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Spatial patterns of migrating Great Crested Newts and Smooth Newts: The importance of the terrestrial habitat surrounding the breeding pond

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Summary

I compared spatial movement patterns of *T. cristatus* and *T. vulgaris* entering and leaving two breeding ponds in Lower Saxony, Germany. Drift fences and pitfall traps were employed to monitor migration activities. Individuals of *T. cristatus* could be identified by their belly pattern. Both newt species preferred forested areas to pasture as the terrestrial habitat, but only *T. vulgaris* used also the open grassland to a substantial degree. The data suggest that adult *T. cristatus* and *T. vulgaris* emigrated to a distance of 5 to 50 meters from the pond, however, a high number of *T. vulgaris* was also found in the direct pond environment. Individual recapture data of *T. cristatus* demonstrated a high degree of home site fidelity for the major part of the adults and subadults. The juveniles of both species preferred the same sites as the adults, indicating some hereditary preference for suitable land habitats. The consideration of the terrestrial habitat should be an integrated part of every conservation strategy for newts.

Key words: *Triturus cristatus, Triturus vulgaris,* migration, orientation, terrestrial habitat, habitat preferences, site fidelity.

Räumliche Migrationsmuster von Kamm- und Teichmolchen: Die Bedeutung des Landlebensraums in der Umgebung der Laichgewässer

Zusammenfassung

Die räumlichen Aktivitätsmuster von an- und abwandernden *T. cristatus* und *T. vulgaris* wurden an zwei Laichgewässern in Niedersachsen verglichen. Zur Kontrolle der Wanderaktivitäten wurden Fangzäune und Eimerfallen eingesetzt. Individuen von *T. cristatus* konnten anhand ihrer Bauchfleckenmuster wiedererkannt werden. Beide Molcharten bevorzugten Waldgebiete vor Grünland als Landlebensraum, aber nur *T. vulgaris* nutzte in größerem Maße (20 bzw. 24 % der Tiere) auch offenes Weideland. Die Ergebnisse legen nahe, dass adulte *T. cristatus* und *T. vulgaris* bis zu einer Entfernung von 5 bis 50 Meter vom Laichgewässer abwanderten. Eine hohe Anzahl an *T. vulgaris* wurde jedoch auch in der direkten Gewässerumgebung aufgefunden. Wiederfänge von *T. cristatus* - Individuen belegen ein hohes Maß an Ortstreue zum Landlebensraum für den größten Teil der adulten und subadulten Tiere. Die Juvenilen beider Arten bevorzugten dieselben Orte wie die Adulten und weisen damit auf vererbte Präferenzen hin. Die Berücksichtigung des Landlebensraum sollte ein integraler Bestandteil jeder Schutzstrategie für Molche sein.

Schlagwörter: *Triturus cristatus, Triturus vulgaris,* Migration, Orientierung, Landlebensraum, Habitatpräferenzen, Ortstreue

Introduction

For most amphibians the breeding pond is the centre point of their population, where they meet more or less every year. Due to that fact, most studies on habitat use of newts focused primarily on characteristics of the breeding ponds (Cooke & Frazer 1976, Dolmen 1980, Atkins 1998, Stumpel & van-der-Voet 1998), although the newts actually spend most time of the year on land. The quality of the terrestrial habitat should be an influential factor in newt survival and lifetime reproductive success and the importance of the surrounding environment of the pond in general has been recognised previously (Dodd & Cade 1998, Marnell 1998, Semlitsch 1998, Joly et al. 2001). Nevertheless quantitative data about terrestrial habitat use are rare (but see Duff 1989, Schiemenz & Günther 1994, Marnell 1998) and most information has the character of anecdotes. To improve our conservation strategies, especially for the endangered crested newt, it is essential to learn more about the site selection by the newts on land.

The aim of this study was to monitor the spatial movement patterns of the two newt species *Triturus cristatus* and *Triturus vulgaris*, migrating between their terrestrial and their aquatic habitat. Newts live inconspicuously on land and it is difficult to follow their tracks. There is only one study, where radio-telemetry was used to track great crested newts emigrating from the breeding pond (Jehle & Arntzen 2000). But due to the size of the transmitter radio-telemetry is still limited to the larger species and life stages, and it normally allows to observe only a small subsample of the entire population for reasons of money and man power.

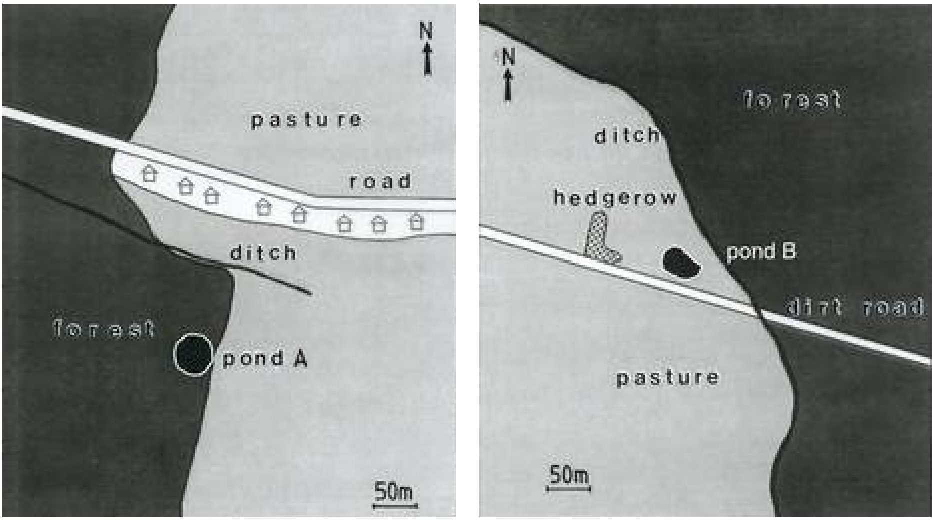

Fig. 1a and 1b: Location and surrounding environment of pond A and pond B.
Lage und Umland der Gewässer A und B.

Therefore, I employed the indirect method of correlating the spatial distribution of migrating newts entering and leaving the pond with their preferred land habitats. I controlled every movement to and from the pond area by a classical system of drift fences and pitfall traps. To make the correlation of the spatial movement patterns with the preferred land habitats plausible, two assumptions should be met: (i) newts are leaving the pond on the site next to their terrestrial habitats and (ii) they wander off more or less in a direct line from the pond. Both assumptions are confirmed by several studies (BLAB 1986, DODD & CADE 1998, JEHLE & ARNTZEN 2000) as well as by own results based on recapture data from more distant drift fences and from experimentally displaced newts (MÜLLNER 1991).

Study sites and methods

Study sites

Field data were collected from February to September 1990 at two ponds in the county of Lüchow-Dannenberg, which is located in the eastern part of Lower Saxony, Germany. This mainly flat area is dominated by the marshes of the river Elbe with pastures, wet forests and some small sandy elevations. A rich amphibian life is known from this region (LEMMEL 1977, FILODA 1981) and both the crested newt, *Triturus cristatus*, and the smooth newt, *Triturus vulgaris*, are found there in great numbers.

The two ponds, where both species of newts were breeding, represent different habitat types (fig. 1): pond A lies near the village Grippel on a forest edge and is partially shaded. It has a dimension of about 0,2 ha. Three sides touch the wet forest dominated by alders and oaks, whereas one side is adjacent to a pasture. Pond B is situated near the village Prezelle, approximately 20 km from pond A, and is surrounded by wet grassland. Its size is about 0,1 ha and it is exposed to sun throughout the day. North and east to it begins a forested area with alders, that alter with oaks at dryer parts. Both ponds were fish-free and possessed a diverse and richly structured vegetation.

Drift fences and controls

Both ponds were totally enclosed by a drift fence. This fence consisted of plastic for the main part, but at pond A a wire-mesh fence with a mesh size of about 0,4 cm had to be used for a section of the enclosure (trap 14 to 37, see fig. 2). The distance between the enclosure and pond A was approximately 2 to 3 meters in spring, but 3 to 6 meters in summer, because the water level had fallen continuously since May and especially on the lower eastern side of the pond, a huge weedy belt had developed around the pond. At pond B the distance between fence and water was 2 meters. Pitfall traps were placed at 5 meter intervals directly at the fence. Nevertheless, at some traps newts were able to pass between fence and trap. They followed the fence until they reached the next trap, where eventually animals of two or three buckets accumulated. To minimise this methodological bias, the numbers of three buckets were pooled for analysis. Once fallen into the trap a “plastic cuff” around the bucket rim prevented the newts from leaving the bucket.

At pond A the enclosure was installed from February to September, and the traps were placed inside and outside the fence. Additionally, in March two lines of plastic fences and pitfall traps were placed in that area of the forest (fig. 2) where most newts had already come from. The barriers had a distance of 40 - 50 m and 90 - 100 m respectively to the pond. As it turned out that pond A contained populations of *T. cristatus* and *T. vulgaris* much greater than expected, pond B was only observed during the emigration of the newts for reason of man power. Drift fences and traps there were installed from June to August and traps were placed only inside the fence.

During the study all traps were checked daily in the morning. For all newts and anurans, species, sex, trap number and other remarks were noted. All individuals of *T. cristatus* and a subsample of *T. vulgaris* were measured and weighed. The ventral spot patterns of *T. cristatus* were registered with a handheld photo-copier (MÜLLNER 1992) and used for individual identification. After handling at the catching site the animals were released at the opposite side of the fence.

Data Analysis

For analysis the position of each trap was determined as its angle to the centre of the pond. The relative frequency of animals captured per trap was calculated, separate for each species, sex and life stage as well as for immigrants and emigrants. To minimise the bias which could occur due to "leaky" traps (s. above), the data of three traps were combined for the plotted figures and further analysis.

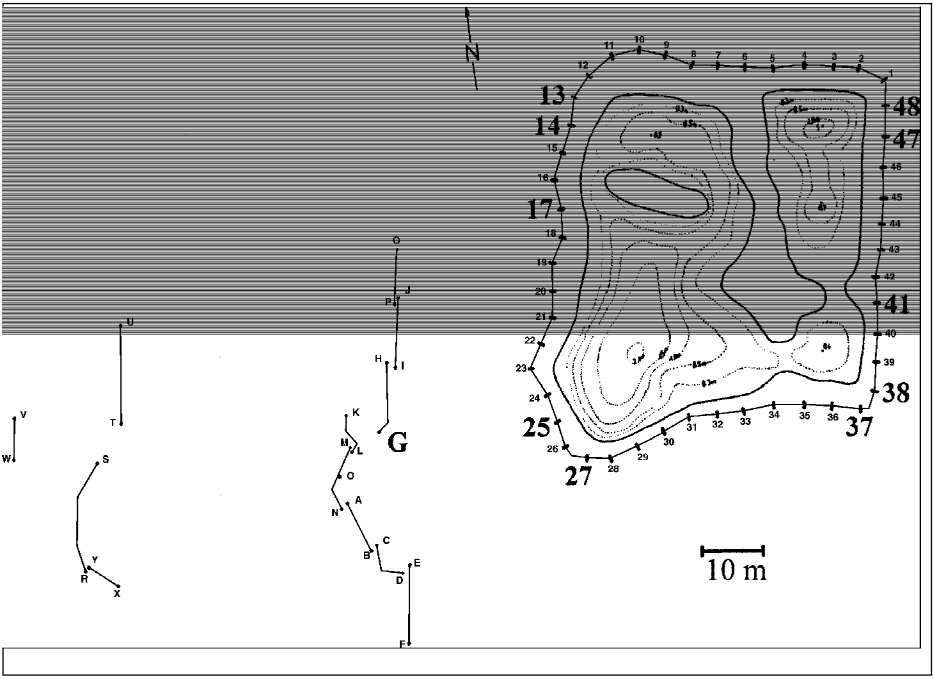

Fig. 2: Location of drift fences and pitfall traps at pond A. The highlighted numbers of traps are mentioned in the text.

Lage der Fangzäune und Fangeimer an Gewässer A. Die hervorgehobenen Nummern der Eimer werden im Text erwähnt.

	Triturus cristatus				***Triturus vulgaris***			
	male	female	sub	juv	male	female	sub	juv
pond A								
immigrating	348	344	202		964	1829		
emigrating	485	323	84	1593*	455	964	0	5415**
pond B								
emigrating	65	41	0	76	37	49	0	1634

Table 1: Number of migrating newts at pond A and B.

sub = subadults, juv = juveniles. * Since the emigration of the juveniles of *T. cristatus* had not yet been totally finished in mid-September, their real number might be slightly higher. ** Certainly much more juveniles of *T. vulgaris* emerged, because they were able to slip through the small meshes of the wire-mesh fence due to their small size and thus could leave the enclosure without being counted at that part of the fence.

Anzahl der wandernden Molche an den Gewässern A und B.

Because newts were caught in distinct traps, their frequencies reflect discrete distributions. In consideration of this type of grouped data, Rayleigh´s test was used to distinguish a given distribution from randomness and chi-square tests were used for the comparison of different distributions (Batschelet 1981). To fulfil the test assumptions of the chi-square test it was sometimes necessary to further pool the data of the traps. Therefore the different degrees of freedom are always given together with the test results. As multiple comparisons with the same data set were made, the chi-square limits had to be corrected by the Bonferroni method (Rice 1989).

Results

Number of migrating newts

At pond A the number of migrating adult and subadult *T. cristatus* was approximately 1000 individuals, with additionally a minimum of 1600 juveniles after metamorphosis (table 1). For *T. vulgaris* nearly 2800 adults but no subadults were counted and at least 5500 juveniles emerged. At pond B, where only emigration was observed, I counted slightly more than 100 adult *T. cristatus*, no subadults and 76 emerging juveniles. For *T. vulgaris* 86 emigrating adults and 1634 juveniles leaving the pond were caught.

At pond A existed an obvious discrepancy between the number of newts immigrating and the number of newts leaving the enclosure for both species (table 1). The higher number of emigrating male *T. cristatus* probably was due to the unusual early start of spring immigration in 1990, where a substantial proportion of males already had entered the pond area before the enclosure was completed. However, the much lower number of emigrating adult *T. vulgaris* and subadult *T. cristatus* is striking. No observations were made to suppose that the newts had been able to overcome the fence in greater numbers during summer or that they were caught by predators. With the exception of efts, no newts could be dip-netted in the pond in August or September to indicate a prolonged aquatic stay (Hagström 1982, Verrel 1985). However, several times I found adult smooth newts of both sexes hiding together under grass tufts or dead wood at the wet and weedy belt around the pond, which had developed in summer. For the subadults of *T. cristatus* no evidence existed that they could have developed to small adults during the aquatic phase and thus were contributing to the high number of pond leaving males. Weights of emigrating male and female *T. cristatus* were significantly higher than weights of immigrating *T. cristatus* (Müllner 1991) and could not have included measurements of many small males.

Spatial movement patterns at pond A

Crested newts and smooth newts both immigrated to and emigrated from pond A in a non-random manner, regardless of sex or life stage. Neither in *T. cristatus* nor in *T. vulgaris* males and females showed a different spatial movement pattern during immigration (*T. c.*: $X^2_{df23} = 22{,}8$; $p = 0{,}48$; *T. v.*: $X^2_{df47} = 58{,}4$; $p = 0{,}12$) or during emigration (*T. c.*: $X^2_{df22} = 28{,}8$; $p = 0{,}15$; *T. v.*: $X^2_{df32} = 39{,}6$; $p = 0{,}17$). Their numbers are therefore pooled in the figures and for analysis. The spatial distributions of adults, subadults and juveniles are presented in figure 3 and will be described for each species separately.

T. cristatus

Adult and subadult *T. cristatus* entering the pond in spring were not randomly distributed (Rayleigh´s test, adult: $z = 7{,}9$; $p < 0{,}001$; subadult: $z = 4{,}4$; $p < 0{,}02$) but showed a significant accumulation at the western side, with the subadults concentrating at the north west. These sides of the pond are adjacent to forest. Only 9,5 % adults and 9,5 % subadults entered the enclosure from the forest edge and the grassland in the east. During emigration adults and subadults again showed a non-random, significant orientation to the western side (adult: $z = 5{,}7$; $p < 0{,}01$; subadult: $z = 3{,}4$; $p < 0{,}05$). But in comparison to the immigration the distribution was more focused to the west and the percentage preferring the pasture was even smaller for adults (3,2 %) as well as for subadults (3,5 %). The distributions of immigration and emigration differed significantly (adult: $X^2_{df15} = 207{,}6$; $p < 0{,}001$, subadult: $X^2_{df11} = 44{,}8$; $p < 0{,}001$).

The freshly metamorphosed juveniles, which recently had developed in the pond, were not distributed randomly ($z = 7396{,}4$; $p < 0{,}001$), but showed a distribution similar to that of the adults. Like those, they oriented primarily to the forest in the south west. But in difference to the adults the remainder was more evenly distributed and a bigger percentage moved towards the pasture (11,5 %). The distribution of emigrating adults and juveniles differed significantly from each other ($X^2_{df15} = 143{,}1$; $p < 0{,}001$).

At the barrier lines inside the forest only few individuals were caught. During immigration this was probably due to the late construction of the drift fences. But also during summer only 31 adults of *T. cristatus* were caught at the first fence line in a distance of 40 - 50 meters from the pond. They represented 8 % of the of all individuals who had left the corresponding section of the enclosure in the south west. In contrast, 18 % of the juveniles of that section passed the first barrier and still 8 % of them were noted at the second barrier in a distance of 90 to 100 meters from the pond, where no adults were caught.

T. vulgaris

Adults of *T. vulgaris* entered the enclosure primarily from the western side, specially from the north west ($z = 78{,}3$; $p < 0{,}001$). But in contrast to *T. cristatus*, a substantial proportion

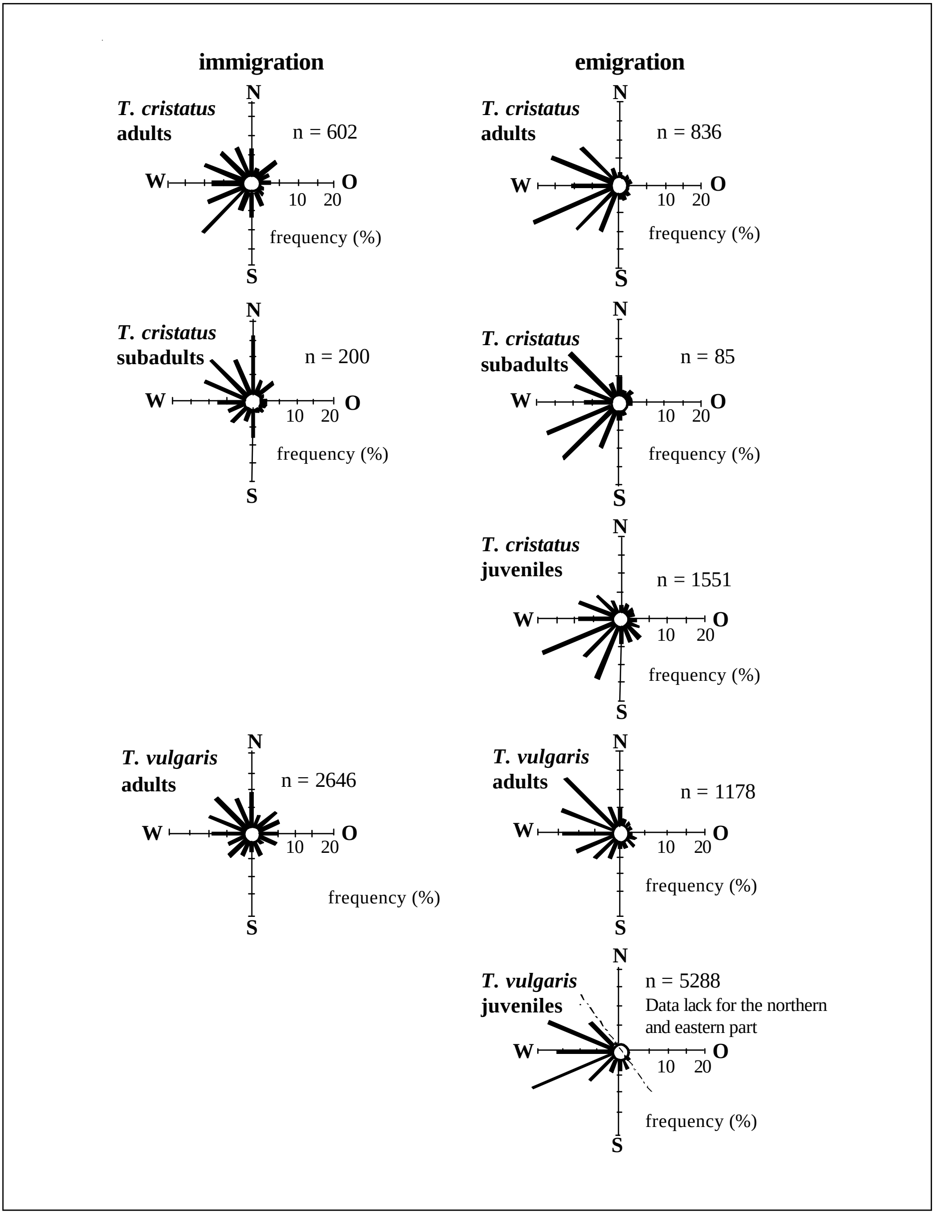

Fig. 3: Spatial distribution patterns of migrating *T. cristatus* and *T. vulgaris* at pond A. Bars represent the relative frequency of newts at a specific angle of orientation.

Räumliche Verteilung der wandernden *T. cristatus* und *T. vulgaris* an Gewässer A. Die Balken repräsentieren die relative Häufigkeit der Molche in einer spezifischen Wanderrichtung.

of 19,6 % immigrated from the pasture in the east. During emigration in summer *T. vulgaris* returned mainly to the north west ($z = 15,5$; $p < 0,001$), but also oriented towards the open grassland. This pasture orientation was less pronounced than in spring and the distribution of immigration and emigration differed significantly ($X^2_{df15} = 393,7$; $p < 0,001$). The spatial patterns of emerging juveniles were lacking for the eastern part of the enclosure for methodological problems (see above), but the existing data suggest that their distribution might be similar to that of the adults.

As for *T. cristatus*, only a few adult *T. vulgaris* were caught in the forest at the first barrier line. At the second line no adults, but several juveniles were counted.

Comparison between *T. cristatus* and *T. vulgaris*

Both *T. cristatus* and *T. vulgaris* showed a non-random preference for forested sites when migrating to the pond in spring or leaving the pond in summer. But of *T. vulgaris* a percentage twice than that of *T. cristatus* moved from and to the open grassland. The distributions of the two species differed significantly from each other during immigration in spring ($X^2_{df15} = 150,8$; $p = 0,001$) and emigration (X^2_{df15}; $p < 0,001$) in summer.

Spatial distribution of emigrating newts at pond B

At pond B only the emigration of the newts was observed. Neither for *T. cristatus* ($X^2_{df5} = 10,9$; $p = 0,053$) nor for *T. vulgaris* ($X^2_{df4} = 6,1$; $p = 0,19$) the orientation of emigrating males and females differed significantly. Their data were therefore pooled. Figure 4 presents the spatial distribution of adults and juveniles in both species.

T. cristatus

Adult *T. cristatus* were not randomly distributed ($z = 8,39$; $p < 0,001$) but oriented primarily towards the north and north east, the closest way from the pond to the forest edge (fig. 1b). Only 7 % of the individuals left for the open pasture in the south and the west. The juveniles showed a pattern similar as their adult conspecifics, i.e. they preferred the nearest forest edge when leaving the pond. But in contrast to the adults they left to a greater percentage (19,7 %) to the open pasture with a marked peak to the western side, where a complex of hedgerows was situated in a distance of approximately 80 meters (fig. 1b). The preferential differences between adults and juveniles were significant ($X^2_{df5} = 23,99$; $p < 0,001$).

T. vulgaris

Adult *T. vulgaris* oriented mainly towards the north east and the eastern side ($z = 1,8$; $p < 0,05$), from where the forest edge could be reached at a distance of 35 to 60 meters. But *T. vulgaris* was also caught to a substantial degree (24,4 %) in traps, which were adjacent to the grassland. The juveniles showed a distribution very similar to the adults with the same high percentage (23,8 %) of individuals moving towards the pasture. The distributions of adults and juveniles did not differ significantly ($X^2_{df8} = 14,77$; $p = 0,064$).

Comparison between *T. cristatus* and *T. vulgaris*

Individuals of *T. cristatus* were leaving the pond more frequently towards the closest forest edge than *T. vulgaris*. Although *T. vulgaris* showed preferences for forested sites

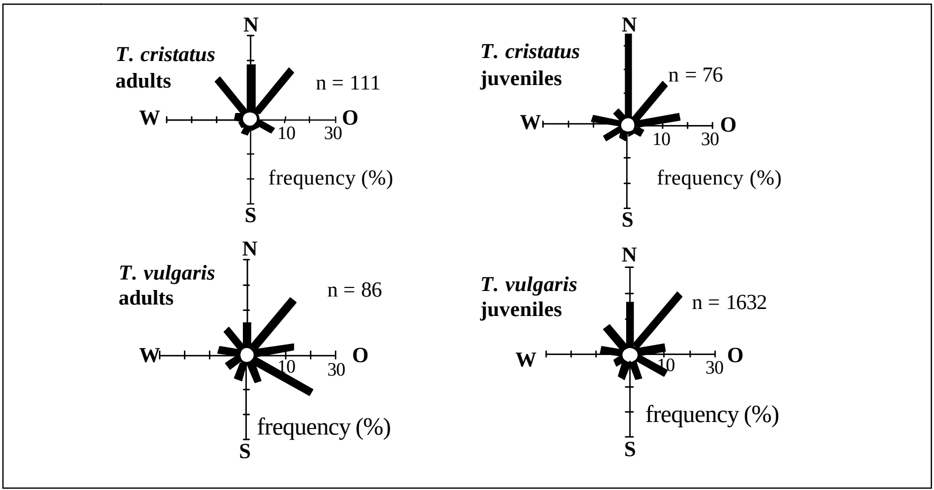

Fig. 4: Spatial distribution patterns of emigrating *T. cristatus* and *T. vulgaris* at pond B. Bars represent the relative frequency of newts emigrating at a specific angle of orientation.

Räumliche Verteilung der anwandernden *T. cristatus* und *T. vulgaris* am Gewässer B. Die Balken repräsentieren die relative Häufigkeit der anwandernden Molche aus einer spezifischen Richtung.

as well, nearly a quarter of the individuals left for the grassland. The difference between *T. cristatus* and *T. vulgaris* was significant for both adults ($X^2_{df6} = 29{,}79$; $p < 0{,}001$) and juveniles ($X^2_{df8} = 38{,}24$; $p < 0{,}001$).

Individual spatial preferences of adult and subadult *T. cristatus*

At pond A all movements concerning immigration and emigration were monitored. In *T. cristatus* 257 individuals could be identified by their belly pattern when entering the pond enclosure in spring and leaving it in summer. For these animals it was possible to compare the site where they came from and where they left the pond area: I calculated the distances between the trap of entering and the trap of leaving the pond area. As figure 5 demonstrates, more than 50 % of male, female and subadult *T. cristatus* left the enclosure with a deviation of less than 20 meters from the trap where they had been found entering in spring. Only a small proportion was leaving the area at the opposite side. Males showed with an average deviation of 22,5 m a slightly higher site fidelity than females with 27,5 m and the distributions of the two sexes differed significantly ($X^2_{df11} = 20{,}9$; $p = 0{,}034$). There was no difference in the distributions of deviation between adults and subadults ($X^2_{df7} = 5{,}4$; $p = 0{,}61$).

Four examples of movement pattern of identified *T. cristatus* may underline these individual site fidelities (compare fig. 2):

- A female came to trap 13 at the north west side of the fence in March, was dip-netted in the north eastern part of the pond in April and emigrated via trap 17 to the forest in summer.

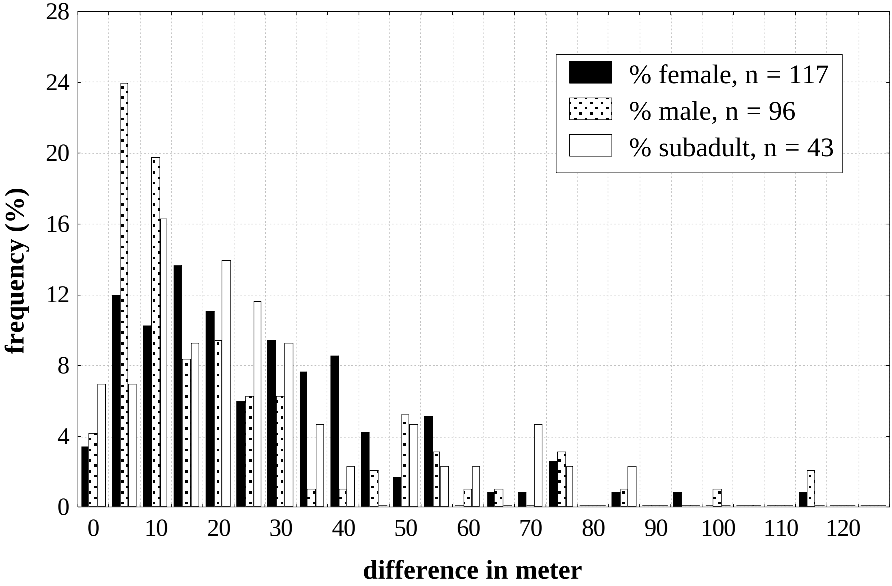

Fig. 5: Spatial deviations of *T. cristatus* between sites of entering and leaving the enclosure of pond A. The total perimeter of the enclosure was 240 meter.

Räumliche Abweichung der Fangorte am Zaun von an- und abwandernden *T. cristatus* an Gewässer A. Der Umfang des Fangzauns betrug 240 Meter.

- A subadult was caught in April in the forest in trap G, and two weeks later at the main drift fence in trap 25. Three months later, at the beginning of August, it was caught in trap 27 and a few days later inside the forest, again in trap G.

Similar results were obtained at the least preferred, eastern side of the fence, which was adjacent to the pasture:

- A male came via trap 48 in spring and left via trap 47 in summer.
- A female entered via trap 38 and left via trap 41.

Discussion

Terrestrial habitat preferences of *T. cristatus* and *T. vulgaris*

At both breeding ponds *T. cristatus* as well as *T. vulgaris* showed a non-random spatial distribution when entering the breeding pond in spring and leaving it in summer. Adults and juveniles of the crested and the smooth newts all gave a clear preference for the woodland sites of the surrounding environment rather than of the grassland as their terrestrial habitat. Forest presents usually a highly structured habitat, which should offer both shelter and a humid microclimate to a much greater extent than pasture. In the forest the newts use old stubs and piles of old leaves as a damp refugia profiting during winter time from the heat produced by decomposing plant material (HAGSTRÖM 1982, VERREL 1985). At both ponds the adjacent deciduous forest contained a diversity of understory plants and many fallen logs, thus presenting probably suitable terrestrial habitats. Also the food abundance might be greater in the forest than in the pasture, but I do not have information about it.

While at pond B the spatial distribution of the newts concentrated along the side facing the forest, the question remains, why the newts at pond A did not distribute in equal numbers to the three woodland sides. Newts are known to prefer deciduous forest to conifer blocks (STRIJBOSCH 1980, DUFF 1989, GROSSE & GÜNTHER 1996), but no conifers existed in the closer environment of pond A. In his investigation in Great Britain DUFF (1989) could demonstrate that there existed a relationship between the numbers of emigrating *T. cristatus* and the percentage of dead wood in the forest section which was chosen by the newts. I did not detect any obvious differences between the forest blocks, but most probably there were some differences in microhabitat quality, like temperature or humidity, invisible for me.

Differences between *T. cristatus* and *T. vulgaris* in their preferences

Woodland seems to be important for both *T. cristatus* and *T. vulgaris* as terrestrial habitat, but my results demonstrate that the smooth newts might be less bound to forest than the crested newts: At pond B almost 25 % of adult and freshly metamorphosed *T. vulgaris* left towards the grassland and at pond A 20 % of *T. vulgaris* entered the pond from the pasture side.

T. vulgaris is known as an euryoecius species, which is found in a wide variety of different habitat types (DOLMEN 1980, BLAB 1986). Its better ability to use pasture as a terrestrial habitat in contrast to *T. cristatus* might be explained by the much smaller size of the smooth newts. This size allows them to use types of microhabitats like grass tufts and the root system of hedges and bushes (BLAB 1986). Shrubs and small hedges were common in the study area often separating blocks of grassland. According to BEEBEE (1981) this type of vegetation is a precondition for the distribution of newts in open grassland or agricultural land. For the crested newt these structures as well as the microclimate might be less suitable in grassland, although apparently a small percentage of *T. cristatus* know to use pasture at both ponds.

It is remarkable that both at pond A and B the crested and the smooth newts selected different parts inside the overall preferred forested area. I cannot offer an explanation for this spatial separation, but as with the intraspecific preferences for a certain forest block, unknown microhabitat characteristics were probably responsible for this patterns.

Distances of the terrestrial habitats from the pond of adult *T. vulgaris* and *T. cristatus*

At pond A only very few adult *T. cristatus* and *T. vulgaris* who had left the pond enclosure were also trapped at the first line of barriers in the forest and none of them reached the second line. This is specially striking because of the great proportion of individuals leaving the enclosure in the south west section next to the forest barriers. It must be therefore concluded that the main proportion of adult newts that had emigrated from the enclosure used a zone of about 8 to 50 meters from the pond as the terrestrial habitat.

While this might be true for almost all adult *T. cristatus*, where apparently all individuals had left the enclosure, my data suggest that a high number of *T. vulgaris* and of subadult

T. cristatus were still staying near the pond and inside the fence. The detected newts inside the enclosure indicate that a great part of the smooth newts used this wet and weedy area within a distance of less than 6 meters to the shoreline as their terrestrial habitat. This suggestion also offers the most convincing explanation for the huge discrepancy in the numbers of *T. vulgaris* entering and leaving the fence at pond A. It might apply for the subadult *T. cristatus* as well, although I could not observe hidden individuals. Observations of other authors confirm that at least smooth newts often migrated only a few meters after leaving the pond (DOLMEN 1981, GRIFFITH 1984, HEHMANN & ZUCCHI 1985, VERREL 1987).

At pond B the direct environment in summer was only a sandy bank without shade, offering little ground cover. No animals were detected inside the enclosure. Most newts probably had reached the forest, which started in a distance of 35 to 60 meters.

For both species much higher emigration distances are reported. BLAB (1986) stated more than 400 m for *T. vulgaris* and KUPFER (1998) observed several hundred meters for *T. cristatus*. DUFF (1989) regularly caught immigrating adult crested newts in distances between 120 and 200 m from their breeding pond. But in comparison JEHLE & ARNTZEN (2000) noted low migration distances with an average of less than 20 meters for radio-tracked, pond leaving *T. cristatus*. It must be concluded that the realised movement activity of newts from the pond depends on the habitat qualities of the surrounding environment. This hypothesis is confirmed by the observations of MADISON & FARRAND (1998) in *Ambystoma tigrinum*. If local refuges and food are abundant in habitats adjacent to the pond, the newts would use them. The variation of known migration distances apparently reflects an adaptive flexibility in response to local habitat conditions. Therefore a difficult question remains to propose “terrestrial buffer zones” (SEMLITSCH 1998), without knowledge of the actually used land habitat.

Dispersal behaviour and emigrating pattern of the juveniles

Juveniles of both *T. cristatus* and *T. vulgaris* were migrating faster and to a much greater distance from the pond than their conspecific adults. In addition, their spatial distributions were more regular than in the adults. Since new ponds become mainly colonised by juveniles (BELL 1977, DOLMEN 1981, BLAB 1986) the rapid “movement on a wide front” (BLAB 1986) might be explained as a strategy of dispersal.

This dispersal behaviour might be in conflict with the preferences for a suitable habitat: In spite of the greater evenness of their spatial distribution in general, a high percentage of the freshly metamorphosed juveniles of both species showed the same clear preferences for a woodland habitat like the adults. This is surprising, as the juveniles lack the familiarity with the quality of their terrestrial surroundings. The result therefore indicates that juvenile newts possess some species-specific heritable preferences for special habitats, that probably become later in life modified by individual experience. The sensory basis of orientation is well known in adult urodeles (review in SINSCH 1991, JOLY & MIAUD 1993), but information is lacking about the orientation cues during the first migration of the juveniles. CZELOTH (1931) supposed olfactorial and visual cues to be important factors. He had demonstrated that juveniles of the smooth newt migrated straight forward to a dark structure at the horizon. This preference could explain the second peak of the distribution pattern of emigrating *T. cristatus* juveniles on the western side of pond B. In that direction a bush and hedgerow complex (fig. 1b) was situated in some distance and the departing individuals might have been optically attracted by that structure.

Site fidelity of adult and subadult *T. cristatus* to a terrestrial habitat

Most adult and subadult *T. cristatus* left the pond area where they had entered it four months earlier and were thus demonstrating a clear site fidelity to their terrestrial habitat. Site fidelity to less preferred terrestrial sites, like the open grassland, also occurred as individual migrating histories have shown. Especially these animals give a strong evidence for an individually developed bound to a special terrestrial site. This philopatry is supported by the small deviations between first and second trapping site after experimental displacements of emigrating newts (MÜLLNER 1991). Although I did not examine individual preferences of *T. vulgaris*, the studies of DOLMEN (1981), GRIFFITH (1984) and BLAB (1986) suggest similar distinct home areas for the smooth newt, that might be used over several years.

Site fidelity can be interpreted as an adaptive strategy in a stable environment in the sense of "I am going back to the site, I already know and where I could survive until now". It is not clear if these philopatric individuals may shift their behaviour in a changing environment. If not, the persistence of the used terrestrial habitats is of high importance. However, there also existed a group of migrating newts which showed a more opportunistic migration behaviour. These animals might be the driving force during the colonisation of new habitats by adults. As ARNTZEN & TEUNIS (1993) could show, adult crested newts are able to occupy new ponds with success over short distances.

Conservation implications

Which consequences should we draw from these results? In my opinion we have to focus our attention much more to the terrestrial habitat a newt population might use than only checking the "right" characteristics of the pond itself. All activities for conservation and specially the planning and realisation of new ponds should consider the presence of a suitable surrounding habitat which must contain a highly structured vegetation and forested zone or at least hedgerows nearby. The striking fidelity of the crested newts to terrestrial sites in their pond surrounding should caution us to assure the persistence of the land habitat as well as that of the breeding pond, if we really want to maintain a viable population. As the destruction and sealing of landscape still continues in Germany, it will not be sufficient to create new isolated ponds in an agricultural or cattle growing "desert". The consideration of the terrestrial habitat should be an integrated part of every conservation strategy for newts.

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