

## HOW DOES A NEWT FIND ITS WAY FROM A POND? MIGRATION PATTERNS AFTER BREEDING AND METAMORPHOSIS IN GREAT CRESTED NEWTS (*TRITURUS CRISTATUS*) AND SMOOTH NEWTS (*T. VULGARIS*)

JAN C. MALMGREN

*Department of Natural Sciences, Örebro University, SE-701 82 Örebro, Sweden*

Migration patterns across a drift fence with pitfall traps were studied between 1997 and 1999 at a breeding pond with populations of great crested newts, *Triturus cristatus*, and smooth newts, *T. vulgaris*, at a study site in south-central Sweden. Metamorphs and older newts emigrated from the pond non-randomly and seemed to avoid exiting where open fields adjoined, but were oriented towards a patch of forest immediately to the east of the pond. Movement patterns changed slightly over the years, but metamorphs were more dispersed and less concentrated than older newts, and did not choose directions identical to those of older newts. Older great crested and smooth newts showed similar directional orientation. Great crested newt metamorphs dispersed towards both edges of the forest patch, and possible explanations for this are discussed. The results suggest that orientation in relation to cues from the surroundings of a breeding pond may be used by newts to make migratory decisions.

*Key words:* Amphibia, behaviour, conservation, dispersion, circular statistics

### INTRODUCTION

Pond-breeding newts of the family Salamandridae are capable of remarkable homing and orientation (e.g. Cummings, 1912; Grant, Anderson & Twitty, 1968; Joly & Miaud, 1993), and make interesting models for studies of migration (see Glandt, 1986; Sinsch, 1991; Dingle, 1996). Adults often show high breeding site fidelity and individuals frequently return to their natal site (Griffiths, 1996), possibly due to their constraining demands for complex landscape structures with high connectivity (Fahrig & Merriam, 1994; Hanski, 1999; Marsh & Trenham, 2001). For example, it has been demonstrated that the occurrence and abundance of newts is related to the presence and width of uncultivated habitat sectors (Oldham, Keeble, Swan & Jeffcote, 2000; Joly, Miaud, Lehmann & Grolet, 2001), which connect or constitute primary landscape elements. When newts are leaving a breeding pond they usually travel in straight lines and seem to move towards favourable habitat patches in the vicinity (Verrell, 1987; Sinsch, 1991; Macregor, 1995; Jehle, 2000; Jehle & Arntzen, 2000). This indicates that individual newts try to optimize the use of available spatial units (Sinsch, 1990) and that suboptimal choices can be costly. An important mechanism to facilitate such migratory behaviour is presumably the ability to use chemical cues (see Joly & Miaud, 1993; Joly *et al.*, 2001). Hayward, Oldham, Watt & Head, (2000) suggested that metamorphs of great crested newts, *T. cristatus*, detect and follow cues left by piloting adults, which could be an important strategy enabling individuals without any experience of the surroundings to find suitable habitats. This requires, however, that

adults can identify areas favourable for dispersal or for terrestrial activities. The present study focuses on questions related to this problem. In particular, are migration patterns directed towards habitat patches that are preferred by newts in different life stages? Furthermore, do newts have stronger directional responses to such habitats as they get older, and are there detectable differences in orientation and dispersion between newts in different stages of life, or even between closely related species? I studied migratory movements across a drift fence with pitfall traps from 1997 to 1999, at a pond in south-central Sweden, as part of a population study of great crested and smooth newts (*T. cristatus* and *T. vulgaris*, respectively). The questions addressed here may be interesting from a general biological perspective, but detailed knowledge about migratory behaviour can also prove critical for conservation efforts (Sutherland, 1998; Marsh & Trenham, 2001).

### METHODS AND MATERIALS

The site used for this study is a circular cattle pond located in Lanna (59°15'N 14°56'E, altitude 110 m), 25 km W of Örebro in south-central Sweden. It contains breeding populations of great crested and smooth newts, and has a surface area of 300 m<sup>2</sup>, with a maximum water depth of approximately 1.8 m in spring and 0.8–1.0 m in warm and dry summers. The central part of the pond has a dense floating mat of water moss (*Drepanocladus*), with a small stand of reedmace (*Typha latifolia*) to the west. An open littoral zone dominated by broad-leaved pondweed (*Potamogeton natans*) and submerged grasses is present around the pond. Within 100 m of its perimeter (Fig. 1A) the pond has open pasture and meadow on its western half, and a spinney of birch (*Betula pubescens* and *B. pendula*), ash (*Fraxinus excelsior*) and aspen (*Populus tremula*) on its eastern half. This forest element, which consti-

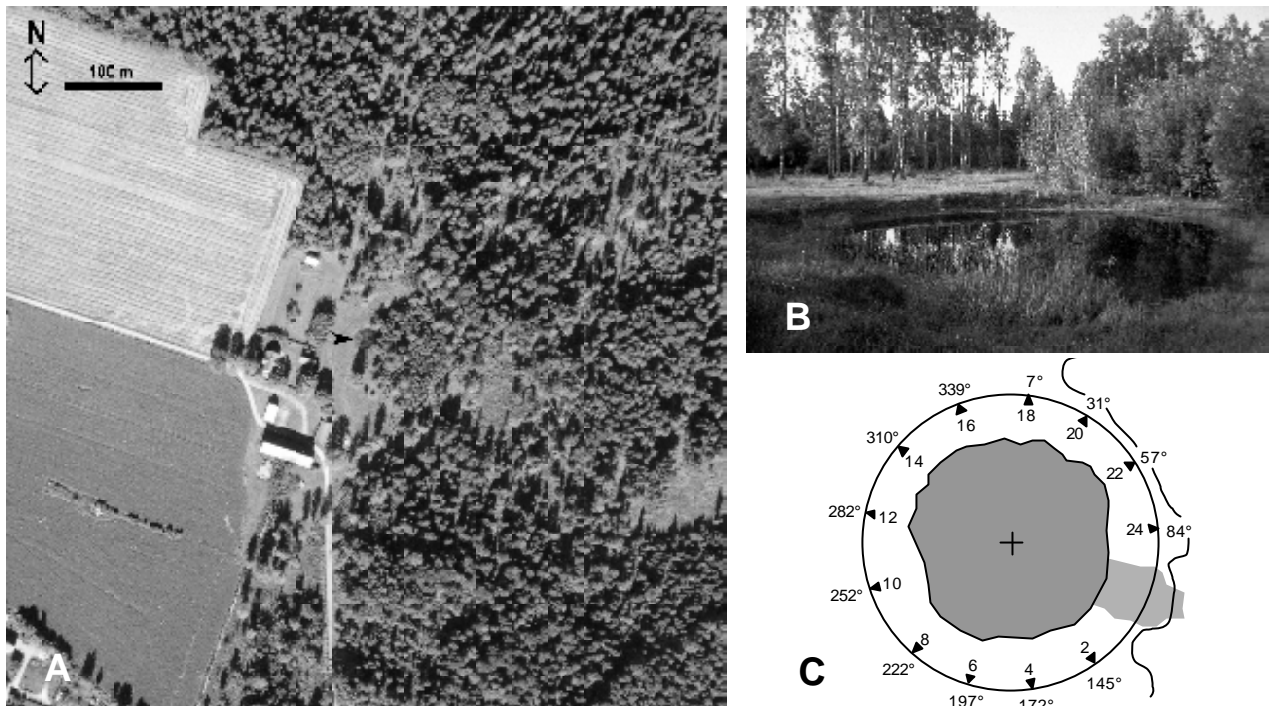


FIG. 1. A, aerial photo of the study site, with the pond at centre (arrow). Photo courtesy of the Swedish National Road Administration. B, photo of the pond taken from the south in the season before drift fences and pitfall traps were installed. C, plan of the pond, with triangles depicting trap locations with associated numbers and compass bearings relative to the pond centre. A trap was not placed in the seasonally flooded southeastern segment (shaded). To compensate for this, the midpoints of trap grouping intervals were used for traps 2 and 24 ( $136.5^\circ$  and  $92.5^\circ$  respectively) in all analyses. The outline of the forest sector immediately adjacent to the eastern half of the pond is drawn into the figure.

tutes a circular patch with a diameter of 100–120 m, covers a sector from approximately  $9^\circ$  to  $137^\circ$  and lies 1–3 m from the perimeter fence. There are a few, single, large birches located in the pasture directly to the north. At a distance of approximately 100 m further to the north, south and east of the pond, a wide band of old forest dominated by spruce (*Picea abies*) and hardwood (see above) replaces the old pasture. At the same distance to the west, the open pasture and meadowland is replaced by extensive arable fields.

The breeding pond was completely encircled by a drift fence with pitfall traps and has been monitored continuously from 1997. The fence was constructed of UV-resistant plastic sheets stretched between poles with wire and presents a barrier 50–60 cm above ground and 10–20 cm below. Plastic 10-litre buckets, buried with the rim at ground level and placed firmly against the fence, were used as pitfall traps ( $n=25$ ). Traps were placed alternately on the inside (facing the pond,  $n=12$ ) and outside of the fence ( $n=13$ ). The distance between traps on each side of the fence was 6 m, and the total length of the fence was approximately 75 m. A single interruption of the even distribution of traps was caused by a boggy and seasonally flooded area at the south-eastern segment of the fence (between traps 2 and 24, which were separated by 12 m; see Fig. 1C). The average distance between the fence and the pond shoreline varied between 3 m and 4 m over the season.

The traps had a 10 cm depth of water at all times and were checked every 1–3 days, when the water was changed and trapped animals were registered. The data presented in this paper are based on newt captures from pitfall traps on the pond side of the fence during three years of outward migration episodes (1997–1999). Great crested and smooth newts were counted, size-classed and sexed before being released on the outside of the fence. Only two size- or age-classes (hereafter referred to as life-stage classes) are used in the analyses presented here – *metamorphs* (i.e. young of the year) and *all other ages* pooled (i.e. post-metamorphs, including juveniles and mature adults).

Since captures were made at a circular fence with a fairly even distribution of pitfall traps, single observations of migrating individuals can be treated as vectors for certain directions. I therefore used circular statistics (Mardia, 1972; Batschelet, 1981; Upton & Fingleton, 1989; Fisher, 1993) to analyse migration patterns in population samples. I assumed that individuals wandered in a fairly straight line from the pond to meet the fence and fell into one of two traps closest to their point of exodus, which is a common supposition of drift fence studies. All traps were further assumed to be equally effective at catching newts, so producing a statistically valid sample of emigrating newts for all directions. Compass bearings for all traps were established and confirmed in winter, relative to the pond

TABLE 1. Emigration dates for great crested and smooth newts (*Triturus cristatus* and *T. vulgaris*) from 1997 to 1999 at a breeding pond in south-central Sweden. Onset (first observed emigrant), end (last observed emigrant) and duration (number of days) of emigration for each year, species and life stage class (metamorphs and all other ages).

	Class	Onset	End	Duration
<i>T. cristatus</i>				
1997	Older	10 June	8 August	59
	Meta.	27 July	23 October	88
1998	Older	21 May	29 July	69
	Meta.	18 June	3 November	138
1999	Older	1 June	19 July	48
	Meta.	30 June	21 October	113
<i>T. vulgaris</i>				
1997	Older	16 June	16 September	92
	Meta.	3 August	16 November	105
1998	Older	1 June	10 September	101
	Meta.	9 August	29 October	81
1999	Older	24 May	23 September	122
	Meta.	23 August	21 October	59

centre. The data were treated as grouped (with 12 angular orientations) in all analyses, and to compensate for the gap in the distribution at the south-eastern segment of the fence, traps 2 and 24 were assigned the values of the midpoints of their grouping intervals (Fisher, 1993), which corresponded to 136.5° and 92.5°, respectively. These bearings were used in all analyses reported here. This procedure contributes statistically to minimizing the effect of too large sample intervals, but may sacrifice intuitive interpretation. Sample distributions were assessed both graphically (by linear histograms and uniformity plots) and formally (test of randomness against any alternative) to establish modality (Fisher, 1993). Rayleigh's uniformity test was used to test the hypothesis of random dispersal against the alternative of preferred directions for samples with unimodal distributions. Samples that had bimodal or multimodal distributions were tested with Rao's spacing test for one-sidedness against the alternative of random dispersal, implemented as a special case of empirical coverage permutation tests (Mielke, 2001), with the statistical software 'Blossom' (Cade & Richards, 1999). This test is an alternative to Rayleigh's test for detecting departures from uniform distributions when multimodality is suspected. However, it may be sensitive to grouped data, so interpretations from the results must be made with caution. Tests of differences in directional orientation between samples were performed through a multi-response permutation procedure (MRPP). This method is based on distance functions (Mielke, 2001), has the advantage of not being sensitive to the underlying modality of the data, and compares grouped data in a way that is analogous to a one-way analysis of variance. The null hypothesis

tested with MRPP is that circular distributions are identical for the samples compared. The test detects departures under the alternative hypothesis, due to differences in mean and median angles, angular dispersion, number of modes or any combination of these effects, where the samples are non-identical. MRPP analyses were run in 'Blossom' by class (metamorphs, all other ages), and for pooled samples of class and species within and across years. The hypothesis of differences in the strength of directionality between samples was tested through a separate test for the concentration parameter, following Fisher (1993). Moreover, chi-square tests were used to test whether the samples were distributed towards the forest element immediately adjacent to the eastern half of the pond, and Student's *t*-test was used to test for differences between classes in the mean duration of the emigration episodes.

## RESULTS

A total of 8600 observations of newts leaving the pond were made at the drift fence during the course of the study (recaptures included). Great crested newt observations numbered 1926 (22%), with metamorphs comprising 63% and all other ages 37%. Smooth newt observations numbered 6674 (78%), divided into 83% metamorphs and 17% all other ages. Onset, duration and end of emigration episodes varied over the years (Table 1). The duration of outwards migration was significantly different between the classes of great crested newts: the mean ( $\pm$  SE) for metamorphs was 113 $\pm$ 27 days, while that for older newts was 59 $\pm$ 12 days (two-tailed *t*-test:  $t=3.47$ ,  $df=4$ ,  $P=0.0256$ ). The overlap of the two classes' periods of emigration varied from 12 days to 41 days. Smooth newts did not show a similar difference between classes in the duration of emigration periods ( $t=1.46$ ,  $df=4$ ,  $P=0.2181$ ): metamorphs emigrated over periods of 82 $\pm$ 25 days and older newts over periods of 105 $\pm$ 17 days. The overlap in emigration periods of newly-metamorphosed and older smooth newts varied between 31 and 44 days. Observations of actual dispersal from the pond were mostly made at dusk, but metamorphs and older newts of both species were occasionally observed at the fence during rainy days. Whether classes and species left the pond at different hours was beyond the scope of this study, mostly due to time and resource constraints.

Dispersal of great crested and smooth newts from the breeding pond was non-random in both life stages and in all years (Fig. 2). The null hypothesis of uniform distributions could be rejected for all samples in favour of modal differences among life stages after graphical assessments and formal tests. All samples of older newts, as well as metamorphs of both species sampled in 1997, had approximately unimodal distributions with preferred directions towards the forest patch (Rayleigh's test, all  $P<0.0001$ ), whereas samples of metamorphs from both species over 1998 and 1999 dispersed one-sidedly (Rao's spacing test, all  $P<0.0001$ ) but tended to

have distributions that were either bimodal (*T. cristatus* 1998, 1999) or even multimodal (*T. vulgaris* 1998, 1999). The proportion of newts caught in traps on eastern (traps 18–4 pooled,  $n=6$ ) vs. western (traps 6–16 pooled,  $n=6$ ) halves of the fence perimeter (i.e. towards or away from the adjacent forest edge, respectively) differed significantly (chi-squared tests, all  $P<0.0001$ ). Thus, there was a strong grouping of newts in traps on the eastern half, facing the adjacent forest (metamorphs 66–79%, adults 81–90%). A similar, but slightly weaker difference was detected in the proportion of newts caught at northern (traps 12–22 pooled,  $n=6$ ) vs. southern (traps 24–10 pooled,  $n=6$ ) halves of the fence (chi-squared tests, all  $P<0.05$ ), with the northern half being preferred (metamorphs 53–67%, adults 58–83%). Overall, this shows that there was a tendency in all samples for newts to orientate towards the forested area immediately adjacent to the pond (which covers bearings  $9^\circ$ – $137^\circ$ , roughly corresponding to the sampling intervals included by traps 18, 20, 22, 24 and 2), as is evident from Fig. 2. Older newts had a strong directional response towards this specific habitat patch, with the exception of smooth newts sampled in 1999. When the life stage classes were compared for the concentration parameter (Table 2), metamorphs consequently showed a significantly weaker directional response than older newts, again consistent in all groups except for smooth newts in 1999 (Fig. 2). Thus, metamorphs were in general more dispersed than older newts, which suggests that age-related factors affect how strongly newts are drawn to certain directions. Furthermore, metamorphs tended to disperse towards the edges of the adjacent forest patch, rather than straight into it as older newts did. This pattern was particularly evident in great crested newts (Fig. 2). A comparison between great crested and smooth newts revealed no consistent interspecific difference in the strength of the directional response (using the concentration parameter), either in metamorphs or in older newts.

Significant differences in movement patterns were observed in both species when circular distributions of emigration directions were analysed within and among life stage classes (Table 3, Fig. 2). Differences were consistent both when the classes were compared for single years and across years (MRPP, all  $P<0.01$ ). Analyses from MRPP and the circular histograms show that older newts of both species were distributed towards the forest patch to the east. The differences between years within this life stage, regardless of species, indicates that the angular distributions in at least one year differs from the others with small chance that this is due solely to sampling variability. In great crested newts, a larger proportion of post-metamorphs moved to the east in 1998 and 1999 than they did in 1997, when the larger proportion moved east-north-east. The difference in older smooth newts is explained by the observation that in 1999 a larger number of newts dispersed towards the edges of the forest patch than they did in 1997 and 1998. Similar reasoning can

be applied to analyse test results from MRPP on metamorphs, where the proportion of individuals moving towards the forest edges comprise the largest contributing factor to explain the differences. When data for all years were pooled, there were differences in the distributions of great crested and smooth newt metamorphs emerging from the pond (MRPP,  $P<0.0001$ ). The major difference among years appears to be due to differences in the proportions of newts that emerged from the pond in relation to the edges or the centre of the adjoining forest patch. The only comparison of distributions where great crested and smooth newts did not differ was when data on all years were pooled for post-metamorphs (MRPP,  $P=0.1572$ ). This observation suggests that older great crested and smooth newts had similarly strong preferred orientations towards the north-eastern sector of the pond perimeter as a route for emergence.

## DISCUSSION

Great crested and smooth newts of all categories emigrated from the pond after breeding or metamorphosis in non-random directions, tending to leave the pond where forest adjoined, rather than open fields. The data suggest that cues from the surroundings were important for orientation, and there were clear age-effects in the way newts selected a route to leave the pond. Metamorphs – which had no prior experience of the terrestrial environment – were more dispersed and less concentrated than older newts, but were still mostly distributed along the eastern half of the pond, towards the forest sector. Older newts, who had previous experience of the surroundings, left the pond from the north-eastern sector, where the fence perimeter adjoined the forest patch most closely. Their strong directionality and consistency over the years in doing so suggest that they were piloting towards familiar habitats and that the forest patch to the east served as either a preferred habitat or a corridor funnelling individuals towards the more extensive forest beyond. That both great crested and smooth newts shared the same general tendency to emigrate in this direction over the years gives some support to this conclusion. Furthermore, that the directionality was greater in newts that had spent at least one year on land than in naïve, newly-metamorphosed newts, may be the result of accumulated experience of the habitat and local conditions, and by effects of natural selection during the first few years of life. Experiments on alpine newts, *Triturus alpestris*, (Joly & Miaud, 1989; Joly & Miaud, 1993) and on radio-implanted marbled newts, *Triturus marmoratus*, and great crested newts, *T. cristatus*, (Jehle, 2000; Jehle & Arntzen, 2000) have demonstrated that adult *Triturus* newts may be faithful to breeding ponds and terrestrial sites, and have navigational abilities during migrations. The results obtained here suggest that the strong directional orientation towards an adjoining forest patch may indeed be a response towards a favourable habitat.

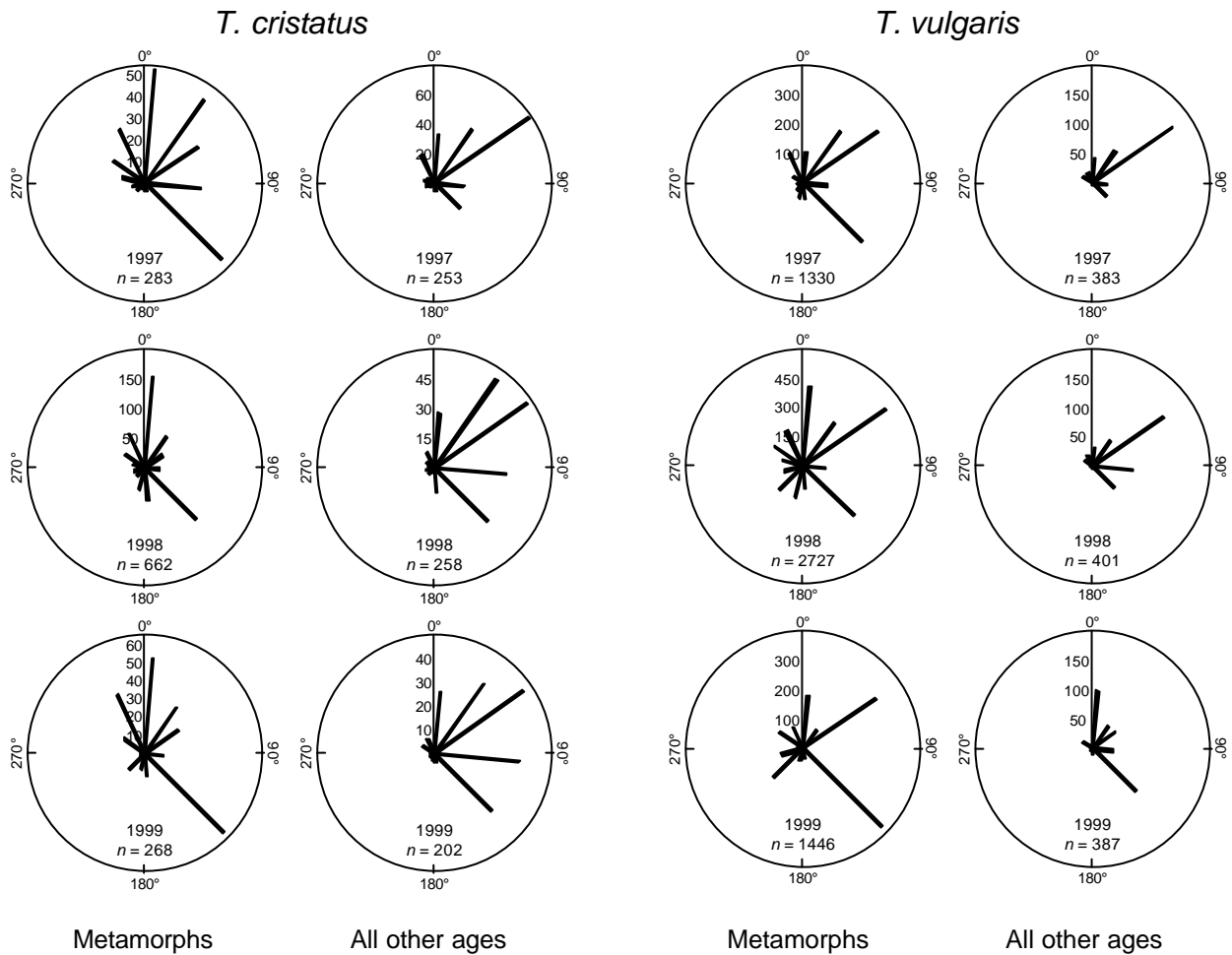


FIG. 2. Circular histograms of migration patterns after breeding and metamorphosis in great crested and smooth newts – *Triturus cristatus* and *T. vulgaris* respectively – at a pond in south-central Sweden for three consecutive years, showing patterns for life stage classes and species. The length of each line radiating out from the circle centre indicates the number of newts moving in that direction. Study year and sample size (n) for each sample are given.

Results from a study of nine radio-implanted adult great crested newts during an emigration episode at the study site during four weeks in July and August 2001 (*unpubl.*) also support this. The latter resulted in 30 point localizations of preferred microhabitats, of which 26 (87%) were situated within the adjoining circular forest patch (max. dia. 120 m) to the east of the pond. Overall, the data indicate that directional preferences by adult newts are potentially reliable indicators of where suitable terrestrial habitats are located.

Even though post-metamorphs of the two species had similar directionality when pooled across years, movement patterns (in terms of circular distributions) changed slightly from one year to the next for all samples. Furthermore, metamorphs did not migrate in directions identical to those taken by piloting post-metamorphs. Instead, metamorphs had a tendency to be distributed in traps adjoining either edge of the eastern forest patch, and this behaviour seemed to be more developed in great crested than in smooth newts.

TABLE 2. Summary results from tests between life stage classes and species, based on the concentration parameter – which is an indicator of the directionality strength. Horizontal and vertical lines connect concentration values for the sample pairs tested, and asterisks denote the associated probability for the null hypothesis that two samples have equal concentrations. NS = not significant ( $P > 0.05$ ), \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

	1997		1998		1999	
	Metamorphs	All other ages	Metamorphs	All other ages	Metamorphs	All other ages
<i>T. cristatus</i>	0.99	1.48	0.45	1.34	0.64	1.56
	NS	NS	**	**	NS	***
<i>T. vulgaris</i>	0.98	2.17	0.53	1.87	0.42	1.06
					NS	

Hayward *et al.* (2000) found that *T. cristatus* metamorphs had the ability to detect and trail chemical cues left by piloting adults in experiments, and postulated that tracking may be an important mechanism for finding suitable terrestrial habitats. The observations reported here do not clearly confirm this, but rather seem to indicate that great crested newt metamorphs possibly detect and avoid using the same migration routes as more experienced individuals, even though the latter are demonstrably reliable indicators of where favourable habitats are situated. Since there is a distance of 3-4 m between the pond perimeter and the fence, the metamorphs do not lack opportunities to track older newts. Alternatively, metamorphs in the field may not be using cues left by older newts at all but following odour cues from other metamorphs, or using visual or chemical cues from the environment as information sources. A second alternative is that metamorphs are prone to migrate through the scrub along the edge of a forest patch, whereas older newts have more to gain by returning to well-known territory as quickly as possible. The tendency to follow trails left

TABLE 3. Comparisons of the directional orientation within and among life stage classes and species for great crested and smooth newts (*T. cristatus* and *T. vulgaris*, respectively) within and among years. Standardized test statistics results from multi-response permutation procedures (MRPP). The *P*-value is the associated probability that two samples have equal circular distributions.

Comparison	Standardized test statistic	<i>P</i>
<i>T. cristatus</i>		
Metamorphs vs. all other ages		
1997	-5.68	0.0012
1998	-27.37	< 0.0001
1999	-14.62	< 0.0001
1997-9	-52.72	< 0.0001
Life stage classes among years		
Metamorphs	-6.15	0.0004
All other ages	-5.44	0.0007
<i>T. vulgaris</i>		
Metamorphs vs. all other ages		
1997	-44.82	< 0.0001
1998	-75.35	< 0.0001
1999	-24.76	< 0.0001
1997-9	-121.59	< 0.0001
Life stage classes among years		
Metamorphs	-59.11	< 0.0001
All other ages	-30.72	< 0.0001
<i>T. cristatus</i> vs. <i>T. vulgaris</i>		
Metamorphs	-13.82	< 0.0001
All other ages	-0.84	0.1572

by adults may also be density-dependent, and the patterns observed by great crested newts in this study could reflect a strategy by metamorphs to minimize competition with older individuals over resources (e.g. food or hiding places). Trailing behaviour is likely to account for some of the variation in natural systems, since adults and metamorphs have a period of overlap in the timing of emigration from a pond, but it may be more complex than previously believed. For example, only metamorphs that emerge early are likely to benefit from trailing older newts if the overlap between emerging metamorphs and older newts returning to terrestrial habitats is limited. If this is taken into account, the data from this study suggest that when the temporal overlap was short (1997) a larger proportion of great crested newt metamorphs emerged in the same directions as older newts, whereas during 1998-99 – when the classes had a greater overlap – metamorphs were more dispersed towards the forest edges. That is, when cues from older newts were likely to be more available, the metamorphs responded with avoidance (i.e. negative feedback). Emigration patterns for smooth newts do not seem equally complex, but rather suggest that large proportions of the metamorphs of this species either followed older individuals or emigrated without taking notice of where newts had travelled before, since many dispersed in the same general direction as older newts. Further experimentation in this field may provide valuable insights into the actual determinants of orientation and terrestrial habitat selection in newts.

Patterns of aquatic microhabitat selection may obscure emigration distributions. However, the vegetation structure and topography of the pond does not suggest that newts were inhibited from emerging in certain directions, but examination of this aspect was beyond the scope of this study. Hayward *et al.* (2000) showed that metamorphs moved away from their larval sites before metamorphosis and concluded that they had begun to be influenced by an orientation mechanism at this stage. They also found that females moved around widely in the pond during breeding and egg-laying, and before leaving the pond (see also Madison, 1998). It appears plausible that this is also applicable here and that orientation towards surrounding habitat elements already takes place before the newts leave the pond.

Although this study is based on observations at a single, isolated breeding pond, which may not be typical, it identifies topics that are in need of further investigation. For example, it seems crucial to determine mechanisms and cues that are involved in producing the non-random orientation relative to the surroundings observed here in all life stages and both species, and I have introduced some possible explanations. I also propose that valuable information can be extracted from drift fence studies where migration patterns in different life stage classes are analysed in relation to habitat availability. Both great crested and smooth newts do seem to have similar requirements in terms of the qual-

ity of the surroundings for dispersal, and their directions may be used as indicators of the presence of suitable habitat patches. The data suggest that newts may become more directional as a forested sector adjoining a pond becomes narrower, or conversely, that dispersal approaches uniformity when a pond is entirely surrounded by equally favourable forest habitat. If this can be demonstrated it could prove useful for conservation purposes and show how important well-designed forest and terrestrial habitat management practices may be in the conservation of newt populations.

#### ACKNOWLEDGEMENTS

I thank Christer Tikkala and Per Bülow for assistance at the study site, and Johan Elmberg, Sven-Åke Berglind and Daniel Gustafson for constructive comments on early manuscript drafts. Two anonymous referees, Clive Cummins and Brian Cade also contributed with comments that sharpened the focus of the manuscript considerably. Permits for the study were acquired from the Swedish National Board for Laboratory Animals (Tierp, C 149/97, C 84/0) and the Swedish Environmental Protection Agency. The study was funded in part by grants from Helge Ax:son Johnsons Fund for Scientific Research, the Swedish Environmental Protection Agency and the Royal Swedish Academy of Sciences.

#### REFERENCES

- Batschelet, E. (1981). *Circular Statistics in Biology*. London: Academic Press.
- Cade, B. S. & Richards, J. D. (1999). *User manual for Blossom statistical software*. Fort Collins: U.S. Geological Survey (Internet: [www.mesc.usgs.gov/blossom](http://www.mesc.usgs.gov/blossom)).
- Cummings, B. F. (1912). Distant orientation in amphibia. *Proceedings of the Zoological Society of London* **1912**, 8-19.
- Dingle, H. (1996). *Migration. The Biology of Life on the Move*. New York: Oxford University Press.
- Fahrig, L. & Merriam, G. (1994). Conservation of fragmented populations. *Conservation Biology* **8**, 50-59.
- Fisher, N. I. (1993). *Statistical Analysis of Circular Data*. Cambridge: Cambridge Univ. Press.
- Glandt, D. (1986). Die saisonalen Wanderungen der mitteleuropäischen Amphibien. *Bonn. Zool. Beitr.* **37**, 211-228.
- Grant, D., Anderson, O. & Twitty, V. C. (1968). Homing orientation by olfaction in newts (*Taricha rivularis*). *Science* **160**, 1354-1356.
- Griffiths, R. A. (1996). *Newts and Salamanders of Europe*. London: T & A D Poyser Ltd.
- Hanski, I. (1999). *Metapopulation Ecology*. Oxford: Oxford University Press.
- Hayward, R., Oldham, R. S., Watt, P. J. & Head, S. M. (2000). Dispersion patterns of young great crested newts (*Triturus cristatus*). *Herpetological Journal* **10**, 129-136.
- Jehle, R. (2000). The terrestrial summer habitat of radio-tracked great crested newts (*Triturus cristatus*) and marbled newts (*T. marmoratus*). *Herpetological Journal* **10**, 137-142.
- Jehle, R. & Arntzen, J. W. (2000). Post-breeding migrations of newts (*Triturus cristatus* and *T. marmoratus*) with contrasting ecological requirements. *Journal of Zoology* **251**, 297-306.
- Joly, P. & Miaud, C. (1989). Fidelity to the breeding site in the alpine newt *Triturus alpestris*. *Behavioural Processes* **19**, 47-56.
- Joly, P. & Miaud, C. (1993). How does a newt find its pond? The role of chemical cues in migrating newts (*Triturus alpestris*). *Ethology Ecology & Evolution* **5**, 447-455.
- Joly, P., Miaud, C., Lehmann, A. & Grolet, O. (2001). Habitat matrix effects on pond occupancy in newts. *Conservation Biology* **15**, 239-248.
- Macgregor, H. (1995). Crested newts - Ancient survivors. *British Wildlife* **7**, 1-8.
- Madison, D. M. (1998). Habitat-contingent reproductive behaviour in radio-implanted salamanders: A model and test. *Animal Behaviour* **55**, 1203-1210.
- Mardia, K. V. (1972). *Statistics of directional data*. London: Academic Press.
- Marsh, D. M. & Trenham, P. C. (2001). Metapopulation dynamics and amphibian conservation. *Conservation Biology* **15**, 40-49.
- Mielke, P. W. (2001). *Permutation methods in statistics*. New York: Springer-Verlag.
- Oldham, R. S., Keeble, J., Swan, M. J. S. & Jeffcote, M. (2000). Evaluating the suitability of habitat for the great crested newt (*Triturus cristatus*). *Herpetological Journal* **10**, 143-155.
- Sinsch, U. (1990). Migration and orientation in anuran amphibians. *Ethology Ecology & Evolution*, 65-79.
- Sinsch, U. (1991). The orientation behaviour of amphibians. *Herpetological Journal* **1**, 541-544.
- Sutherland, W. J. (1998). The importance of behavioural studies in conservation biology. *Animal Behaviour* **56**, 801-809.
- Upton, G. J. G. & Fingleton, B. (1989). *Spatial data analysis by example. Volume 2: Categorical and directional data*. Chichester: John Wiley & Sons.
- Verrell, P. A. (1987). The directionality of migrations of amphibians to and from a pond in southern England, with particular reference to the smooth newt, *Triturus vulgaris*. *Amphibia-Reptilia* **8**, 93-100.