 1990 were analysed by Oldham *et al.* (1991), partly as the result of commercial interest (British Coal). These covered eight years of recorded translocations, and included some cases undertaken earlier, before the enactment of the Wildlife & Countryside Act. Together these yielded a total of 86 exercises. The results were disappointing, with 26% – all from the pre-1982 period – having no quantitative records, and another 26% with records but with no attempt at monitoring. A further 20% involved garden ponds, important in a local sense, but unlikely to support viable long-term populations in their own right. For the remaining 25 field ponds (29% of the total) there were records of numbers moved and an effort to monitor. However, in eight of these cases the level of success could not be determined because there were already great crested newts at the recipient site and no means of distinguishing between residents and introduced animals. This leaves some 17 translocations (of between 8 and 540 newts, mean of 133) involving field ponds. Of these, 10 (12% of the original total) appeared to be successful, as newts were

present in the receptor pond at least one year following translocation. However, at the time of the study, in 1990, the mean monitoring period was only three years. Furthermore, although newts were observed at the 10 sites in subsequent years, they were rarely counted (four cases). There was only a single case where the data indicated that a breeding population was established at the new site following translocation.

Absence of adequate guidance was reflected in the reasons for the failure of 14 of the translocations (seven each for garden and field ponds). In all but one case, the failures were the result of poor translocation technique. All could have been predicted, even at that time, based on the known characteristics of the host site (e.g. presence of fish or ducks) – an unnecessary and regrettable waste of effort and resources.

Five years later, in 1995, an identical survey covering the English Nature records for the preceding five years, was conducted by May (1996). All the translocations were now covered by the licensing section and the level of recorded detail had improved accordingly. There was an increase in the extent of the practice, 92 cases compared to 52 in the equivalent period in the earlier study, and quantitative information was now available for every case. However, monitoring was still not universal, occurring in only 64% of cases, and there was no consistency in the monitoring procedure. Ideally, the success of translocation depends upon evidence of a self-sustaining population at the new site. Practically, this would have been very difficult to demonstrate, especially within the period of the survey. However, the return of adults in subsequent years and then, in turn, the presence of eggs, larvae and metamorphs provide increasingly convincing evidence of the successful establishment of a population at the new site. Most of the evidence (78% of monitored cases) came from the return of adults; in only one of the cases studied was the emergence of metamorphs used as an indicator of success. Using the minimal criterion of the presence of at least one adult newt in the year following translocation, 92% of the 59 monitored cases (59% of all cases) were judged to be successful. Again, procedures were sometimes used which could have been predicted to lead to failure, with existing knowledge, such as the removal of newts to a site only 250 m distant and with no newt barriers.

The proportions of cases falling into each category, from the 178 records in both surveys, are illustrated in Fig. 1.

CASE STUDY OF GREAT CRESTED NEWT TRANSLOCATION

A public inquiry into a planning application for an opencast coalmine in Lancashire resulted in a ruling by the Secretary of State for the Environment that further work should be conducted on the effects of translocation. A proposal was prepared by a biological consultant which involved setting aside parts of the

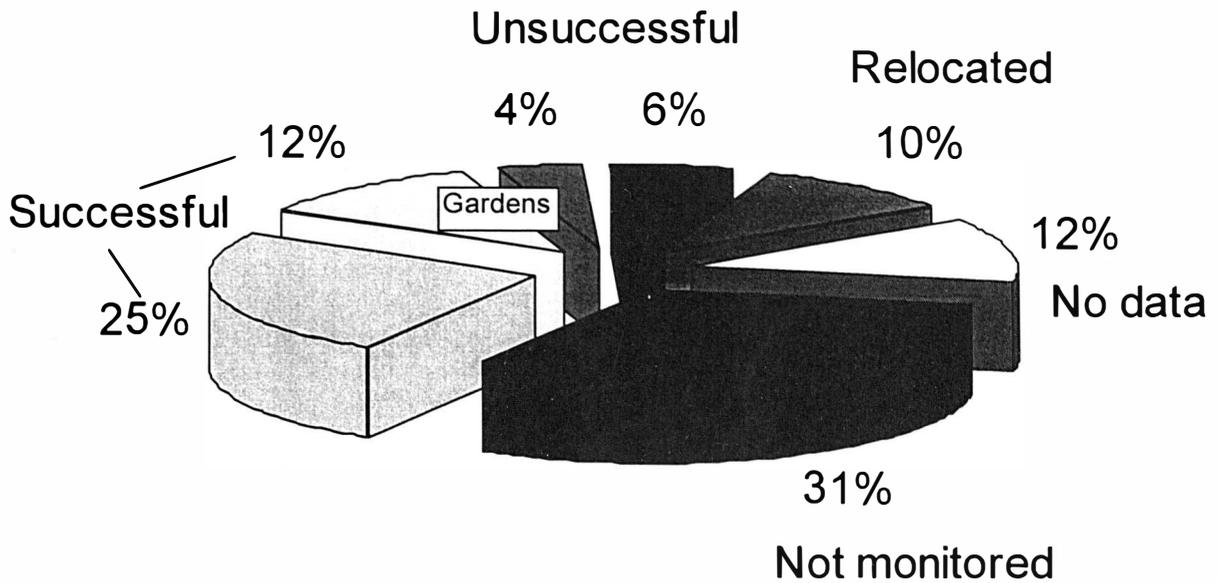


FIG. 1. The outcome of 178 translocations of crested newt populations in the UK before 1996. 'Relocated' newts were transferred to sites with existing populations. Most of the receptor sites were field ponds except for those labelled 'gardens'. (Data from Oldham *et al.*, 1991; May, 1996)

proposed opencast site as conservation areas specifically for great crested newts (Humphries *et al.*, 1991). Starting in 1991, newts were removed from several ponds within the proposed opencast coal site, their belly patterns were photographed, and then the animals were deposited into a single fenced conservation area, situated at one corner of the site. The effects of this translocation were investigated by monitoring the sites of recapture of a sample of the population (Horton & Branscombe, 1994).

The pilot conservation area – described by Horton & Branscombe (1994) – was 5 ha with a landscape typical of non-intensive agricultural use, containing pasture, hedgerows and five ponds (three permanent, two seasonal). The habitat was diversified by planting trees and shrubs and by introducing hibernacula. Three additional ponds were constructed. The conservation area was fenced using a polythene/chicken wire barrier, with newt pitfall traps inside and outside, to determine patterns of movement. A defect in the fence, overlooked by Horton & Branscombe (1994), was a four-metre gap on the south side, left to permit access of site vehicles. Newts were also monitored inside the conservation area by pitfall traps at fences surrounding some of the ponds, and by bottle-trapping (Griffiths, 1985) within the ponds.

Newts were intercepted during their seasonal migration to ponds on the proposed opencast site, using a combination of fences and traps. The interception programme continued for three years (1991 to 1993), but the current report is concerned only with the first two years, when 1090 newts were caught. They were all identified using photocopied belly patterns, then weighed, and following immersion in water for at least 12 hrs, transferred to a central release point inside the

conservation area in each of the years. Those captured at the outer perimeter of the conservation area (a total of 216 newts in 1991 and 1992) and captures at the inner perimeter (whether new animals or recaptures) were also placed at the central release point. Those caught within the conservation area in bottle traps and outside the fences around individual ponds were placed into the ponds (473 newts in 1992).

The paper by Horton & Branscombe (1994) and an earlier internal report (Branscombe & Horton, 1992) provide an account of the procedures used in the pilot project and of the numbers of animals involved in the translocations. The current paper attempts an analysis of the results of matching belly pattern photographs of the newts captured during 1991 and 1992. This was undertaken by De Montfort University on behalf of British Coal and was originally described in an internal report to the company (Oldham, 1993). The objective was to determine whether, in the early stages of the experiment, the conservation area would be likely to sustain a viable great crested newt population. We looked for evidence of a healthy adult population in the conservation area, as indicated by appropriate levels of survival, growth and metamorph production, and examined the population density supported by the habitat. The results of monitoring also provided an opportunity to examine the impact of site fidelity – whether there was a tendency for translocated animals to return to their home pools or to accept the pools in the conservation area as breeding sites.

Following privatization of the coal industry in 1994 the site became the responsibility of RJB Mining Ltd and the experiment was abandoned. To date, the proposed conservation areas have not been established and the opencast site has not been developed.

DATA ANALYSIS

BELLY PATTERN ANALYSIS

The total collection of photocopies was sorted into sets based on site, year and sex; only males were used in the present exercise. The next subdivision was based upon belly pattern. Two attributes were selected: the presence or absence of (1) longitudinally oriented groups of mid-ventral spots; and (2) low spot density on the posterior half of the belly. These criteria were applied successively and each sub-sample was further sub-divided into three groups. Two of them were comprised of animals clearly either possessing or not possessing the first attribute, (positive and negative groups). The third contained newts whose categorization was in doubt (intermediates). During the matching exercise, each site/date set was matched, in turn, with each of the other appropriate sets. Animals caught at the opencast site ponds were matched against those captured in the conservation area in the same year, and against those captured at any site in the following year. The positive and negative groups from each set were matched, respectively, against the positives and negatives of the other sets, whilst the intermediates were matched against both positives and negatives.

Once a match was detected, the individual patterns are so distinctive that a direct comparison of photocopies left no doubt about its validity. However, the matching process involved nearly 1000 animals, even when restricted to one sex; it was time-consuming and arduous, and the possibility of missing a match was very real, especially when photocopies were of poor quality. Control trials, involving photocopied and toe-clipped animals showed that as many as 14% of matches were missed on initial scanning (Oldham & Nicholson, 1984). However, there is no reason to suspect that individuals from one location were more likely to be missed than those from any other location, so results involving proportions are unlikely to be biased by any lack of matching efficiency.

POPULATION PARAMETERS

Information on population size, survival, and patterns of newt movement were obtained by monitoring at the conservation area barrier and within the conservation area, coupled with belly pattern matching. The monitoring exercise provided information on the production of metamorphs. Knowledge of barrier efficiency and the likelihood of capture within the conservation area are important in the determination of population parameters. Much of the evidence hinges on the recapture history of the male newts introduced into the conservation area in 1991 from both the source ponds on the opencast site and from the outer perimeter of the conservation area. They were recaptured, in both 1991 and 1992, in the conservation area ponds, at fences surrounding some of these ponds, at the inner and outer perimeter of the conservation area, or – in some cases – back at the source ponds.

RESULTS

BARRIER EFFICIENCY

The males represented 47% of the total catch of newts on the proposed opencast site in 1991. Of those transferred into the conservation area in 1991 (Fig. 2a, 2b), 59 were recaptured in 1992 (Fig. 2d) – about half (53%) still inside the conservation area, at the ponds, but the remainder outside it, either at the outer perimeter (9%) or back at the source ponds (39%). The suggested fence efficiency of 53% is a rough estimate and depends both upon uniform motivation to leave the conservation area and a comparable probability of capture inside and outside of it in 1992. In fact, for the relatively small proportion of natives amongst the recaptures (about 20%), motivation to leave the conservation area might have been lower than for the translocated animals (see below). Secondly, the probability of capture outside the conservation area might be lower than that for inside, owing to lower survival of animals travelling towards the distant ponds. If both these possibilities apply then on both counts the fence efficiency of 53% described above is an overestimate. The efficiencies of the barriers surrounding the conservation area and the source ponds were probably similar to that at the conservation area, as they were both constructed in the same way.

LIKELIHOOD OF CAPTURE

Three hundred and thirty-eight male newts were introduced into the conservation area in 1991 during the translocation exercise – 286 from the source ponds and 52 from the outer perimeter (Fig. 2a,b). Of these 131 were recaptured in the conservation area later in the same year. Monitoring during the same period in 1992 (Fig. 2d) provided an additional 59 recaptures, 33 of which were recaptured for the first time since release in 1991. The 33 animals are known to have been present in the conservation area in 1991, but not recaptured in that year. This gives us an estimate of $44 \pm 13\%$ (mean \pm 95% confidence limits) for the likelihood of capturing newts from the male population in 1991.

POPULATION DENSITY

All the ponds on the proposed opencast site were studied intensively for several seasons prior to 1991 and all known great crested newt breeding sites were completely encircled with drift fences. Hence, assuming that newts breed every year, the catches at these fences, corrected for observed fence efficiency, can be used to estimate the density of adult great crested newts in the existing agricultural landscape of the site. There were approximately four ponds km^{-2} (0.04 ha^{-1}) in the study area. If we assume newts to be dispersed within a radius of 500 m from the breeding ponds (e.g. Oldham & Nicholson, 1986; Baker & Halliday, 1999), then their density in the opencast site is approximately five adults ha^{-1} . This compares with densities of between five and 32 adults ha^{-1} on agricultural sites in Leicestershire

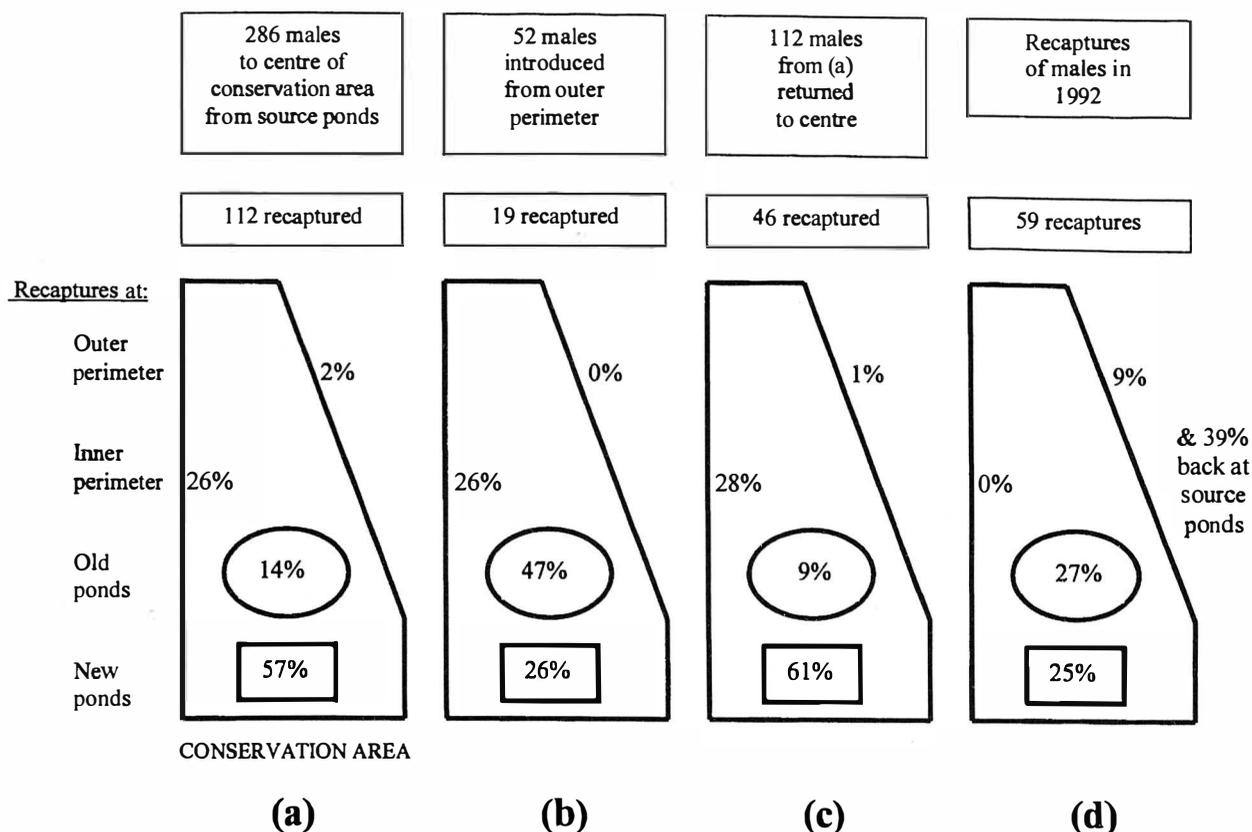


FIG. 2 Locations of recaptured newts following translocation: (a) from ponds mainly in the south and west into the centre of the conservation area in 1991; (b) from the outer perimeter of the conservation area, involving newts moving in from surrounding habitat in 1991; (c) returned again to the centre of the conservation area in 1991 after the first recapture (from (a)); (d) in 1992, involving newts first identified in 1991. The old ponds have existed for many years, whilst the new ponds were constructed early in 1991. Newts were collected from the inner and outer perimeter either from pitfall traps or from the base of the fence.

(Oldham, unpublished) and up to 1000 or more adults ha^{-1} in very good habitat (Latham *et al.*, 1996).

Adult newt density within the conservation area itself in 1991 can be estimated from four components. Two of these are known precisely: the numbers introduced from both the opencast site ponds (610) and from the outer perimeter of the conservation area (100). The third component, numbers "leaking" into the area past the conservation area perimeter fence, can be estimated from the calculated barrier efficiency (53%, see above) and adds about 50 newts. The fourth component, natives already present before the barrier was constructed, is more difficult to determine. However, it can be estimated crudely from the numbers of unidentified males caught within the conservation area, after correcting for sex ratio, inward leakage, likelihood of capture and pattern matching efficiency. The estimate for natives so obtained, of about 300 animals ($60 ha^{-1}$), provides a considerably higher density of newts than the overall value for the opencast site of $5 ha^{-1}$. This might be expected, however, given the high concentration of newt ponds in the conservation area, 20 times higher than outside, even before construction of the new ponds. Added to the numbers introduced, the overall adult total in the conservation area was estimated as 1060, about $210 ha^{-1}$. Even allowing for escapes, which would re-

duce the density to about $750 (150 ha^{-1})$, this is probably higher than ideal in the context of this agricultural landscape.

SURVIVAL

Individuals were "marked" photographically in early 1991, and monitored in the conservation area both later in 1991 and again in an equivalent period in 1992, using comparable effort. Of 338 marked males, 131 were recaptured at least once in 1991, but only 59 were recaptured in 1992 (Fig. 2). The difference provides a male survival estimate of $45 \pm 9\%$, comparable with the value of about 50% for adults quoted by Arntzen and Teunis (1993). There is no reason to believe that the survival of females differed significantly.

METAMORPH PRODUCTION

Metamorph emergence within the conservation area is described by Horton & Branscombe (1994). One hundred and thirty-five metamorphs were observed leaving the three newly created ponds in 1991 (the other three ponds were not monitored), and 567 from all six ponds in 1992. This information on metamorph emergence is relevant to recruitment into the adult population in 1993 at the earliest.

SOMATIC CONDITION OF NEWTS IN THE CONSERVATION AREA

Mass changes in a sample of 65 male newts recaptured during the 1991 season between early March and mid-July, during periods ranging between one day and 133 (median=44) days varied between the extremes of 52% gain and 29% loss. The median and mean changes in mass were both 18% gain. The largest gains occurred early in the season (an average of 1.6% per day during March), the smallest towards the end (0.2% between mid-April and mid-July). Horton & Branscombe (1994) noted that the mean masses of newts caught inside the conservation area were similar to those from outside it.

HOMING AFTER TRANSLOCATION

There is direct evidence that newts passed the conservation area barrier and had returned to their original ponds of capture by the following season. Of the 23 males known to have returned to a pond outside the conservation area, the majority (65%) were recaptured at the pond at which they were intercepted in 1991. Most of the remainder reached an alternative pond more or less *en route* to their original pond of capture. The distances moved ranged between 200 m and 500 m (median 400 m). No recaptures were made at source ponds 900 m distant. About half the translocated animals did not escape from the conservation area, although they may have attempted to do so. There is evidence of such attempts in the 29 males recaptured at the inside barrier of the conservation area in 1991. These constituted 26% of the 112 males recaptured in 1991 (Fig. 2a); most of the remainder were in the ponds. All recaptures (including the 112 males) were returned to the central release point within the conservation area (Fig. 2c). Forty-six males were recaptured yet again, of which 28% were found at the inner perimeter and most of the remainder in the ponds, a similar recapture distribution to that following first translocation.

If the numbers of animals actually escaping are taken into account (about 47%, see *Barrier efficiency*, above) and added to those apparently attempting to escape (26% of the remainder), we have about 60% of the introduced animals tending to leave the area. Some continued their efforts to escape (Fig. 2c), despite being returned twice to the centre of the area and therefore having further opportunities to enter the new ponds. This expression of site fidelity is further indicated by the behaviour of the newts originally caught at the outer perimeter of the conservation area (Fig. 2b) – presumably for the most part, natives of the original conservation area ponds. None of these animals was recaptured in ponds outside the conservation area in 1992. Furthermore, of the males from this set, which were recaptured in ponds in the conservation area, 9 (47%) were found in the three original ponds, rather than the three newly constructed ponds (Fig. 2b). The equivalent number for the introduced males was 16

(14%, Fig. 2a). Although the numbers recaptured are small, there was a significant tendency ($\chi^2=12.0$, $P<0.01$) for natives to be caught in the old ponds, and “foreigners” in the new ponds. This tendency appeared to have disappeared by the second year (Fig. 2d), when the proportions of recaptures in the new and old ponds were similar. In the first year following translocation site fidelity appears to be strong. Nevertheless, at least 28% of the 286 males (i.e. 80 of the recaptures) introduced from the external ponds (Fig. 2a) evidently accepted the conservation area ponds, especially the new ones, and used them as breeding sites.

Collectively, these data suggest that the newts transferred into the conservation area differed in their behaviour from the presumed natives of the area, those caught at the outer perimeter. If the translocated animals are treated as a separate set, then the proportion escaping or attempting escape rises to 70%, instead of 60% for the combined data.

DISCUSSION

One of the most striking aspects of the pilot project is the strength of the newts' tendency to return towards their previous breeding sites, and their ability to surmount carefully prepared barriers in doing so. Also striking, however, are the indications of the success of the translocation procedure. Despite the high density of newts in the conservation area there was evidence of acceptance of newly created ponds, reasonable metamorph emergence, individual mass gain and mortality comparable with other populations.

The calculated efficiency of the barriers used in this project are similar to those of between 18 and 69% (means of 42% for influx and 32% for exodus) determined in six studies of the great crested newt, using similarly constructed barriers (Amtkjaer, 1981; Verrell & Halliday, 1985; Franklin, 1993; summarized by Arntzen *et al.*, 1995). Most of the barriers in these studies were made in the course of research projects, inevitably constrained by a shortage of financial resources and often concerned only with obtaining a large sample of the population, not a total sample. It is possible to provide efficient barriers, and during population rescue, it behoves the responsible parties to make adequate provision using robust barriers in this regard.

In the population study by Arntzen & Teunis (1993), juvenile survival (from the age of one to two years) was approximately 20% and adult survival approximately 50%, similar to the present study. At these rates, an annual production of 2.5 metamorphs per adult would be needed to maintain a stable population, equivalent to an annual production of at least 1875 metamorphs needed at the conservation area to maintain the 1991 population level. No estimates of fence efficiency are available for the metamorphs, but being so much smaller, they are even more likely than the adults to evade capture and the estimate of annual metamorph production (567) is probably a serious underestimate. The observed level of metamorph production in 1992

may have been adequate to maintain the population. In the following year, however, metamorph production reduced to 182 (Horton & Branscombe, 1994) and this may be a reflection of overpopulation in the conservation area.

The recorded median gain of 18% body mass of males in the conservation area in the 1991 season occurred mainly during their aquatic phase. This information must be considered against the background of mass loss commonly reported for newts during the breeding season (e.g. Arntzen *et al.* 1999). Mass gain in the current study is particularly encouraging in view of the relatively high density of newts in the conservation area. It emphasises the importance of aquatic habitat enhancement in conservation management for great crested newt conservation.

Fidelity of adult amphibians to their breeding sites is well-reported (e.g. Twitty *et al.*, 1967; Oldham, 1967; Heusser, 1969; Sinsch, 1992). In extreme cases, individuals have been known to return to locations from which breeding sites have been obliterated (e.g. Jungfer, 1943; Heusser, 1964). There is some evidence, however, to suspect that fidelity might not be so marked in the great crested newt. Franklin (1993) has shown that new sites may be colonized by great crested newts within one year of their creation. This was also the case in the present study. The new ponds were made in the winter prior to the 1991 breeding season, yet 57% of the recaptured males (at least 22% of those introduced) used them (Fig. 2a). "Native" newts tended to use the old ponds (Fig. 2b). There was, however, marked variation in the acceptance of new sites by translocated adults. Allowing for catching efficiency it would seem that roughly 30 or 40% of the introduced animals quickly accepted the new ponds, whilst about 50% escaped from the area, some of them returning successfully to their previous breeding site. The remainder were captured at the inner boundary of the conservation area fence, apparently attempting to return. These animals attempted to return to their original site on more than one occasion, following replacement at the central release point (Fig. 2c). This tendency by part of the population might reduce the rate of population establishment at new receptor sites and it emphasizes the need to couple translocation with efficient barriers preventing the return of translocated newts.

In the current study, the maximum distance of translocation was 900 m and newts escaping from the conservation area returned only as far as 500 m. It is possible that animals transferred a greater distance, with cues from the home site unavailable, may accept the new site more readily than those that have been moved only a short distance.

The great crested newt spends a substantial part of its life in water. Terrestrial habitat is nonetheless important, especially for the largely terrestrial juvenile phase. In the present project efforts were made to enhance both (details in Horton & Branscombe, 1994), but with

particular emphasis on the aquatic habitat. This strategy appears to have been successful, enabling individuals to breed and produce metamorphs in the first year of the project.

Finally, it is important to recognise that most of the above work is based upon the adult component of the population. We still have no reliable method of capturing a high proportion of the juveniles during the period, lasting from two to three years, between metamorphosis and sexual maturity. The only method of ensuring that this large component of the population is incorporated into the translocation is to continue trapping for at least three years.

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4. For all papers the title page should contain only the following: title of paper; name(s) of the author(s); address of the Institution where the work was done; a running title of five words or less, and the name and address of the corresponding author with (if available) an email address. The text of the paper should begin on page 2 and be produced in the following order: Abstract, Keywords, Text, Acknowledgements, References, Appendices. Full papers and reviews should have the main text divided into sections. The first subhead will be centred in capitals, the second shouldered in lower case, and the third run on in italics. Footnotes are not permitted. *Short Notes* (generally less than six manuscript pages and accompanied by a single data set) should be produced as continuous text. A *sans serif* font (e.g. Universe or Helvetica) is preferred.
5. The usual rules of zoological nomenclature apply.
6. Tables are numbered in arabic numerals, e.g. TABLE 1; they should be typed double spaced on separate sheets with a title/short explanatory paragraph above the table. Horizontal and vertical lines should be avoided.
7. Line drawings and photographs are numbered in sequence in arabic numerals, e.g. FIG. 1. Colour photographs can only be included at cost to the author. If an illustration has more than one part each should be identified as (a), (b), etc. The orientation and name of the first author should be indicated on the back. They should be supplied camera-ready for uniform reduction of one-half on A4 size paper. Line drawings should be drawn and fully labelled in Indian ink, dry-print lettering or laser printed. Illustrations produced using other types of computer printer are not usually of suitable quality. A metric scale must be inserted in micrographs etc. Legends for illustrations should be typed on a separate sheet.
8. References in the text should be given as in the following examples: "Smith (1964) stated —"; "—as observed by Smith & Jones (1963)." "—as previously observed (Smith, 1963; Jones, 1964; Smith & Jones, 1965)". For three or more authors, the complete reference should be given at the first mention, e.g. (Smith, Jones & Brown, 1972), and *et al.* used thereafter (Smith *et al.*, 1972). For the list of references the full title or standard abbreviations of the journal should be given. Articles 'submitted' or 'in prep' may not be cited in the text or reference list. The following examples will serve to illustrate the style and presentation used by the Journal.

Bellairs, A. d'A. (1957). *Reptiles*. London: Hutchinson.

Boycott, B. B. & Robins, M. W. (1961). The care of young red-eared terrapins (*Pseudemys scripta elegans*) in the laboratory. *British Journal of Herpetology* 2, 206–210.

Dunson, W. A. (1969a). Reptilian salt glands. In *Exocrine glands*, 83–101. Botelho, S. Y., Brooks, F. P. and Shelley, W. B. (Eds). Philadelphia: University of Pennsylvania Press.

Dunson, W. A. (1969b). Electrolyte excretion by the salt gland of the Galapagos marine iguana. *American J. Physiol.* 216, 995–1002.
9. Final acceptance of a paper will depend upon the production by the author of a typescript, illustrations and computer diskette ready for the press. However, every assistance will be given to amateur herpetologists to prepare papers for publication.
10. Proofs should be returned to the Managing Editor by return of post. Alterations should be kept to the correction of errors; more extensive alterations will be charged to the author.
11. Twenty-five offprints and one complimentary copy of the Journal are provided free of charge. Further copies (minimum of twenty-five) may be purchased provided that they are ordered at the time the proofs are returned.
12. All submissions are liable to assessment by the editorial board for ethical considerations, and publication may be refused on the recommendation of this committee. Contributors may therefore need to justify killing or the use of other animal procedures, if these have been involved in the execution of the work. Likewise, work that has involved the collection of endangered species or disturbance to their habitat(s) will require full justification.

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SCIENTIFIC STUDIES OF THE GREAT CRESTED NEWT: ITS ECOLOGY AND MANAGEMENT

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