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

R. HAYWARD[1,2], R. S. OLDHAM[1,3], P. J. WATT[4] AND S. M. HEAD[2]

[1] *Department of Biological Sciences, De Montfort University, Scraptoft, Leicester LE7 9SU, UK*

[2] *The Northmoor Trust, Little Wittenham Nature Reserve, Little Wittenham, Abingdon, Oxfordshire OX14 4RA, UK*

[3] *The Old Vicarage, Coleorton, Leicestershire LE67 8FD, UK*

[4] *Department of Animal and Plant Sciences, Uiversity of Sheffield, Sheffield S10 2TN, UK*

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 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

Correspondence: Rachel Hayward, 4 Parcnoweth, Cury, Nr Helston, Cornwall, TR12 7BW, UK. *E-mail*: rachel@cury.demon.co.uk

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.

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
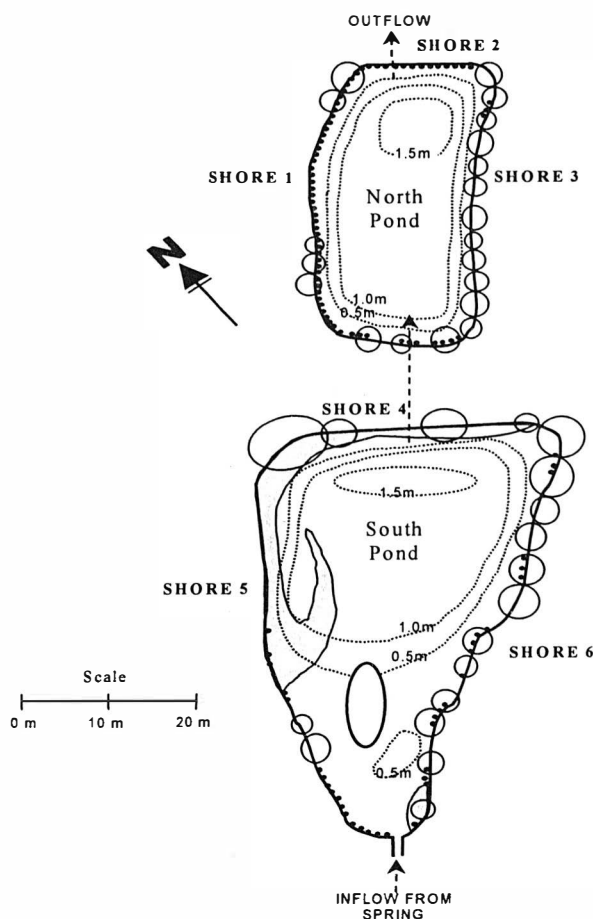

FIG 1. Map of the Little Wittenham study site. Thin dashed lines indicate water depth; thick dashed lines indicate water flow; circles and ellipses indicate overhanging trees; hatched areas indicate *Carex riparia* and black dots indicate *Carex distans*, the two major types of marginal vegetation.

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 to 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
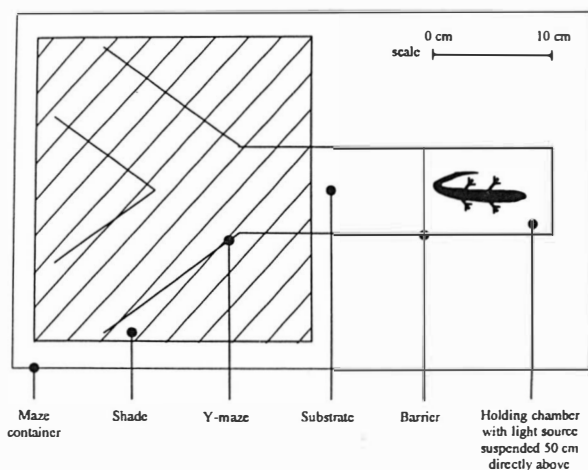
FIG 2. Y-maze used to test metamorph ability to follow cues
left on substrate previously traversed by a foreign adult newt.
The substrate was damp filter paper, changed for each test.
The light gradient, created by the light source and the shading
of the arms of the maze, provided the stimulus for the 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 deter-
mine 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 corru-
gated 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 re-
lease 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 differ-
ent 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 direc-
tion (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 re-
sponse 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, assum-
ing 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. Com-
parisons are indicated by double headed arrows and
resulting probability levels.

North Pond. (Fig. 3) Female dispersal was signifi-
cantly different from egg distribution around the pond
(χ^2=28.58, df=2, P<0.01). Egg and larval distribution
patterns in the North Pond were not significantly differ-
ent from each other (χ^2=4.66, df=2, P>0.05).
Metamorph dispersal followed a pattern significantly
different from the distribution of the larvae (χ^2=6.643,
df=2, P<0.05). Metamorph dispersal was significantly
different from that of adult female dispersal (χ^2=11.91,
df=2, P<0.01), but not significantly different from that
of adult male dispersal (χ^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 fe-
male dispersal were significantly different along the
east and west shores (χ^2=25.14, df=1, P<0.01, applying
Yates' correction). The eggs and larvae, when compar-
ing all three shores, had significantly different
distribution patterns (χ^2=1.88, df=2, P<0.01), though
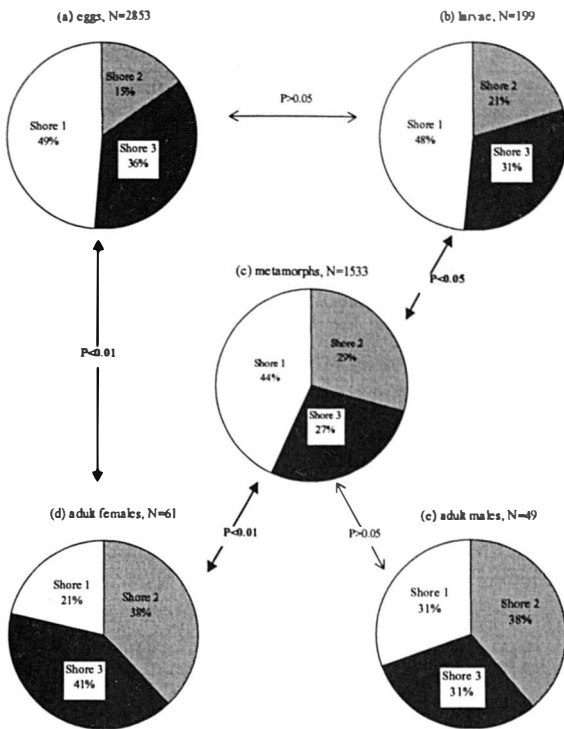the patterns of dispersion of eggs and larvae along east

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.
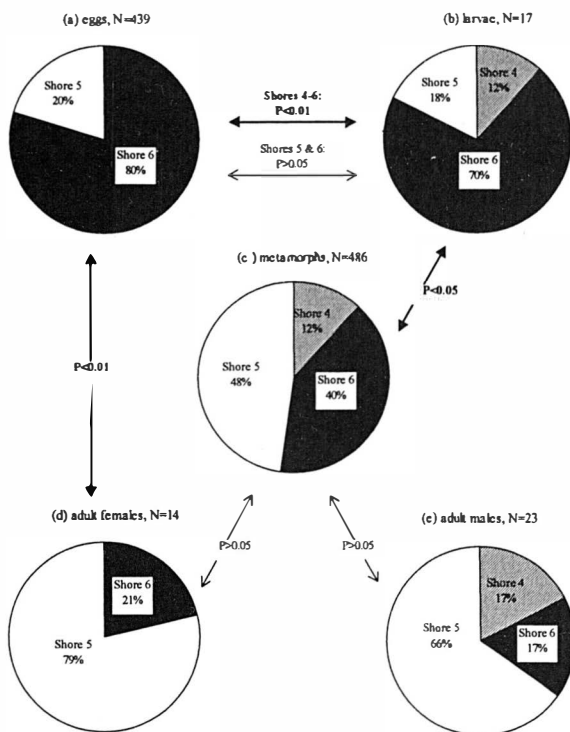

FIG 4. Dispersion patterns of the different life stages of the crested newt in the South Pond and a summary of their comparisons. Dispersion patterns were compared using chi-squared contingency tables. Bold arrows and probability levels indicate significant differences between the dispersion patterns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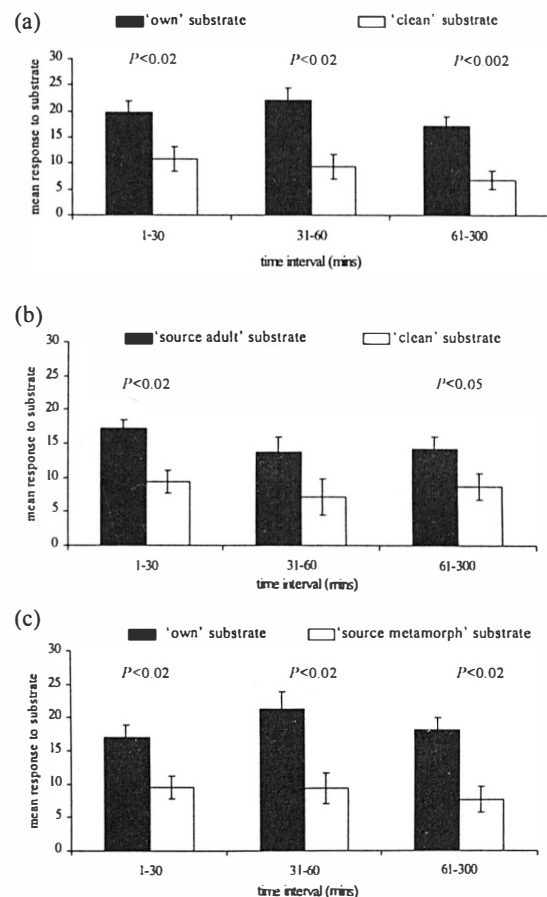

FIG 5. Responses of metamorphs in substrate preference tests, $N=24$: (a) own (i.e. previously used) substrate vs. clean substrate; (b) source adult substrate vs. clean substrate; (c) own (i.e. previously used) substrate vs. source metamorph substrate. Vertical lines show SE.
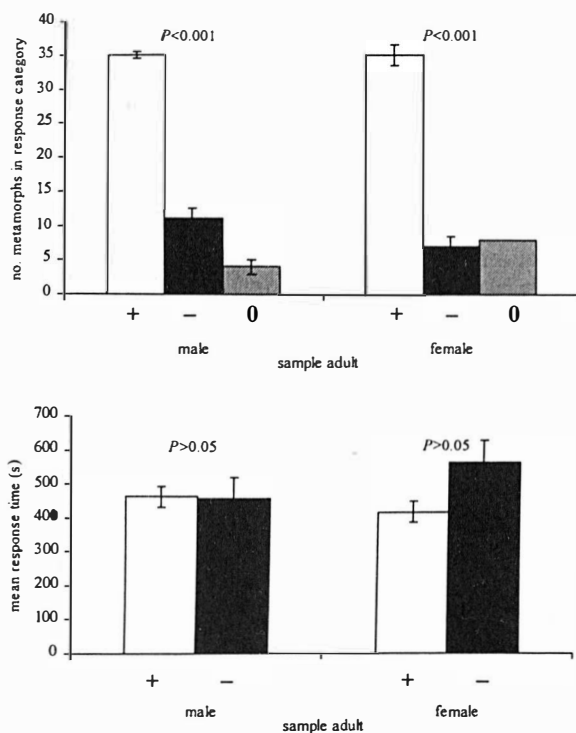
FIG 6. Responses of metamorphs in Y-maze tests: (a) numbers of test metamorphs in each response category (N=100) – metamorphs following the same path as source adults scored '+' (open bars), those taking the opposite path scored '-' (dark bars) and those not responding with in the time limit scored '0' (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 (χ^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 (χ^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 (χ^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 Pfennig (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. Pfennig'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.

ACKNOWLEDGEMENTS

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