

Migration strategy of the Great crested newt (*Triturus cristatus*) in an artificial pond

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Abstract

In animals, migration is an evolutionary adaptation to manage seasonally varying habitats. Often driven by climatic changes or resource availability, amphibians then migrate from their hibernation sites to their breeding grounds. This research focused on the migratory habits of the Great crested newt (*Triturus cristatus*). The study explored factors like gender, body size, and environmental determinants, noting that immigration and emigration events proved distinct during the year. Results unveiled that males typically reached ponds first, with temperature being pivotal: males preferred up to 5 °C, females around 10 °C, while juveniles moved as temperatures increase. Wind velocity affected larger newts, around 120 mm, prompting them to migrate with stronger winds. Notably, heavy rainfall favored migration of newts of roughly 60 mm size. Humidity displayed gender-based trends: males associated positively with average levels, females showed aversion above 50%, and juveniles leaned towards drier conditions. Emigration patterns mirrored these findings, emphasizing roles of temperature, wind, and humidity. The effect of moonlight is not statistically significant. These findings provide valuable insights into the environmental factors influencing the migration of *T. cristatus*, which may guide future conservation efforts.

Kurzfassung

Bei Tieren ist die Migration eine evolutionäre Anpassung an saisonal wechselnde Lebensräume. Oft sind es klimatische Veränderungen oder die Verfügbarkeit von Ressourcen, die dazu führen, dass Amphibien von ihren Überwinterungsplätzen zu ihren Brutgebieten wandern. Diese Studie befasste sich mit den Wanderungsgewohnheiten des Kammmolchs (*Triturus cristatus*). Die Studie untersuchte Faktoren wie Geschlecht, Körpergröße und Umweltfaktoren und stellte fest, dass sich Ein- und Auswanderungsereignisse im Laufe des Jahres unterscheiden. Die Ergebnisse zeigten, dass die Männchen in der Regel zuerst die Teiche erreichten, wobei die Temperatur ausschlaggebend war: Die Männchen bevorzugten Temperaturen bis zu 5 °C, die Weibchen etwa 10 °C, während die Jungtiere mit steigenden Temperaturen abwanderten. Die Windgeschwindigkeit wirkte sich auf größere Molche (ca. 120 mm) aus und veranlasste sie, bei stärkerem Wind zu wandern. Vor allem Molche mit einer Größe von etwa 60 mm bevorzugten bei ihrer Wanderung starke Regenfälle. Die Luftfeuchtigkeit zeigte geschlechtsspezifische Tendenzen: Männchen assoziierten sich positiv mit durchschnittlichen Werten, Weibchen zeigten eine Abneigung gegen Werte über 50%, und Jungtiere neigten zu trockeneren Bedingungen. Die Auswanderungsmuster spiegeln diese Ergebnisse wider und unterstreichen die Rolle von Temperatur, Wind und Feuchtigkeit. Der Einfluss des Mondlichts ist statistisch nicht signifikant. Diese Ergebnisse bieten wertvolle Einblicke in die Umweltfaktoren, die die Migration von *T. cristatus* beeinflussen, und können als Grundlage für künftige Schutzbemühungen dienen.

Key Words

emigration, immigration, moon phase, rainfall, temperature, *Triturus cristatus*, wind

Schlüsselwörter

Auswanderung, Einwanderung, Mondphase, Niederschlag, Temperatur, *Triturus cristatus*, Wind

Introduction

Migration is an adaptive behavior seen in animals that enables them to deal with environments that change seasonally (Alerstam and Lindström 1990; Duellman and Trueb 1994). This phenomenon also includes breeding migrations, like amphibians in temperate regions that annually transition from terrestrial habitats to wetlands for offspring development (Russell et al. 2005; Dingle 2014). Migrations serves multiple purposes, such as congregating individuals for mating, facilitating the use of alternate resources, or helping avoid physiological limitations that might impact survival (Grayson et al. 2011). Species' migratory responses can differ due to variations in physiological tolerance and desiccation resistance, especially in the context of changing climates (Todd and Winne 2006). Changes in rainfall, for instance, can impact pond-breeding amphibian populations by affecting their habitats and increasing larval mortality (Semlitsch and Wilbur 1988; Carey and Alexander 2003; Daszak et al. 2005). Understanding how climatic factors influence over-land migration patterns in diverse amphibians is crucial to assessing future impacts of climate change and possible strategies for mitigation. The great crested newt (*Triturus cristatus*) is a notable amphibian species which has suffered significant population declines (Beebee and Griffiths 2000; Arntzen et al. 2009). Movement behavior is of paramount importance in conservation biology as it governs the spatial interactions between individuals, other organisms, and the environmental elements around them (Vojar 2007; Nathan et al. 2008). The seasonal activities and migratory patterns of *T. cristatus* have been recorded for more than a century, with historical records dating back to study in 1897 (Dürigen 1897). *T. cristatus* move to ponds for breeding (Kupfer and Kneitz 2000). The migration period usually takes place between February and April (Langton et al. 2001). The early migrations of *T. cristatus* often occur at night when the air temperature rises above 4–5 °C. Migration activity peaks during and immediately following successive humid nights (Jehle et al. 2011). Ralph (1957) found that the lunar cycle significantly influenced salamander activity patterns. Deeming (2008) similarly revealed that *T. cristatus* showed heightened activity just prior to the new moon.

It's worth mentioning that the migration of newts, including crested newts, is not a synchronized process, and individuals can be seen migrating several months after their initial arrival at the pond (Langton et al. 2001). On average, male newts tend to reach the pond a few days before the females, a behaviour believed to enhance their chances for successful mating. This early arrival tactic might give males a competitive edge in securing partners during the mating season. Newts use their breeding ponds for more than just reproduction; they also use them for feeding, an essential method of resource location (Jehle et al. 2011).

Adults of various species frequently display non-random migration patterns when departing from breeding sites, illustrating a propensity to both enter and exit the same locations and expressing a preference for specific habitats as transit routes over others (Marty et al. 2005; Sztatecsny and Schabetsberger 2005; Rittenhouse and Semlitsch 2006). After the adults leave the breeding pond, the larvae undergo metamorphosis and transition to a terrestrial environment distant from the pond. A portion of the juveniles will remain near the breeding site, eventually reaching sexual maturity and returning to reproduce in their birth pond, thus becoming part of the local breeding adult population. The remaining surviving juveniles will disperse into the adjacent terrestrial habitat, presumably to colonize ponds beyond their birth site (Rittenhouse and Semlitsch 2006). Despite the information provided, it remains unclear which climatic factors significantly impact migration.

Our study was centred on immigration and emigration activity of *T. cristatus*. The research was conducted at a location known for its suitability to *T. cristatus* and where these species have been documented in the past (Weber et al. 2019). Our objective was to understand whether there exist any differences in immigration and emigration based on gender. Furthermore, we investigated migration patterns including direction of individuals varying in length (as per snout to vent length). Lastly, we delved into the possible impacts of environmental factors on migration, paying specific attention to aspects such as temperature, rainfall, humidity, wind, moon phase, and the week of the year. A thorough understanding of migratory behavior can prove instrumental in shaping and directing conservation strategies (Marsh and Trenham 2001).

Materials and methods

The research was conducted in the artificial pond located in Czech Republic in the village of Tověř (49°38.433'N, 17°19.691'E), which is situated northeast of the town of Olomouc at an elevation of 227 meters above sea level. This pond is a small retention reservoir with a water surface area of approximately 500 m². Since it lacks a permanent water inflow, its water levels are dependent on current rainfall, the usual depth in spring is 1.8 m, sometimes in warm summers it completely dries up. The pond was eutrophic with algal growth on the surface. From the south and northeast sides, the shore of the pond has a gentle slope. The littoral zone of the pond is mainly dominated by pondweed (*Lemna minor*), and submerged grasses are also present in the area surrounding the pond. Based on the Habitat Suitability Index (HSI) assessment, which evaluates the suitability of habitats for the occurrence of *T. cristatus*, the Tověř locality is classified as “good”. The water body does not contain any fish. However, waterfowl, particularly mallards (*Anas platyrhynchos*), can be found in the area. One of the potential amphibian predators present at the site is the grass snake (*Natrix natrix*). In addition to the great crested newt, other syntopic amphibian species found here include the common newt (*Lissotriton vulgaris*) and the alpine newt (*Ichthyosaura alpestris*). The fire salamander (*Salamandra salamandra*) has also been observed in the vicinity. Among the frogs, individuals of the European fire-bellied toad (*Bombina orientalis*), the European tree frog (*Hyla arborea*), the common toad (*Bufo bufo*), the European green toad (*Bufo viridis*), and the agile frog (*Rana dalmatina*) have been captured in this area.

The monitoring took place from 4 March to 18 November 2017, for a total of 259 days. During this study, amphibians were captured using drift fencing lined with pitfall traps (n=47) around the whole pond. The 75 cm

high PE (polyethylene) UV-resistant half-sheet was used as a guidance drift fence during the study. Approximately 10 cm of the drift fence was embedded in the ground to prevent individuals from burrowing under the barrier. As part of the trapping method, white plastic buckets measuring 30 cm in height and 25 cm in diameter were buried around the perimeter of the pond as traps. These trapping buckets were spaced approximately 3 meters apart and were sunk into the ground so that the top of the bucket was level with the ground (Crosswhite 1999). Plastic buckets were positioned on both sides (inside n=24, outside n=23) of the drift fence to capture individuals during both emigration and immigration. Each bucket was equipped with a small, moistened sponge and a small number of leaves to retain moisture and provide shelter for the animals. The drop traps were numbered sequentially from 1 to 47, creating a directional rosette of migrants. The traps were divided into two sections based on the different environments representing potential wintering sites. The section with the forest was designated for traps numbered 1 to 25, while the section near the village was assigned to traps numbered 26 to 47 (Fig. 1). Every morning the sex and length of each of the *T. cristatus* were recorded, along with the corresponding trap number in which it was found. The length of the individual was measured from snout to vent (SVL). Individuals with indistinct adult sex characteristics were considered as juveniles in size between 10–80 mm. For each captured individual, an identification photograph of the belly was taken for capture-mark-recapture purposes (used for another study), then individuals were released immediately in the direction of their migratory path. It was assumed that individuals would move in a relatively straight line from the pond towards the fence and fall into one of the two nearest traps, which is a common assumption in drift fence studies. Additionally, all traps were considered equally effective at capturing newts, thus providing a statistically representative sample

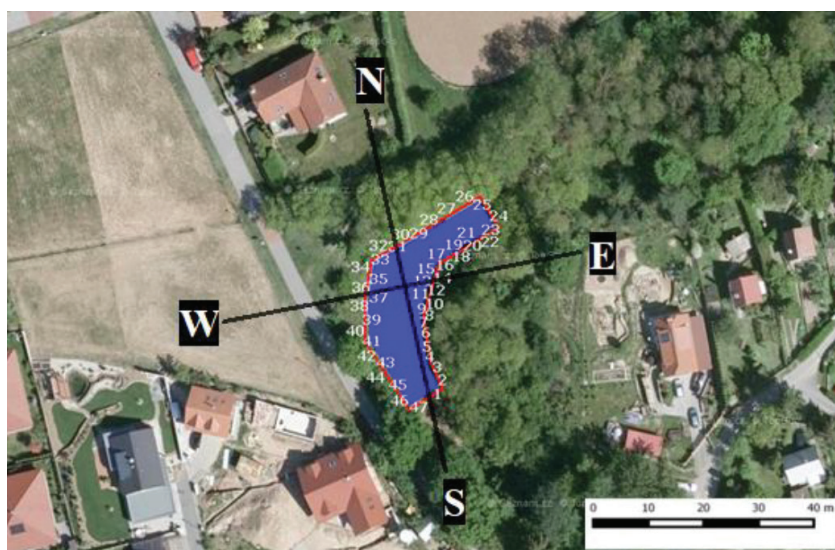


Figure 1. Map of the site with marked water area (blue), drift fence (red), individual trapping containers (white numbers) and distribution of cardinal directions.

of migrating newts in all directions (Malmgren 2002). Meteorological data used for this study were measured at location on DAVIS Vantage PRO meteorological station. Air temperature (°C) and humidity (%) were measured at 2 m above ground level, wind speed (m/s) at 10 m above ground level, and precipitation (mm) at 1 m above ground level with length of sunshine (h). Daily averages were used for temperature, humidity, and wind speed, while the total daily rainfall was considered for precipitation.

The effect of meteorological data on migration activity of different body size and both sexes were evaluated using Canonical Correspondence Analysis (CCA) using Canoco for Windows 5.0. Models for both immigration as well as emigration activity of newts were done. Body size and sexes were used as species data, whereas environmental data were factors: week of the year (week), average temperature (T_avg), minimum temperature (T_min), maximum temperature (T_max), average wind strength (F_avg), maximum wind strength (F_max), precipitation (SRA), average humidity (H_avg), direction from forest (forest) and length of sunshine (light). Environmental variables that significantly explained variation of activity of newts were used to calculate predictive Generalized Additive Models (GAM). The direction of migration (both immigration and emigration) was visualized in program Oriana for Windows with applied Rayleigh-Test.

Results

Migration based on sex

During the immigration process, the highest number of captures was observed for males, with 543 individuals recorded. Females followed closely with 532 captures, while only 21 juveniles were observed arriving in the pond. In terms of emigration, 530 males, 386 females, and 191 juveniles were recorded as captures. The sex ratio of *T. cristatus* individuals found at the Tovér site was 1.21:1, with a slight majority of males compared to females. The primary immigration of *T. cristatus* to the study site, accounting for 75.36% of the total number of immigrants, occurred between March 4th and March 31st, spanning a period of 27 days. During this period, a total of 390 females (accounting for 73.31% of the total arrivals), 433 males (79.74%), and 3 juveniles (14.29%) arrived at the study site. A subsequent small increase in

immigration was observed from around April 28th to May 8th. On the other hand, the primary emigration period for individuals began on June 5th and lasted until July 12th, totalling 37 days. During this time, approximately 40.43% of the overall outmigration was attributed to the leaving individuals. During this period, 336 females (representing 87.05% of the total number of females leaving) and 421 males (79.14%) departed. However, no juveniles were observed to emigrate during this period. The juveniles experienced an emigration wave from August 7th to September 6th ($n=130$; i.e., 68%), followed by a shorter period from September 15th to September 27th. Autumn migrations of tens of individuals have also been recorded. *T. cristatus* individuals were observed immigrating to the pond predominantly from the southwest, which includes village area (Rayleigh test; mean direction \pm IC95 is $\mu=215.111\pm 11.27^\circ$; length of vector $r=0.211$; $p<0.0001$). Conversely, during emigration, individuals predominantly departed to the southeast, where the forest is situated (Rayleigh test; $\mu=148.598\pm 8.84^\circ$; $r=0.265$; $p<0.0001$) (Fig. 2).

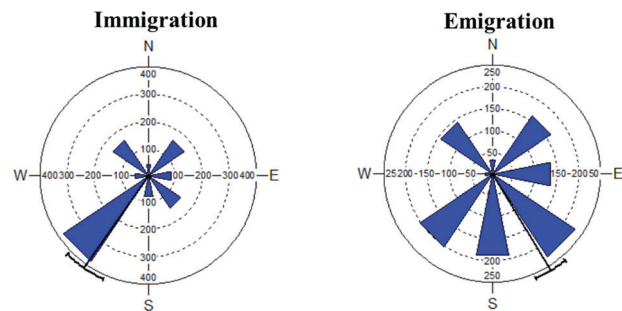


Figure 2. Directional rosettes of immigration and emigration for all individuals of *T. cristatus*. The black section shows the mean angle of migration, and the arcs extending to either side represent the 95% confidence intervals of the mean.

When examining the direction of immigration separately for each sex, we find that for females (Rayleigh test; $\mu=209.735\pm 17.43^\circ$; $r=0.196$; $p=0.510$) and juveniles (Rayleigh test; $\mu=39.639\pm 67.54^\circ$; $r=0.153$; $p=0.616$), the results are non-significant, indicating no clear preference. However, for males, there is a significant preference (Rayleigh test; $\mu=219.5\pm 13.94^\circ$; $r=0.241$; $p<0.0001$) that aligns with the overall direction of immigration, indicating a preference for coming from the southeast, which corresponds to the direction from the village (Fig. 3).

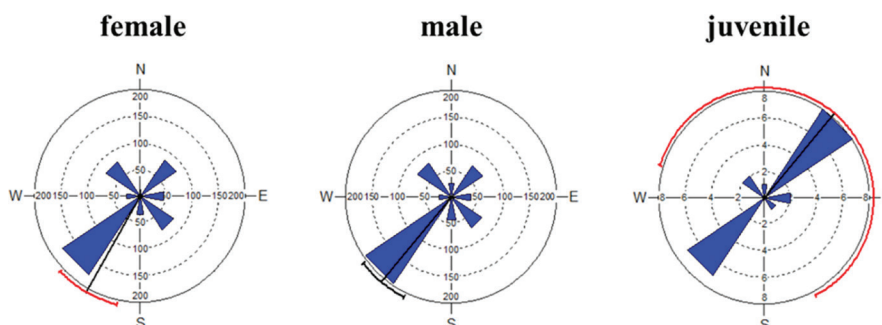


Figure 3. Directional rosettes in immigration, by gender. The black section shows the mean angle of migration, and the arcs extending to either side represent the 95% confidence intervals of the mean. Red colour sings nonsignificant results.

Migration based on body length

The average length (SVL) of the male individuals captured during the study was 102.3 mm, while the average size of the female individuals was 108.4 mm. The average length for juveniles was 61.1 mm (Table 1). Significant difference in size were found between all sex groups (Tukey’s range test, $p < 0.05$). The average increase in body length between immigration and emigration period observations was identical at 7 mm for both males and females.

Table 1. Size structure (SVL) in mm for immigration and emigration (Q1 = lower quartile, Q3 = upper quartile, med = median).

sex	Immigration					Emigration				
	max	min	med	Q1	Q3	max	min	med	Q1	Q3
female	141	60	105	98	115	142	78	112	105	117
male	124	54	99	92	105	126	10	106	102	110
juvenile	70	48	62	59	68	76	39	62	56	66

The highest number of females (n=149) immigrated in the length of around 100 mm; the highest number of males (n=152) also immigrated in this length. As for juveniles, the highest number (n=11) was observed with the SVL around 60 mm. For emigration, both males and females shifted up by one average length. Most females (n=152) emigrated in body size around 110 mm, followed by 242 males in the same size. Among juveniles, SVL around 60 mm was the most preferred size, with 84 captures.

Migration based on environmental factors

The Canonical Correspondence Analysis (CCA) model, when applied to single environmental factors during immigration, displays explanatory variables accounting for 8.8%. It highlights several influential factors under simple term effects, including week of the year, average, minimum and maximum temperature, average humidity and length of sunshine. No notable preference for these factors is observed among males and females. However, the immigration of juveniles is seen to be dependent on the week of the year and males immigrate to the pond at lower temperatures (Fig. 4).

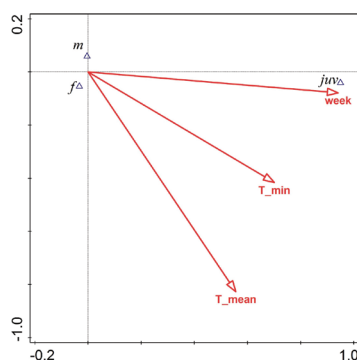


Figure 4. CCA model for immigration for sex with the environmental factors (the week in year (week), average temperature (T_mean), minimum temperature (T_min)). Only significant variables are shown.

In the Generalized Additive Model (GAM) for the sequence of the week of the year, it’s observed that males arrive first at the pond, followed by females. Juveniles started immigration around mid-year. One of the key factors here is the average temperature, as the GAM indicates that females predominantly arrive at around 10 °C, males prefer cooler temperatures up to 5 °C, and the number of juveniles was observed to increase as the temperature rises from 10 °C. The GAM for minimum and maximum temperature were similar as GAM for average temperature. Males show a positive correlation with average humidity, whereas females display a negative correlation when humidity levels are 50% or higher. Juveniles seem to prefer lower humidity (Fig. 5). A GAM analysis between factors and body length shows that smaller males immigrate to the pond first followed by larger females. The largest individuals immigrate at temperatures between 10 and 15 °C, corresponding to females. It is also apparent that immigration of larger individuals above 100 mm decreases with increasing humidity up to 80%, but then increases again with increasing humidity (Fig. 6).

The Canonical Correspondence Analysis (CCA) model applied to individual environmental factors during emigration accounts for 26.15% of the variation. The significant factors within simple term effects include the week of the year, maximum and average wind strength, precipitation, average humidity, length of sunshine and minimum, maximum, and average temperature. In this model, males emigrated from the pond during lower rainfall, stronger winds on warmer days. Females emigrated on sunny days with warmer temperatures. For juveniles, the week of the year was important and they emigrated at higher humidity and precipitation (Fig. 7).

The Generalized Additive Model (GAM) for the order of week in the year reveals that males typically emigrated by the 25th week, followed by a decrease in emigration and a new surge starting around the 35th week. Females peak in their emigration around 20th week and then start their emigration again in the 35th week. Juveniles have an emigration peak during the 35th week. Male emigration decreases with increasing mean temperature, showing a slightly increase at 20 °C, while females prefer temperatures between 15–20 °C for their emigration. Juvenile emigration firstly decreases up to 20 °C, then increases with rising temperatures. The GAM for minimum temperature mirrors that of the mean temperature, with males preferring cooler temperatures for emigration, females around 15 °C, and juveniles leaving as the minimum temperature rises. In the GAM for maximum and mean wind strength, males tend to favour stronger winds for emigration, whereas females cease their migration at higher wind strengths. In terms of precipitation, juveniles tend to emigrate during heavier rainfall, while females and males demonstrate a decrease in emigration during such conditions. Regarding humidity, males find it optimal to emigrate around 60% average humidity, while females cease emigration as humidity increases. Contrarily, juvenile emigration elevates with increasing humidity (Fig. 8). The GAM further show that larger in-

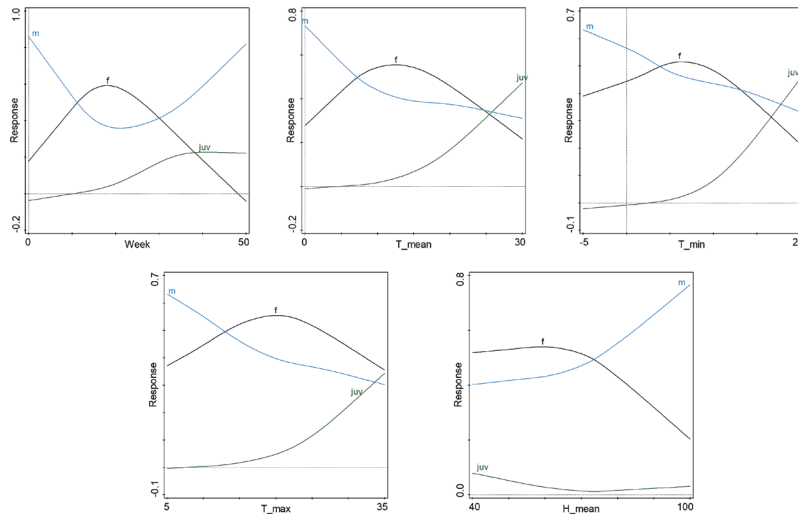


Figure 5. GAM of immigration activity for the week (Week), average temperature (T_mean), minimum temperature (T_min), maximum temperature (T_max), average humidity (H_mean)). Only significant variables are shown.

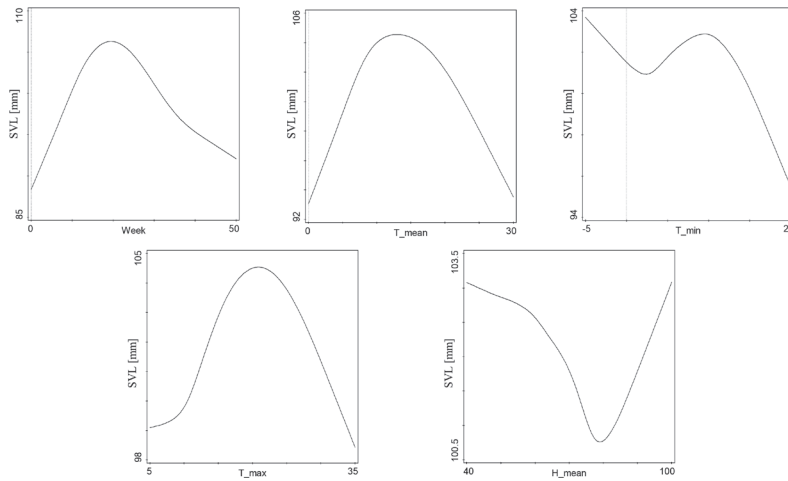


Figure 6. GAM of size of the newts of immigration activity for the week (Week), average temperature (T_mean), minimum temperature (T_min), maximum temperature (T_max), average humidity (H_mean)). Only significant variables are shown.

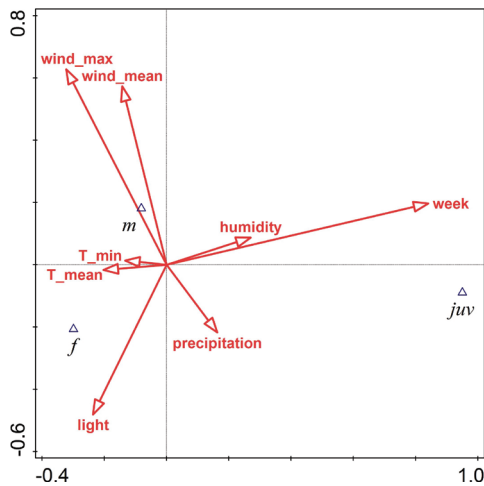


Figure 7. CCA model for emigration for sex with the environmental factors (the week in year (week), average temperature (T_mean), minimum temperature (T_min), maximum wind strength (wind_max), average wind strength (wind_mean), average humidity (H_mean), precipitation (precipitation), light (light)). Only significant variables are shown.

dividuals emigrate during week 20, with a resurgence of emigration during week 35. Individuals above 100 mm peak emigration at 15 °C and continue to emigrate at higher wind strengths. Conversely, emigration of larger individuals decreases with increasing mean humidity, which can also be seen in the GAM for precipitation, where larger individuals stop migrating with increasing precipitation (Fig. 9).

The last factor we investigated was the impact of the lunar phase (illumination). We noted that as the moon’s phase or brightness increased, there was a rise in the number of both immigrants and emigrants, encompassing all genders. Nevertheless, the correlation discovered between moonlight and both immigration and emigration proved to be statistically non-significant. For immigration, we found a correlation coefficient $r = 0.42$, but with a p-value of 0.5, being not statistically significant. Similarly, the correlation for emigration was also statistically non-significant, with a correlation coefficient $r = 0.049$ and a p-value of 0.53 (Fig. 10).

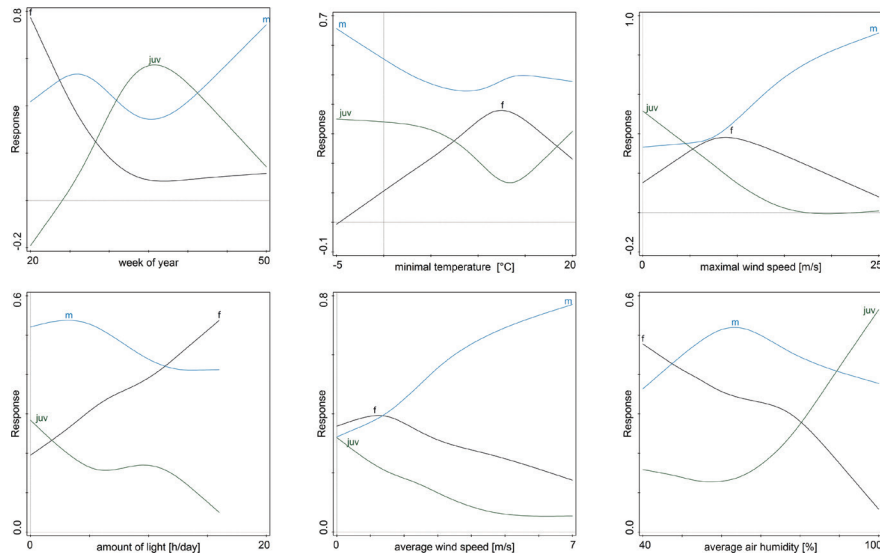


Figure 8. GAM of emigration activity for the week of year, minimum temperature, maximum wind speed, amount of light, average wind speed, average humidity. Only significant variables are shown.

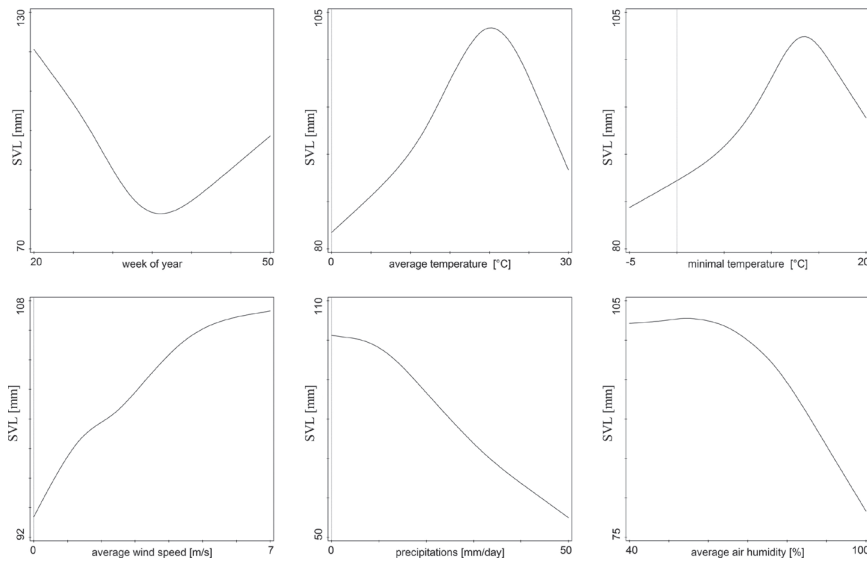


Figure 9. GAM of size of the newts of emigration activity for the week of year, average temperature, minimum temperature, average wind speed, precipitations, average humidity. Only significant variables are shown.

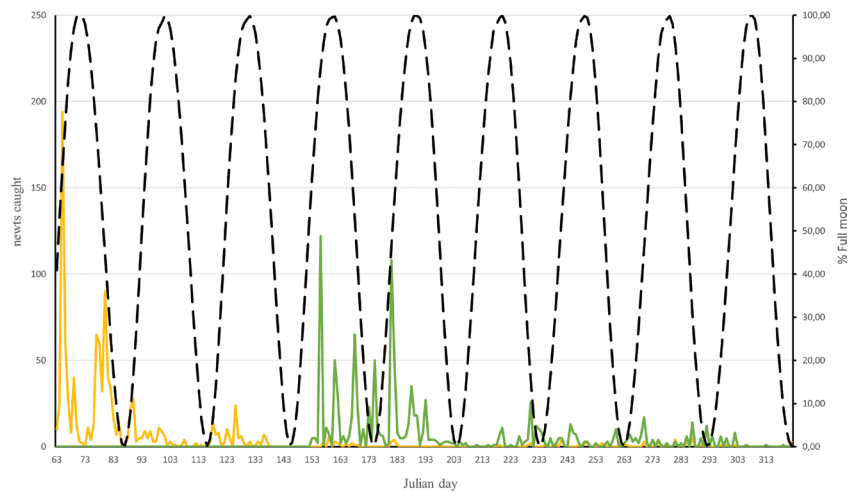


Figure 10. The number of newts (orange line for immigration, green line for emigration) caught plotted against the phase of the moon (dashed line).

Discussion

Our study noted that the major immigration period occurred between March 4th and March 31st. This accounted for a significant 75.36% of the total immigration events, over a period of 27 days. This immigration period is somewhat earlier compared to study (Verrell and Halliday 1985), where the majority of adult newts had entered the pond by May 5th. Our results are, however, broadly in line with the patterns reported by Blab and Blab (1981), who documented spring immigration lasting from February to May. Blab and Blab (1981) also observed an emigration period running from mid-July to mid-October, followed by a second immigration wave during October and early November. These findings appear to generally align with the data obtained in our study, offering similar migration patterns for this species. Our results indicated that male *T. cristatus* arrived at the pond in advance of the females, which is similar in other species of newts (Diego-Rasilla 2003; Diego-Rasilla and Luengo 2007) and salamanders (Douglas 1979; Sexton et al. 1990). This could suggest a selective advantage for males to reach the breeding grounds earlier, potentially increasing their opportunities to mate with various females. Alternatively, females may be selectively inclined to arrive later to broaden their selection group of potential mates (Douglas 1979; Russell et al. 2005).

In our study, we observed that the main emigration period began on June 5th and ended on July 12th, spanning a total of 37 days. This period accounted for roughly 40.43% of the overall outmigration, with individuals predominantly leaving during this time. Interestingly, no juveniles were noted to emigrate during this primary emigration phase. Instead, we recorded a significant juvenile emigration wave from August 7th to September 6th, during which approximately 68% (n=130) of the juveniles left. This was followed by a secondary, shorter wave from September 15th to September 27th. Autumn immigration suggests that certain individuals remain in the habitat over the winter period, indicating potential overwintering within the water. This finding may help to explain the phenomenon noted by Verrell and Halliday (1985), when fewer amphibians are captured upon leaving a pond than entering it, particularly when using a drift fence to intercept migrating individuals. While the exact reason for this discrepancy is not entirely clear, factors like predation could explain it. Our findings align with study research in Western France (Arntzen 2002), which suggested that males tend to leave the ponds before females despite a slightly longer overall aquatic phase. Our results are, however, shorter than the seven-month aquatic phase reported by Griffiths and Mylotte (1987) in an upland area. The observed emigration pattern is also consistent with study Verrell and Halliday (1985), which recorded emigration from late April to early November, with metamorphosed larvae departing the ponds starting in early August. In agreement with our study, they also mentioned an autumnal migration period, with several males and females captured outside of the drift fence in November.

Our findings suggest that migration directions of *T. cristatus* individuals can be influenced by the presence of specific environmental factors such as developed land, forests, and possibly the shelters that gardens provide during the terrestrial period. The use of gardens in the village's area as overwintering sites is intriguing and shows that these amphibians can adapt to utilize human-modified habitats for their survival needs. This adaptability can provide crucial survival strategies in a rapidly changing world where natural habitats are increasingly being modified or lost. However, there is also evidence to suggest that *T. cristatus* may not necessarily exhibit directional preference when moving to and from a pond (Verrell and Halliday 1985). This disparity might be explained by differences in local environmental conditions across different study sites. Some studies have suggested that newts, when leaving a breeding pond, tend to move in straight lines towards favorable habitat patches, indicating their efforts to optimize the use of available space (Verrell 1987; Sinsch 1991; Macgregor 1995; Jehle and Arntzen 2000; Jehle et al. 2011). It's interesting to note that while metamorphs of *T. cristatus* might have the ability to follow cues left by adults (Hayward et al. 2000; Oldham et al. 2000), this behavior was not observed in this study. Instead, juveniles exhibited a non-preferred direction of migration, it could be part of dispersion, suggesting different factors influence their movements, potentially including the surrounding habitat's structure and resources. The finding that *T. cristatus* individuals of all sizes exhibit non-random migration directions when emigrating from the pond (Malmgren 2002) aligns well with our results. This study, like ours, noted that these newts prefer to leave the pond in areas where forests adjoin rather than open fields, indicating the importance of these specific habitat types. Furthermore, despite having no prior experience in the terrestrial environment, juveniles showed a preference for areas near the forest during dispersal, again supporting the notion that specific environmental cues or conditions may guide their migration directions.

Our results confirm that females are generally larger than males. This concurs with the findings in study Verrell and Halliday (1985), where adult females entering the water were significantly longer than males. Moreover, our study notes that females emigrating from ponds also tend to be slightly larger than males. The growth observed between immigration and emigration periods was identical for both sexes, registering an increase of 7 mm. This indicates that the environmental conditions during these periods were conducive to growth for both genders equally. When it comes to juveniles, their average length in our study was significantly larger than previous research, with a recorded SVL of 61.1 mm. This contrasts with the results of Verrell and Halliday (1985), where juvenile length ranged from 40 to 51 mm. This stage of *T. cristatus* can span two to five years, characterized by rapid growth (Dolmen 1983; Francillon-Viellet et al. 1990). By Arntzen and Teunis (1993) the growth of juveniles over

the summer was swift, with an average increase in SVL of 8.3 mm over a span of 10 weeks.

Our study found that female *T. cristatus* tend to start their migration at around 10 °C, while males seem to prefer cooler temperatures of up to 5 °C, and juveniles start their migration as temperatures increase. Initial migrations occur post-sunset at temperatures above 4–5 °C, with most activity during consecutive humid nights (Jehle et al. 2011). It's also interesting to mention that the temperature threshold for migration in crested newts is higher compared to smaller newt species (Griffiths and Raper 1994). Migration in *T. cristatus* has been found to be influenced by the daily minimum temperature, with significant newt movement observed when temperatures reach or exceed 5 °C. On the other hand, limited movement was reported during cooler periods from late March to late April (Verrell and Halliday 1985). During March, when most incoming individuals were captured, the number of animals caught each day showed a positive correlation with the minimum temperature. The correlation coefficient (Pearson *r*) was 0.6, indicating a moderate positive relationship, and the correlation was statistically significant ($p < 0.001$) (Verrell and Halliday 1985). In colder springs, the migration period was short, lasting 23 days compared to early and warm springs where it lasted 40 days (Dervo et al. 2016).

Our research reveals complex connections between weather conditions and the migratory behaviours of *T. cristatus*. We discovered that rainfall and humidity play substantial roles in influencing behaviours, but their effects vary across different body size and genders. For example, newts between 50 and 70 mm prefer heavier rainfall, while larger newts decrease their arrival frequency with increasing rainfall. Our data also imply that precipitation affects emigration patterns, with juveniles tending to emigrate during heavier rainfall, while both genders show decreased emigration under such conditions. Juvenile amphibians, due to their smaller size and resultant greater surface area to volume ratios, are theoretically more prone to desiccation risks during day-time migrations compared to their adult counterparts (Spight 1968). Consequently, it might have been anticipated that these young amphibians would be less inclined to migrate during the day. Regarding humidity, optimal emigration conditions for males occur around 60% average humidity, while females halt emigration as humidity increases. Conversely, juvenile emigration rises with increasing humidity. Smaller individuals (to 80 mm) require higher humidity for emigration, whereas larger individuals (over 110 mm) stop emigration when humidity surpasses 60%. These findings challenge some previous research. While many studies correlate rainfall with amphibian breeding timing (Byrne 2002; Vaira 2005; Scott et al. 2008) others report no such link (Gittins et al. 1980; Reading 1998). Verrell and Halliday (1985) concluded rainfall wasn't necessary for *T. cristatus* migration. Often, nocturnal rainfall triggers migrations as it lowers desiccation risks for migrating amphibians (Semlitsch and Pechmann 1985).

Amphibians' water balance heavily relies on sufficient moisture, thereby making them vulnerable to desiccation, particularly during periods without rain (Jørgensen 1997; Hillyard 1999). A multitude of studies indicate that amphibian migrations often correlate with heavy rainfall (Todd et al. 2011). However, not all species respond similarly, with recently metamorphosed *B. terrestris* showing a weak correlation between migration and rainfall due to their higher desiccation tolerance (Thorson and Svihla 1943). Interestingly, even periods of no rain can trigger migration in certain amphibians, like recently metamorphosed *Bufo quercicus*, particularly after prolonged dry spells (Greenberg and Tanner 2005). Our findings reveal that these relationships are more nuanced, pointing to the importance of considering both humidity and size classes in understanding amphibian migrations. In conclusion, we underscore that rainfall is typically the most critical determinant of amphibian movements. Notwithstanding, responses to climatic factors, such as rainfall, vary considerably among amphibian species and age classes, with some demonstrating a greater dependence than others.

While our findings did not display a significant correlation between the moon's phase and immigration/emigration numbers, it's worth noting that we haven't considered possible interference from cloud cover. Clouds can obscure the moon's illumination and thus might impact the activity patterns of the animals, or human activity in this case. This could be a relevant factor that may affect the visibility of the moon and hence potentially influence our observed results. Future research could explore this aspect to gain a more comprehensive understanding of the influence of lunar phases on migration patterns. There have been previous studies showing that the moon's phase can affect the behavior of certain species. By Ralph (1957) salamanders' activity patterns were determined by the lunar cycle. Deeming (2008) observed that *T. cristatus* were most active right before the new moon. The pattern of heightened activity during the darkest nights could potentially be a survival strategy, reducing the risk of predation when individuals move away from breeding ponds to forage or migrate between ponds (Deeming 2008). Another possible explanation could be the influence of secondary phenomena like insect activity. Certain insects are known to have activity patterns that align with the lunar cycle, often peaking during full moon phases. If the organisms under study – salamanders, newts, or another species – rely on these insects as a primary food source, then their migration and foraging patterns might align more closely with the activity patterns of their prey rather than directly with the moon's phase or brightness. This indirect influence could create a seeming correlation between lunar phases and migration patterns. To properly assess this, future research could delve into a multivariable analysis considering these potential ecological interactions (Deeming 2008).

Finally, our study underscores that climatic conditions may play a crucial role in the migratory behaviours of *T. cristatus* as notable amphibian species. The documented

decline in amphibian populations worldwide might be directly or indirectly associated with climate change, considering that key climatic elements like precipitation and temperature significantly influence essential processes in amphibian population dynamics (Blaustein et al. 2001). By Dervo et al. (2016) the migration phenology of *T. cristatus* was noticeably affected by the combined impact of temperature and precipitation. They observed an overall trend towards an earlier commencement of breeding migration with increasing temperatures. As climate patterns continue to alter, it's plausible that amphibian phenology could also evolve in response to these changing selection pressures, as has been witnessed in various other organisms (Bradshaw and Holzapfel 2001). However, despite the robust phenological reactions of amphibians to climate change, there's a lack of detailed information on whether these responses stem from genetic adaptations or are entirely due to phenotypic plasticity (Urban et al. 2014). The study Todd et al. (2011) alerts to the potential consequences of rapid shifts in regional weather patterns on amphibian migrations. Such changes could differentially impact species, potentially leading to altered arrival times of reproductive adults or varying success rates of migrations. Thus, the study reinforces the need for conservation efforts to consider these climatic impacts and the differing responses of amphibian species to environmental changes.

Conclusions

Our study provides a comprehensive examination of the migratory patterns of *T. cristatus*, noting that a significant portion of immigration events occur over a period of 27 days, starting from March 4th. Our data align with previous studies, revealing similar migration patterns. Protandry, with males reaching breeding grounds before females, was observed, indicating potential mate selection advantages. Emigration was prevalent during a 37-day period from June 5th, while juveniles mainly emigrated from August to September. Autumn migration with overwintering within water habitats was also confirmed. In addition, the influence of environmental factors such as land development, forests, and human-made shelters was noted on migration directions. *T. cristatus* showed the ability to adapt to human-modified habitats. However, juveniles demonstrated non-preferred migration directions, indicating the influence of local habitat structure and resources. Temperature played a significant role in migration, with gender and size-specific preferences. Furthermore, rainfall and humidity considerably influenced migratory behaviours with variable effects across different sizes and genders. Our data suggested no significant correlation between moonlight and immigration/emigration, although an upward trend was observed. More research, considering factors like cloud cover, is suggested to understand this aspect better. Finally, the study emphasized the crucial influence of climatic conditions on

amphibian migration, underscoring the need for further research and effective conservation strategies amid global climate change.

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