Palacký University Olomouc

Faculty of Science

Migration strategy of the Great crested newt (*Triturus cristatus*)

Ph.D. Thesis

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DEDICATION

To my grandfather Jindřich Otmar

This thesis should be cited as:

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Annotation:

The European great crested newt (*Triturus cristatus*) has experienced a significant decline. Despite extensive research, many aspects of this species remain enigmatic, particularly in the context of current rapid climate changes. Understanding the survival and abundance of newts, which rely on aquatic habitats for breeding and terrestrial environments for other life stages, is challenging. This thesis delves into migration behaviour of *T. cristatus* and monitoring options of this species. Our research confirmed that male newts typically reach breeding ponds first, with temperature being a critical factor: males favour temperatures up to 5 °C, females around 10 °C, and juveniles migrate as temperatures rise. Heavy rainfall seems to encourage the start of newt's migration around 60 mm in size. Humidity affects genders differently: males prefer average humidity levels, females avoid levels above 50%, and juveniles tend toward drier conditions. Similar trends were observed in emigration patterns. We also confirmed autumn migration. Interestingly, 31.94% of female and 18.64% of male newts showed a reduction in body size when leaving ponds, averaging 6 mm and 6.4 mm, respectively. Other information is that newts do not seem to memorize migration paths. To enhance monitoring efforts, we evaluated the efficacy of three funnel trap types (prism, umbrella, and Ortmann's) for capturing *T. cristatus*. The umbrella–shaped trap proved most effective, outperforming the others, including the commonly used prism–shaped trap. Surprisingly, bait type had negligible impact on capture rates. Additionally, we implemented Passive Integrated Transponder (PIT) tagging for *T. cristatus* and tested passive telemetry systems in natural conditions. Results indicate that males are more active than females, with a recorded instance of a male traveling up to 20 meters in 78 seconds. This thesis enhances our understanding of *T. cristatus* migration and contributes to developing more effective conservation strategies for this threatened species.

List of Publications

This thesis is based on the work contained in the following papers and manuscript:

Weber L, Růžička J, Tuf IH, Rulík M. 2023. Migration strategy of the Great crested newt (*Triturus cristatus*) in an artificial pond. *Herpetozoa* 36:345–356.

Weber L, Botorová M, Rulík M. 2023. Comparing trap and bait efficiency to record the great crested newts (*Triturus cristatus*). *Knowledge & Management of Aquatic Ecosystems* 2023:(424), 26.

Weber L, Šmejkal M, Bartoň D, Rulík M. 2019. Testing the applicability of tagging the Great crested newt (*Triturus cristatus*) using passive integrated transponders. *PlosOne* 14(7), e0219069.

Weber L, Růžička J, Tuf IH, Rulík M. 2024. Should I stay or should I go? Movement strategy of the Great crested newt (*Triturus cristatus*)**. (Manuscript – submitted in Amphibian and Reptile Conservation)

Declaration

I hereby declare that I am author of this dissertation and that I have used only those sources and literature detailed in the list of references.

Lukáš Weber

Olomouc, January 2024

Financial Support

The contribution of Lukas Weber to the papers included in this thesis was as follows:

Paper I   70 %

Paper II   75 %

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Paper IV   80 %

Co–author agreement

Doc. Martin Rulík, Ph.D., the supervisor of this Ph.D. thesis and co–author of paper I–IV fully acknowledges the stated contribution of Lukáš Weber to these manuscripts.

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MSc. Jan Růžička

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1. Introduction

Despite its small size and primarily nocturnal nature, the great crested newt (*Triturus cristatus*) garners significant interest. Researchers from various countries have dedicated years to monitoring *T. cristatus* populations in the wild. For example, the migratory behaviours and seasonal routines of the *T. cristatus* species have been observed and documented extensively for over a hundred years, starting with the initial study conducted by Dürigen in 1897. Despite such a long history of research, numerous aspects of this remarkable species remain a mystery. Especially considering the current rapid changes in climate, we cannot predict whether a species will become extinct or how its abundance will evolve. Enhancing our understanding of *T. cristatus* is crucial, as they are a flagship species, and this knowledge could contribute significantly to the conservation of other amphibian species as well. Their extensive research has revealed that these newts can have a lifespan of up to 17 years and can travel more than a kilometre within several weeks. Additionally, these efforts have greatly enhanced our understanding of the characteristics of the small water bodies inhabited by the *T. cristatus* (Langton et al. 2001; Gustafson 2011; Jehle et al. 2011).

T. cristatus like numerous amphibians worldwide, is experiencing a decline across its distribution. (Kuzmin 1994; Beebee 1997; Beebee and Griffiths 2000, 2005; Edgar and Bird 2006; D' Baker 1990). The factors contributing to these declines are varied and intricate, differing across species and locations (Griffiths et al. 1996; Stuart et al. 2004; D'Amen et al. 2010, Gustafson 2011). In Europe the main factors are: habitat alteration, over–exploitation, invasive species, climate change, disease, and environmental pollutants, as well as habitat destruction, fragmentation, and pathogens (Oldham and Swan 1997; Kiesecker et al. 2001; Lips et al. 2005; Edgar and Bird 2006; Hamer and McDonnell 2008). *T. cristatus* is listed in Annex II of the European Habitats Directive, which can establish of protected areas for its preservation. Comprehending its habitat needs is essential for evaluating its conservation status and guiding management and development efforts. The species could serve as a key indicator or umbrella species for other pond–breeding amphibians and for broader pond–based biodiversity, aiding in the monitoring of amphibian habitats and landscapes (Pearson 1995; Caro and O'Doherty 1999; Houlahan et al. 2000; Roberge and Angelstam 2004; Gustafson et al. 2006; Malmgren 2007).

Surveys have shown that many newt habitats have been lost due to landscape changes, leading to habitat destruction, isolation, and fragmentation. This impacts newts and other amphibians at both individual and population levels (Beebee and Griffiths 2000; Edgar and Bird 2006; Malmgren 2007). The metapopulation structure of *T. cristatus* and their short migration distances make them especially susceptible to habitat changes (Laan and Verboom 1990; Joly et al. 2001; Ficetola and De Bernardi 2004; Schabetsberger et al. 2004; Karlsson et al. 2007). Hence, understanding factors that influence their habitat selection, survival, and reproduction is vital for preventing further habitat loss and for effective restoration and creation of suitable habitats. This includes considering physical, chemical, and biological aspects of aquatic habitats (Gustafson et al. 2006; Gustafson et al. 2009), as well as examining the terrestrial habitat (Gustafson et al. 2011) including the migration paths.

1.1 Distribution and biology

Newts and salamanders have a wide global distribution, found on every continent except Australia and Antarctica (Griffiths 1996). *T. cristatus* is native to northern and central Europe, extending eastward to the Ural Mountains (Griffiths 1996; Arntzen 2003; Gasc et al. 2004;). Within Europe's temperate zones, *Triturus* genus newts inhabit agricultural lands, provided there are ponds, both natural and man–made, suitable for breeding. Forested areas within these agricultural landscapes are commonly used by newts for aestivation and hibernation, as recorded by Miaud (1990) and Joly and Miaud (1993). However, the separation of forests and ponds in these landscapes requires newts to cross open fields for habitat transition. Traditionally, these fields were mostly pastures, but recent shifts towards grain crop cultivation have led to the reduction of pasture lands. This land–use change has resulted in the loss of some cattle ponds and the encirclement of others by cultivated fields, adversely affecting newt populations in these regions (Joly et al. 2001).

Newts depend on aquatic environments for breeding and development, and terrestrial habitats for post–breeding activities and juvenile growth (Gasc et al. 2004; Thiesmeier and Kupfer 2000). The connectivity between these habitats is essential for their dispersal and migration. The relationship and quality of these habitats, along with their surrounding areas, are crucial for the species' survival but have not been thoroughly studied (Kupfer and Kneitz 2000; Joly et al. 2001; Hartel et al., 2010a, 2010b). In the Czech Republic, *T. cristatus* originally had a widespread distribution, from lowlands to elevations of

800 meters, except in some parts of southern Moravia (AOPK ČR 2024). Currently, its occurence has significantly diminished, though it remains more prevalent in regions like Podkrušnohoří, Doupovské hory, the Ostrava area, between Kladno and Rakovník, in southern Bohemia, central Moravia, and around Cheb and Plzeň (Figure 1).
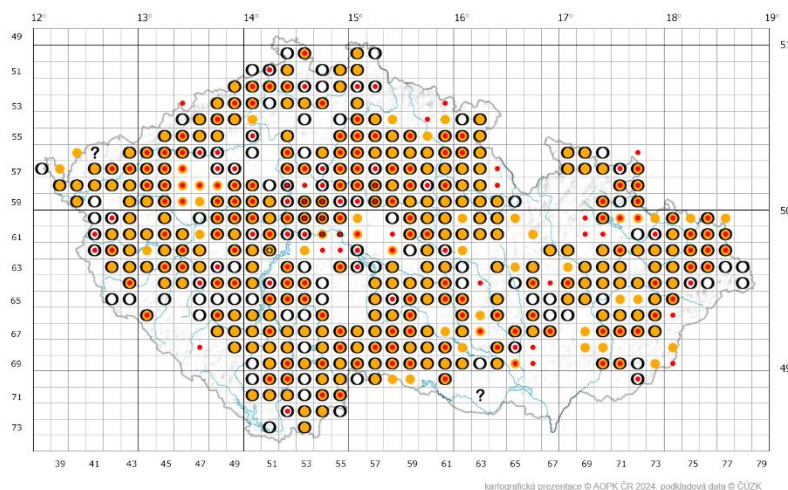
Figure 1. Distribution of *T. cristatus* in the Czech Republic (findings since 2010 are marked in bold in the circle).

The length of an adult *T. cristatus* is 11 to 15 cm, with some reaching up to 16 to 18 cm (Griffiths 1996; Thiesmeier and Kupfer 2000). In this species, females are usually larger than males (Griffiths 1996; Malmgren and Thollesson 1999). During the aquatic phase, male *T. cristatus* exhibit a serrated crest along their back and tail and a silver stripe on the tail sides, features that are attractive in courtship displays (Malmgren and Enghag 2008). Conversely, females have a slightly heightened tail but lack the males' distinctive crests. *T. cristatus* eggs are distinguishable from other amphibians by being light–coloured, about 2 mm in diameter, and encased in a gelatinous layer, resulting in a total width of 4–5 mm (Fog et al. 2001). The larvae possess a long tail with a black elongated tip and black spots on the crest and tail. Initially, they have external gills, which they lose before metamorphosis. As they go to the terrestrial phase, their body length ranges from 40 to 90 mm, taking on a miniaturized adult form (Baker 1990; Langton et al. 2001) (Figure 2). Some individuals of *T. cristatus* may show a reduction in body length after the transition from water to land which can point the trade–off between movement efficiency in water and on land (**Paper IV**). The need for effective movement in both aquatic and terrestrial environments can compromise the overall performance of semi–aquatic species (Gillis and Blob 2001). Physical adaptations for efficient swimming might hinder terrestrial mobility

and vice versa, with body length being a significant factor (Gvoždík and Damme 2006). However, in that study authors did not find evidence of a compromise between relative swimming and running speeds at the interspecific level. In *T. cristatus*, which display indeterminate growth, there is a suggested correlation between body size and age (Duellman 1989). This observation opens avenues for evolutionary research, particularly regarding the role of body size in mate selection (Halliday and Verrell 1988). The preference of females for larger, older males could indicate a selection for mates with heritable longevity traits (Howard 1978). However, amphibians typically experience rapid growth before reaching maturity and then slowdown in growth (Marvin 2001), suggesting that adult size may be more indicative of juvenile growth rates than of age (Halliday and Tejedo 1995). Although body size varies among mature adults (Arntzen 2000), natural selection might favour early reproduction, thereby influencing growth and reproductive success.
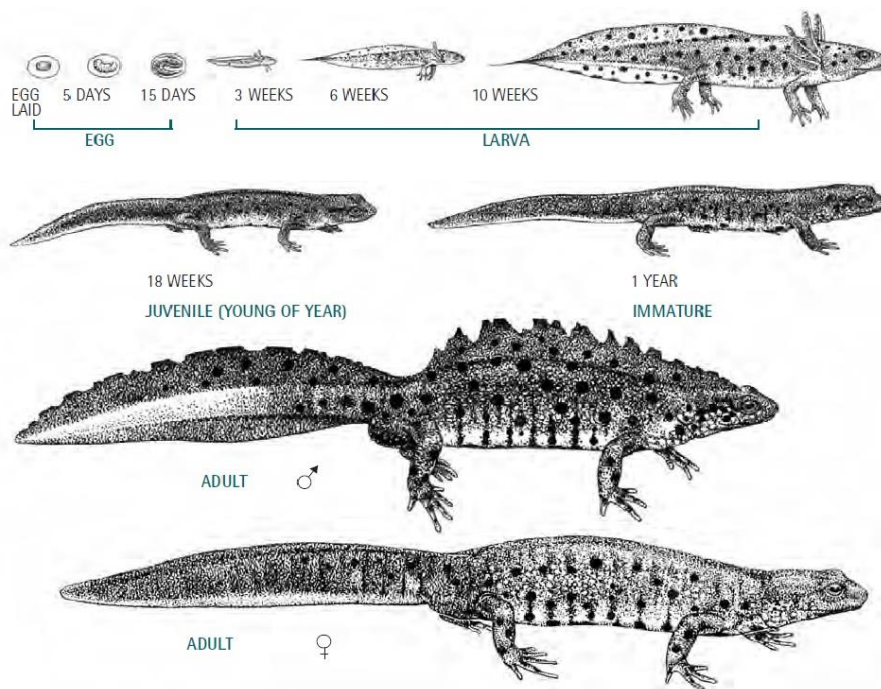
Figure 2. Life stages of *T. cristatus* (according to Langton et al. 2001, modified).

In temporary habitats, amphibians tend to be larger (Thorson 1955). During the aquatic phase, weight changes are common due to reproductive activities, with females typically gaining and males losing weight (Jehle et al. 2011). However, it's important to note that these patterns can vary significantly among individuals (Mullner 1991). Newts begin the breeding season in better body condition, which diminishes due to the energetic costs of reproduction (Arntzen et al. 1999). Environmental factors like breeding pond temperature

can influence condition at metamorphosis (Reading 2007). The actual problem is that milder winters may lead to lower body conditions, potentially due to increased metabolic rates (Reading 2007). Differences in condition scores between sexes may indicate reproductive potential in females and energy reserves in males, reflecting their varied habitat use (Jarvis 2015).

In amphibian breeding populations, sex ratios are often balanced, but some populations exhibit a slight male bias, especially early in the breeding season (Arntzen 2002; **Paper I**, **IV**). Balanced sex ratios are crucial for population dynamics and influence the intensity of mate competition. When the sex ratio is skewed, competition for mates becomes more intense in the predominant sex, leading to stronger sexual selection for advantageous traits (Grayson et al. 2012). In the *Triturus* genus, males are capable of mating with multiple females, although there are limitations such as the availability of spermatophores (Halliday 1987). For *T. cristatus*, optimal mating opportunities mostly occur in the evenings (Griffiths 1985).

Newts, which typically inhabit small ponds and heterogeneous cultural landscapes with low–intensity usage, are increasingly losing their habitats in modern landscapes. This reduction has led to the destruction of many newt localities, resulting in heightened isolation and fragmentation that adversely affects newts at both individual and population levels (Bernes 1994; Ihse 1995; Hull 1997; Beebee and Griffiths 2000; Benton et al. 2003; Löfvenhaft et al. 2004; Edgar and Bird 2006; Loman and Anderson 2007; Malmgren et al. 2007). Due to its metapopulation structure and limited migration ranges, *T. cristatus* is particularly vulnerable to these habitat changes (Laan and Verboom 1990; Joly et al. 2001; Ficetola and De Bernardi 2004; Schabetsberger et al. 2004; Karlsson et al. 2007). During its terrestrial life stages, *T. cristatus* generally remains close to its breeding sites. Although some may travel over a kilometre away, most are found within 250 meters of their pond, with significant activity occurring even closer (Baker et al. 2011). Optimal breeding ponds offer abundant submerged vegetation, and a pH above 5.5. However, newts are adaptable to various pond types, including water tanks, disused pools, and flooded quarries (Baker et al. 2011). Female *T. cristatus* typically lay around 250 eggs per season, but approximately half may fail due to chromosomal issues (Langton et al. 2001). The larvae, primarily feeding on zooplankton, inhabit the ponds during summer and are usually found in the free water column, making them susceptible to fish predation. They undergo metamorphosis from July to September, and post–metamorphosis, while many newts move

to land, some either remain in or return to the pond during their juvenile stage (Thiesmeier and Kupfer 2000; Malmgren 2002; **Paper I**, **IV**). They reach sexual maturity within two to three years (Griffiths 1996; Jehle and Arntzen 2000; Baker et al. 2011), with juveniles typically remaining on land, though some return to their birth pond before adulthood (Griffiths 1996; Langton et al. 2001; **Paper I**).

In larger populations, high larval counts can hinder larval growth, survival, and post–metamorphic outcomes like decreased size at metamorphosis (Cayuela et al. 2020). This can subsequently diminish juvenile recruitment and overall population size (Ousterhout and Semlitsch 2016, **Paper IV**). Some of the studies show annual survival rates for newts vary between 25–100% based on location and year (Baker 1999; Griffiths et al. 2010). Adults generally survive more than juveniles, but consistent patterns aren't clear. High adult counts don't guarantee juvenile numbers, and low juvenile rates don't predict adult decreases (Jehle et al. 2011). Newt populations are influenced by factors like predation, migration, climate, and resources, complicating generalizations and necessitating further research (Griffiths et al. 2010, **Paper IV**).

1.2 Ecology

T. cristatus undergoes both terrestrial and aquatic life stages. In aquatic environments, they engage in courtship, breeding, and larval development. The terrestrial phase includes hibernation and the rest of their life cycle (Malmgren 2007). Newts emerge from hibernation when temperatures rise and migrate to aquatic habitats during the first warm nights of spring, adapting physically and behaviourally for aquatic life (Thiesmeier and Kupfer 2000; Malmgren 2007). *T. cristatus* undergoes both terrestrial and aquatic life stages. In aquatic environments, they engage in courtship, breeding, and larval development. The terrestrial phase includes hibernation and the rest of their life cycle (Malmgren 2007). Newts emerge from hibernation when temperatures rise and migrate to aquatic habitats during the first warm nights of spring, adapting physically and behaviourally for aquatic life (Thiesmeier and Kupfer 2000; Malmgren 2007). Older individuals of *T. cristatus* arrive at ponds earlier and stay for shorter periods compared to their younger counterparts (Stoefer and Schneeweiss 2001; Sinsch et al. 2003; Paper IV), with males typically being the first to enter and juveniles among the first to leave. Factors such as water depth, predator presence, and food supply also influence residence time in ponds (Jehle et al. 2011; Gustafson 2011).

Courtship, mainly nocturnal and peaking at dusk, involves males displaying and competing near the shoreline in shallow water. Females mate with multiple males throughout the period, ensuring enough spermatophore for egg fertilization (Hedlund 1990; Malmgren 2007). Initially, females prefer larger males but become less selective as the season progresses (Malmgren 2007; Malmgren and Enghag 2008). They lay eggs individually in submerged vegetation, wrapping them in leaves for protection (Miaud 1993; Miaud 1994; Langhelle et al. 1999; Marco et al. 2001). Preferred plants include floating sweet grass, water mint and broad–leaved pondweed (Langton et al. 2001), with a typical yield of 200 to 300 eggs per season (Thiesmeier and Kupfer 2000; Langton et al. 2001). Larval development depends on water temperature, but about half the embryos don't survive to become larvae (McGregor and Horner 1980; Malmgren 2001). Larvae feed initially on planktonic crustaceans, later expanding their diet to include larger aquatic invertebrates (Griffiths and Mylotte 1987; Griffiths et al. 1994; Griffiths 1996). Predatory fish, dragonfly nymphs, and water beetles pose significant threats to newt eggs and larvae, influencing adult newts to avoid breeding in fish–inhabited waters (Cooke and Frazer 1976; Miaud 1993; Thiesmeier and Kupfer 2000; Cooke 2001; Malmgren 2001). Around three months after hatching, newt larvae transition to lung–breathing and undergo morphological changes for terrestrial life, like skin thickening (Malmgren 2007).

Post–breeding, adults actively forage on land, feeding on worms, centipedes, and other small invertebrates (Griffiths 1996; Thiesmeier and Kupfer 2000). Predators include snakes, birds, and mammals (Gleed–Owen 1996; Jehle and Arntzen 2000; Thiesmeier and Kupfer 2000; Webley 2007), but their skin glands provide some defence. Newts are mostly nocturnal and hide in leaf litter, logs, or underground to avoid predators and dehydration (Jehle 2000; Jehle and Arntzen 2000; Schabetsberger et al. 2004; Gustafson 2011). Hibernation occurs in warm, deep sites, including human–made structures, when temperatures fall below 2°C (Thiesmeier and Kupfer 2000; Jehle and Arntzen 2000). The hibernation duration varies with temperature and rainfall, with field studies recording individuals up to 16 or 18 years old (Hagström 1979; Thiesmeier and Kupfer 2000). Here it is worth noting that elevated temperatures, in the context of climate change, pose significant risks to amphibians, including increased mortality, changes in activity patterns, and reduced female fecundity (Reading 2007). Griffiths et al. (2010) also reported that male *T. cristatus* experienced lower survival rates following winters with unusually high temperatures. Additionally, amphibian larvae as faster as pond drying can shorten their metamorphic

phases (Rowe and Dunson 1995). Such changes in pond dynamics can disrupt larval growth (Boone et al. 2002), and alterations in predation dynamics may occur due to size–dependent vulnerabilities. The risks of premature breeding, such as exposure to unpredictable spring weather, are offset by the potential benefits of extended growth periods for larvae (Corn and Muths 2002).

Aquatic habitats of *T. cristatus* were studied more often, focusing on various physical, chemical, and biological aspects (Griffiths 1996; Thiesmeier and Kupfer 2000; Malmgren 2001, 2007; Gustafson 2011). *T. cristatus* prefer stagnant small water bodies like shallow ponds or small lakes, typically 50–250 m² in size (Thiesmeier and Kupfer 2000; Langton et al. 2001; Denoël and Ficetola 2008). Optimal conditions include a shallow shoreline, abundant vegetation, and water retention until late autumn (Griffiths 1997; Denoël and Lehmann 2006; Malmgren 2007). Periodic drying benefits by reducing predators and vegetation overgrowth (Beja and Alcazar 2003; Ficetola and De Bernardi 2004) as fish predation is a significant threat, especially to developing larvae (Beebee 1985; Baker and Halliday 1999; Joly et al. 2001; Malmgren 2001; Skei et al. 2006).

Research on pond biodiversity highlights that physical, biological, and landscape characteristics significantly influence the flora and fauna , more so than chemical properties of the water (Laan and Verboom 1990; Pavignano et al. 1990; Denoël and Ficetola 2007). Nevertheless, the interaction of physical and chemical factors plays a crucial role in pond life which can affect *T. cristatus* presence (Angelibért et al. 2004; Scheffer and van Geest 2006). High water temperatures in ponds are primarily a result of high exposure to sunlight; ponds receiving more sun tend to be warmer, leading to increased productivity suggesting that warmer ponds often host greater biodiversity (Werner and Glennemeier 1999; Oldham et al. 2000; Thiesmeier and Kupfer 2000). These conditions might signal habitats rich in both species and nutrients. Research by Gustafson et al. (2006) highlighted the *T. cristatus* as an indicator of abundant macrophyte diversity in ponds, possibly because this species prefers warmer, more productive environments. These conditions are advantageous as they foster higher growth rates and improved survival of eggs and larvae (Skelly et al. 1999; Werner and Glennemeier, 1999). In the northern distribution areas of *T. cristatus*, water temperature could be a critical factor for reproductive success. The breeding season's length is influenced by the amount of sunlight the aquatic habitat receives, with rapid warming in spring leading to shorter egg and larval development times (Griffiths and De Wijer 1994; Griffiths 1996). Acidified waters prohibit many species from reproducing, or even using

them as habitats, and this is also a likely scenario for *T. cristatus* (Skei et al., 2006). High levels of nitrogen (N) and phosphorus (P) indicate abundant nutrients, crucial for high productivity. Phosphorus typically limits primary production in aquatic ecosystems, but when ample, nitrogen may become the limiting factor (Brönmark and Hansson 2017). However, nutrient–overloaded ponds can suffer from eutrophication, leading to plant overgrowth, low oxygen levels, and poor water quality (Engelhardt and Ritchie 2001; Knutson et al., 2004). Gustafson et al. (2009) indicate that ponds supporting *T. cristatus* reproduction have lower nitrogen and phosphorus levels than those where the species is present but not reproducing. This suggests a preference for moderately nutrient–rich environments, aligning with Gustafson et al. (2006) observations. Other factor is concentration of ammonium, which affecting larval development, varies with temperature and pH; higher pH levels increase its toxicity (Berg, 1996). Biological factors also impact pond chemistry and physical conditions, such as how vegetation cover can affect temperature and oxygen levels (Angelibért et al. 2004; Gustafsson and Boström 2011). For example, temperature stratification could occur in some small and shallow ponds due to a shield formed by floating plants (Angelibért et al. 2004). Availability of food and shelter, along with predation and competition, are crucial in determining amphibian distribution (Griffiths et al. 1993). Minor variations in nutrient levels or the presence of certain species can trigger significant ecosystem changes due to cascading effects (Aronsson and Stenson 1995; Cottenie and De Meester 2004).

Adequate terrestrial habitat should provide foraging opportunities, protection from predators, suitable shelters, and hibernation sites (Langton et al. 2001; Gustafson 2011). *T. cristatus* needs foraging sites, shelters and hibernation, and pathways between aquatic and terrestrial habitats. While terrestrial habitat studies are less common, research suggests that the newt thrives in areas with dense vegetation or abundant ground cover like leaf litter and logs (Jehle 2000; Jehle and Arntzen 2000; Joly et al. 2001; Malmgren et al. 2007; Hartel et al. 2010a). These habitats, including forests, woodlands, wetlands, and grasslands, offer hiding spots and prey (Griffiths 1996; Latham and Oldham 1996; Thiesmeier and Kupfer 2000; Langton et al. 2001). Even less ideal environments like coniferous forests or industrial areas can be adequate only if they provide suitable microhabitats. Open fields with high predation and desiccation risks are typically avoided due to lack of coverage (Jehle and Arntzen 2000; Oldham et al. 2000; Joly et al. 2001; Malmgren 2002). Proximity

to a breeding pond is essential (Kupfer 1998; Jehle 2000; Langton et al. 2001; Malmgren 2002).

Metapopulation dynamics, involving multiple connected breeding populations and alternative ponds within dispersal range, are crucial for the newt's survival (Sjögren 1991; Vos and Chardon 1998; Joly et al. 2001; Marsh and Trenham 2001; Semlitsch 2002; Denoël and Lehmann 2006). A "pondscape" comprising both aquatic and terrestrial habitats, including both natural and human–made ponds, is vital for habitat diversity and migration facilitation (Swan and Oldham 1993; Joly et al. 2001; Malmgren 2002). This landscape should ensure adequate terrestrial habitats near aquatic ones (Boothby 1997; Griffiths and Williams, 2000; Langton et al. 2001), although the exact size needed for a viable newt population is still undetermined.

1.3 Migration

Migration in animals is an adaptive response to seasonally changing environments, a behaviour that includes breeding migrations in amphibians moving from land to wetlands for offspring development (Alerstam and Lindström 1990; Duellman and Trueb 1994; Russell et al. 2005; Dingle 2014). Migrations also serve various functions such as facilitating accessing alternative resources and avoiding survival–threatening physiological constraints (Grayson et al. 2011). Species exhibit different migratory strategy depending on their physiological tolerance and ability to resist desiccation, especially under varying climatic conditions (Todd and Winne 2006).

Amphibians face challenges when migrating between terrestrial and aquatic habitats, such as high energy costs and increased mortality risks in unfamiliar territories (Ims and Yoccoz, 1997; Holt, 1996). The ease of traversing these transitional areas is crucial for maintaining population sizes and ecological connectivity (Merriam, 1984; Baudry and Merriam, 1988). In small, dispersed amphibian populations, immigration is vital for reducing local extinction risks, with habitat proximity and matrix connectivity playing significant roles in movement success (Foley 1992; Joly et al. 2001). Movement behaviour is pivotal in conservation biology since it determines how organisms engage with both other species and their environment (Vojar 2007; Nathan et al. 2008).

Dispersal and migration, facilitated by shorter distances between habitats, can help sustain amphibian populations at specific sites, counterbalancing low local reproductive

rates (Levins 1970; Gill 1978; Hanski 1991). Dispersal includes movements from birth or breeding locations to other breeding sites, encompassing both natal and breeding dispersals (Clobert et al. 2009; 2012; Matthysen 2012). It's essential for gene flow and influences the eco–evolutionary dynamics of spatially distributed populations (Bowler and Benton 2005; Ronce 2007). After these facts we have to view at amphibians through a metapopulation ecology lens, as a network of interconnected sub–populations, highlights the importance of habitat connectivity for overall population health, particularly in fragmented landscapes (Baker et al. 2011).

Terrestrial behaviours with migration aspect remain less understood, despite their importance (Denton and Beebee 1994; Dodd and Cade 1998; Semlitsch 1998; Semlitsch 1985; Pechmann et al. 1991; Law and Dickman 1998, **Paper I**, **IV**). Post–breeding, newts migrate overland, often utilizing small mammal burrows and preferring habitats with bare soil, indicative of underground refuges. Their migration patterns, observed through methods like drift fences, reveal preferences for certain directions and habitats (Dodd and Cade 1998). Our understanding of urodele migration orientation is informed by observed behaviours. These animals typically follow a direct route in their terrestrial–aquatic migrations, as shown in studies by Shoop (1968), Madison and Shoop (1970), Shoop and Doty (1972), Douglas and Monroe (1981), Kleeberger and Werner (1982, 1983), and Madison (1997). Most newt individuals demonstrate site fidelity to specific aquatic locations, a behaviour documented by Joly and Miaud (1989), with similar fidelity to terrestrial sites suggested by Joly et al. (2001). Experimental studies have identified two primary orientation mechanisms in amphibian navigation: pilotage using chemical cues from the target site and possible magnetic compass orientation, as evidenced by research from Hershey and Forester (1980), Phillips (1986a, 1986b, 1987), McGregor and Teska (1989), Phillips and Borland (1992), and Joly and Miaud (1993). In contrast, study Sinch (2014) describes that given their limited movement range, most amphibians are unlikely to use Earth's magnetic field for navigation. Some studies have indicated that newts typically move straight towards suitable habitats after leaving breeding ponds, efficiently utilizing space (Verrell 1987; Sinsch 1991; Jehle et al. 2011; Jehle and Arntzen 2000). However, in other studies *T. cristatus* may not consistently exhibit directional preference when moving to and from ponds (Verrell and Halliday 1985) and furthermore there is no significant evidence that *T. cristatus* navigate to and from ponds in a body size–dependent manner (**Paper I**, **IV**). Dispersal often involves random–walk strategies (Brown et al. 2014).

Attempts to alter the homeward orientation e.g. of the European common toad using magnetic fields have been unsuccessful (Sinsch 1987; Landler and Gollmann 2011). Instead, amphibians often rely on visual and olfactory landmarks for navigation within familiar areas (Joly and Miaud 1993; Hayward et al. 2000). To date, there's no indication that these animals navigate using a cognitive map or that linear features like hedgerows and ditches act as effective corridors in newt migration, especially through cultivated fields (Joly et al. 2001, **Paper I**). In addition, some studies suggest newts might use syntopic amphibian species as orientation reference points (Diego–Rasilla and Luengo 2007).

Ensuring expansive and uninterrupted habitats is essential for facilitating newts' migration between terrestrial and aquatic sites. Finally, migration influences climate conditions (Jehle et al. 2011, **Paper I**, **IV**). Understanding the effects of climatic factors on amphibian over–land migration patterns is vital for assessing the future impacts of climate change and developing mitigation strategies. Changes in rainfall, for example, can significantly affect pond–breeding amphibian populations by altering their habitats and increasing larval mortality, as observed in studies by Semlitsch and Wilbur (1988), Carey and Alexander (2003), and Daszak et al. (2005).

The terrestrial life stage of adult *T. cristatus* encompasses four phases: dispersal from the breeding site in late summer, a foraging period, winter hibernation, and a return migration to the pond (Duff 1989). *T. cristatus* shows a lengthy aquatic breeding period and an extended terrestrial sub–adult phase (Bouton 1986; Francillon–Vieillot et al. 1990; Law and Dickman 1998). They typically inhabit areas from 200 to 800 meters of their breeding ponds (Cooke and Frazer, 1976; Jehle, 2000; Jehle and Arntzen 2000; Thiesmeier and Kupfer 2000; Schabetsberger et al. 2004) and often establish in newly created ponds within 1000 meters of existing populations (Laan and Verboom 1990). Some studies estimated their annual dispersal rate at about 1 kilometre (Arntzen and Wallis 1991; Halley et al. 1996; Jehle and Arntzen 2000). However, *T. cristatus* migrations can span up to 1290 meters annually (Kupfer 1998), surpassing the previously estimated dispersal distance of 1 km/year. During hot, dry conditions, newts remain underground, eschewing surface foraging even in heavy rainy weather. This behaviour may be attributed to predator avoidance and unfavourable climatic conditions (Aebischer et al. 1993; Jehle and Arntzen 2000, **Paper IV**). The species' ability to rapidly increase its population in new habitats demonstrates its adaptability and opportunistic breeding behaviour (Arntzen and Teunis 2003), despite some challenges in adapting to new environments (Hagström 1980).

The survival of *T. cristatus* thus depends on the accessibility of two distinct habitats: aquatic zones for breeding and development, and terrestrial areas for post–breeding activities and juvenile growth. For population sustainability, these habitat types must be within feasible migration distances (Gustafson 2011). In terrestrial migrations, they likely target quality microhabitats and shelters, such as safe hibernation sites (Malmgren 2002). Studies have shown that most newt movements occur within forested areas, avoiding open fields in favour of woodlands or semi–natural meadows and pastures (Jehle and Arntzen 2000; Malmgren 2001; Joly et al. 2001; Malmgren 2002), although the availability and quality of these microhabitats can vary significantly (Jehle et al. 2011).

The migration period of *T. cristatus* typically occurs between February and April (Langton et al. 2001; **Paper I**, **IV**). These immigrations often happen at night, especially when air temperatures exceed 4–5 °C, with peak activity during and following humid nights (Jehle et al. 2011). The lunar cycle also plays a significant role in influencing newt activities, a correlation noted by Ralph (1957), and Deeming (2008) reported increased *T. cristatus* activity preceding the new moon. Notably, newt migration, including that of crested newts, is an unsynchronized process. Individuals may migrate several months post their initial arrival at the pond (Langton et al. 2001). Male newts typically arrive at the pond a few days prior to the females, likely to improve mating success. This strategy potentially offers males an advantage in securing mates during the breeding season (Jehle et al. 2011).

Adults of *T. cristatus*, often show non–random migration patterns when departing from breeding sites, frequently using the same entry and exit points and favouring specific habitats as transit routes (Marty et al. 2005; Sztatecsny and Schabetsberger 2005; **Paper I**, **IV**). Juvenile *T. cristatus* often display a non–specific direction of migration, possibly as part of their dispersal process, suggesting that various factors, including the surrounding habitat's structure and resources, influence their movements (Paper I, IV). This behaviour is consistent with study Malmgren (2002), who observed that juvenile of *T. cristatus* showed non–random migration directions when they were leaving ponds, with a preference for forested areas over open fields. This indicates the significance of certain habitat types. Interestingly, despite lacking prior terrestrial experience, juveniles exhibited a preference for forest–adjacent areas during dispersal, hinting at the role of environmental cues in guiding their migration (Paper I, IV). Some juveniles remain near the breeding site, reach sexual maturity, and return to reproduce in their natal pond, integrating into the local adult breeding population. Others disperse to adjacent terrestrial habitats, possibly colonizing

new ponds. The migration paths of *T. cristatus* are often shaped by various environmental factors, such as developed land, forests, and potential shelters in gardens during their terrestrial phase (Gustafson 2011). The use of village gardens as overwintering sites underscores these amphibians' ability to adapt to human–modified environments, a crucial trait in a world where natural habitats are increasingly compromised. Studies indicate that upon leaving breeding ponds, newts often travel in straight lines towards favourable habitats, implying a strategic use of space (Verrell 1987; Jehle and Arntzen 2000; Jehle et al. 2011). Interestingly, *T. cristatus* metamorphs might even be capable of following trails left by adults (Hayward et al. 2000; Oldham et al. 2000; **Paper I**, **IV**).

Verrell and Halliday (1985) observed that most adult newts had entered ponds by May 5th. Other study documented a spring immigration period spanning from February to May (Blab and Blab 1981). Additionally, an emigration phase was noted from mid–July to mid–October, followed by a second immigration wave in early autumn (Jehle et al. 2011, **Paper I**). This autumn migration suggests that some individuals might overwinter in aquatic environments, potentially explaining situation when fewer amphibians are captured leaving than entering ponds, especially when using drift fences (Verrell and Halliday 1985; **Paper I**). While the exact causes of this discrepancy remain unclear, predation among other factors might play a role.

Regarding gender–specific migration timing, male *T. cristatus* typically arrive at breeding ponds before females (Jehle et al. 2011; **Paper I**), a pattern echoed in other newt species (Diego–Rasilla 2003; Diego–Rasilla and Luengo 2007) and salamanders (Douglas 1979; Sexton et al. 1990). This behaviour may provide males with a selective advantage by increasing mating opportunities. Conversely, females might delay their arrival to ensure a wider selection of potential mates (Douglas 1979; Russell et al. 2005). Interestingly, despite males having a slightly longer aquatic phase, they tend to leave ponds before females (Arntzen 2002, **Paper IV**).

Verrell and Halliday (1985) noted that adult female *T. cristatus* entering the water were generally longer than males, a trend also seen in females emigrating from ponds. Regarding migration temperatures, female *T. cristatus* typically start migrating at around 10 °C, while males prefer cooler temperatures up to 5 °C. Juveniles begin their migration as temperatures rise, with initial movements occurring post–sunset at temperatures above 4–5 °C, and peak activity during successive humid nights (Jehle et al. 2011; **Paper I**). Moreover, the

temperature threshold for migration in crested newts is higher than that of smaller newt species (Griffiths and Raper 1994).

Rainfall and humidity significantly influence amphibian behaviours, with these effects varying by body size and gender (Byrne 2002; Scott et al. 2008; Todd et al. 2011; **Paper IV**). Amphibians depend on moisture for water balance, making them particularly susceptible to desiccation in dry periods (Jørgensen 1997; Hillyard 1999). Newts measuring between 50 and 70 mm show a preference for heavier rainfall, while larger newts reduce their arrival frequency as rainfall increases (**Paper I**). Juveniles are more likely to emigrate during heavier rainfall, but adults demonstrate decreased emigration in such conditions. Juvenile amphibians, due to their smaller size and higher surface area to volume ratio, face a greater risk of desiccation during day–time migrations compared to adults (Spight 1968). Nocturnal rainfall is known to trigger migrations by reducing desiccation risks (Semlitsch and Pechmann 1985), leading to the expectation that juveniles would be less likely to migrate during the day. As for humidity, males find optimal emigration conditions at around 60% average humidity, whereas females tend to stop emigrating as humidity rises (**Paper I**). Contrastingly, juvenile emigration increases with rising humidity. Smaller individuals (up to 80 mm) need higher humidity levels for emigration, while larger individuals (over 110 mm) cease emigrating when humidity exceeds 60%. This variation in response highlights the complexity of environmental influences on amphibian migration behaviours (**Paper I**) and requires further research.

Previous research has indicated that lunar phases can influence the behaviour of amphibian species. Ralph (1957) found that salamanders' activity patterns were linked to the lunar cycle. This pattern, with heightened activity during darker nights, might serve as a survival strategy, minimizing predation risks during movements away from breeding ponds for foraging or inter–pond migrations (Deeming 2008; **Paper I**). An alternative explanation could involve secondary factors like insect activity, which often peaks during full moon phases. If the studied species, such as salamanders or newts, depend on these insects for food, their migration and foraging behaviours might indirectly align with their prey's lunar–driven activity patterns, rather than directly with the moon's phase or brightness (**Paper I**). This relationship could result in an apparent correlation between lunar phases and migration patterns. Future studies should consider a multi–variable approach to explore these potential ecological interactions (Deeming 2008). Another factor that might affect these observations is cloud cover, which can obscure moonlight and thereby

influence animal activity patterns. Additionally, human activities could affect the visibility of the moon, potentially impacting the observed behaviours. Future research could investigate these elements to better understand the role of lunar phases in migration patterns (**Paper I**).

Climatic conditions are increasingly recognized as critical in influencing the migratory behaviours of *T. cristatus*, a significant amphibian species. The global decline in amphibian populations is potentially linked to climate change, given that climatic factors like precipitation and temperature play a pivotal role in amphibian population dynamics (Blaustein et al. 2001; **Paper I**). Some studies found that the migration phenology of *T. cristatus* is significantly impacted by both temperature and precipitation, with a trend towards earlier breeding migrations as temperatures rise (Dervo et al. 2016; **Paper I**, **IV**). This observation suggests that, in the face of ongoing climatic shifts, amphibian phenology might also evolve, a phenomenon already seen in various other species (Bradshaw and Holzapfel 2001). However, there's still a gap in understanding whether these responses in amphibians to climate change are a result of genetic adaptations or solely phenotypic plasticity (Urban et al. 2014). We must keep in mind the potential effects of rapid regional weather pattern changes on amphibian migrations (Todd et al. 2011). These climatic shifts could have disparate impacts on different species, possibly leading to changes in the timing of reproductive adult arrivals and the success rates of migrations. This underscores the importance of incorporating these climatic factors and varied species responses into conservation strategies.

1.4 Conservation and monitoring

T. cristatus has seen a widespread decline in Europe, including in Great Britain, Norway, Germany, Austria, and Russia, as evidenced by numerous studies (Beebee 1997; Beebee and Griffiths 2000; Thiesmeier and Kupfer 2000). Therefore, accurate and reliable data on the population trends of *T. cristatus* are crucial for its effective conservation and management under the EU Habitat Directive (Ortmann et al. 2006). Key to their conservation is understanding factors affecting habitat selection, survival, and reproduction. This involves examining aquatic and terrestrial habitats' physical, chemical, and biological features and understanding how landscape features influence species dynamics, particularly habitat permeability to dispersal (Gustafson et al., 2006; Gustafson et al., 2009; Gustafson et al., 2011; Pither and Taylor 1998). Both aquatic and terrestrial

environments regulate populations, with their influence varying based on spatial arrangement and habitat availability (Semlitsch 1998; Skelly and Meir 1997).

The newt's susceptibility to habitat fragmentation poses a significant risk of local extinction (Shaffer 1987), with population dynamics being influenced by land use changes, such as a notable reduction in pond numbers due to agricultural and urban development (Hull 1997; Hamer and McDonnell, 2008). Environmental factors like air pollution, introduction of fish in ponds, afforestation, and loss of dead wood have further degraded their habitats (Griffiths 1996; Latham and Oldham 1996; Jeffries 1998; Schabetsberger et al. 2004; Brönmark and Hansson 2017). Agricultural runoff leading to eutrophication and habitat overgrowth has also impacted these newts (Oldham 1994; Relyea 2005; Kadoya et al. 2011; Brönmark and Hansson 2017).

Conservation strategies must focus on both aquatic and terrestrial environments, considering nutrient levels, pond management, and surrounding land use (Cooke and Frazer 1976; Baker and Halliday 1999; Kupfer and Kneitz 2000; Thiesmeier and Kupfer 2000; Lesbarrerés et al. 2010). The newts' limited dispersal abilities and biphasic life cycle necessitate a comprehensive approach to habitat management, emphasizing the importance of diverse, semi–natural landscapes, pond connectivity, and the physical quality of the landscape they traverse (Møller and Rørdam 1985; Latham and Oldham 1996; Bowne and Bowers 2004; Karlsson et al. 2007; Bloechl et al. 2010; Ribeiro et al 2011). Conservation efforts should aim for a mosaic of high–quality aquatic and terrestrial habitats with corridors to ensure viable populations (Swan and Oldham 1993; Jehle 2000; Joly et al. 2001; Langton et al. 2001; Malmgren 2002; Marsh and Trenham 2001; Smith and Green 2005; Griffiths et al. 2010; Gustafson 2011). When planning new ponds, understanding amphibian navigation is crucial. While adults have been observed colonizing newly built ponds within short distances (Lenders, 1996; Gressler, 1997; Baker and Halliday, 1999), the role of juveniles in initial colonization remains less clear.

Effective conservation management for endangered newt species hinges on establishing robust monitoring methodologies and assessing trap efficacy to gather accurate data (**Paper II**). Evaluating various sampling techniques is crucial for successful amphibian monitoring (Antonishak et al., 2017). Monitoring during the breeding season is particularly important due to the increased visibility of migrating adults or egg masses (Miller and Grant, 2015; Davis et al., 2017). The rise in the importance of tracking

amphibian populations has led to significant advancements in monitoring techniques, such as those developed by the United States Geological Survey's Amphibian Research and Monitoring Initiative and the efforts by Partners in Amphibian and Reptile Conservation (Graeter et al. 2013). Monitoring often focuses on the breeding season when adults and egg masses are observable in breeding sites (Miller and Grant 2015; Davis et al. 2017).The success of these efforts is influenced by factors such as the newts' body size, home range, activity patterns, trap avoidance, and weather conditions (Crosswhite et al. 1999). Amphibian monitoring employs methods like drift fences with pitfall traps, aquatic funnel traps, visual encounter surveys, and dip–net surveys (Heyer et al. 1994; Hutchens and DePerno 2009). Dip–netting is commonly used in Europe for capturing breeding newts (Malmgren et al. 2005; Briggs et al. 2006; Goverse et al. 2006; Skei et al. 2006; Denoël et al. 2013). However, some studies have highlighted the effectiveness of fish traps and drift fences (Baker 1999) and the advantages of funnel traps like Ortmann's trap for cost–effectiveness and efficiency (Ortmann 2009; Drechler et al. 2010; **Paper II**). Most surveys for detecting newts are conducted at night to improve detectability (Halliday 2006; Manenti et al. 2019; **Paper II**).

Newt studies thus depend on effective surveying and monitoring techniques, considering their amphibious nature and the challenges in securing representative samples (Kålås et al. 2010; Arntzen and Zuiderwijk 2020; Dervo et al. 2014). Techniques such as capture–mark–recapture (CMR), employing unique pattern mapping photography, are crucial for estimating critical demographic parameters, aiding in conservation decisions (Williams et al. 2002; Nichols 2014). Studying abundance dynamics necessitates strategic long–term sampling and suitable data analysis models (Cayuela et al. 2019). Population growth can be influenced by density, and multiple surveys at each location during each sampling season might be necessary for reliable abundance measures, though this can be time–consuming (Kellner and Swihart 2014; Ficetola et al. 2018; Falaschi et al. 2021; Falaschi et al. 2022). Efficient and informative population monitoring is especially crucial for vernal pools where newts populations are declining (Mitchell et al. 2006; Adams et al. 2013). These ecosystems are increasingly at risk due to changing precipitation patterns caused by climate change, underscoring the need for effective monitoring (Brooks 2004; Hayhoe et al. 2007; Anderson et al. 2015; Davis et al. 2017).

Adult newt survey methods include active sampling, where surveyors directly capture animals, and passive sampling using traps. Passive methods, like drift fences encircling pools with fences and traps, are effective but resource–intensive (Dodd 1991; Gibbons et al. 2006; Grayson et al. 2011). Active methods, such as visual encounter surveys and dip–net surveys, offer more flexibility and require less resources but depend on the skill of the surveyor and can potentially harm habitats (Heyer et al. 1994; Grant et al. 2005; Bennett et al. 2012; Antonishak et al. 2017). The choice between passive and active survey methods depends on resource availability, effort requirements, and the goal of achieving high encounter rates or studying both larval and adult amphibians (Luhring et al. 2016; Wilson and Pearman 2010; Bennett et al. 2012). The effectiveness of drift fences has been found to vary (Arntzen et al. 1995; Baker 1999; Jehle et al. 1997; Crosswhite et al. 1999). On the other hand, in some instances, dip–netting has proven to be more efficient than using un–baited funnel traps (Bevelheimer et al. 2008). In the Czech Republic, national conservation guidelines advise using a mix of chicken liver–baited funnel traps and dip netting for newt capture (Jeřábková and Boukal 2011). Aquatic funnel traps, traditionally used for larval amphibians, have also proven effective for adult amphibians (Heyer et al. 1994; Antonishak et al. 2017). Funnel trapping is a standardized and efficient method for amphibian surveys and trend monitoring, preferable to dip–net surveys which can disrupt aquatic vegetation and increase water turbidity (Adams et al. 1997; Arntzen and Zuiderwijk 2020). These traps are recommended in dense vegetation or debris–laden areas where dip–netting is difficult and have been shown to correlate with adult amphibian population density (Adams et al. 1997; Wilson and Pearman 2010). Research indicates that umbrella–shaped funnel traps are more effective for capturing *T. cristatus* than the Ortmann's trap and the commonly used prism–shaped trap. This is likely due to their larger size and openings (Drechler et al. 2010; Pellet et al. 2010; Baker 2013; **Paper II**). In contrast, the prism–shaped trap, often employed for caudate amphibians, shows the lowest efficiency, potentially leading to underestimations of *T. cristatus* populations due to its smaller entrance and size (Bock et al. 2009; Pellet et al. 2010; Baker 2013; **Paper II**).

Aquatic funnel trapping is thus widely utilized for surveying amphibians in ponds, a method that's become crucial for conservation due to declining amphibian populations (Adams et al. 1997; Anderson et al. 2015; Davis et al. 2017). Introduced in 1973, these traps have varied in design, ranging from collapsible crayfish traps with small mesh to commercially available cylindrical traps, box funnel traps with fine mesh, plastic beverage

bottle traps, nylon mesh traps, and those made from acrylic sheets (Calef 1973; van Gelder 1973; Richter 1995; Adams et al. 1997; Arntzen and Zuiderwijk 2020). Un–baited funnel traps are commonly used in studies to capture caudate amphibians, though some research uses baits like shrimp or salmon eggs (Adams et al. 1997). Baits such as chicken liver, animal entrails, fish parts, salami, dog food, and raw beef are also employed (Jeřábková and Boukal 2011; Baker 2013; Sannolo and Gatti 2017). The use of baits in amphibian trapping has yielded mixed results. Some studies found no significant difference between baited and unbaited traps, while others suggest that baits might attract predators, thereby reducing capture efficiency (Grayson and Row 2007; Pellet et al. 2010; Antonishak et al. 2017; Sannolo and Gatti 2017; Adams et al. 1997). Considering *T. cristatus* color vision, the color of the bait and trap could influence capture rates (Williams 2014; Antonishak et al. 2017). Moreover, glow sticks as light bait may increase captures by visually attracting adult amphibians, necessitating further research on the efficiency of different coloured lights (**Paper II**). However, using them in traps, a practice adopted from larval fish studies, on the other hand can introduce biases and affect trap standardization due to preferences for certain sizes and groups, or water turbidity (Hernandez and Lindquist 1999; Marchetti and Moyle 2000; Marchetti et al. 2004; Bennett et al. 2012). Despite these challenges, glow sticks have been shown to increase newts captures, transforming passive traps into more active sampling devices (Bennett et al. 2012; **Paper II**).

Nevertheless, funnel trapping presents certain limitations. A study in France indicated a possibility of "trap shyness," with a decrease in amphibian captures over time (Arntzen and Zuiderwijk 2020). There's also the risk of spreading diseases like chytridiomycosis, which can be reduced by disinfecting traps with solutions such as 1% Virkon® (Johnson et al. 2003; Dejean et al. 2010). Aquatic funnel trapping remains a reliable and straightforward method for studying pond amphibians, effective even in vegetated areas, though the trap rates might not always reflect the true abundance due to varying capture probabilities (Seber 1982; Adams et al. 1997). The Ortmann's trap, particularly with chicken liver bait, has proven highly effective in trapping duration and preventing escape (Drechler et al. 2010; **Paper II**). The trap's opacity may make it an attractive hiding place, whereas newts tend to escape quickly from the umbrella–shaped trap due to its larger openings (Griffiths 1985; Baker 2013).

The monitoring strategy should align with the study's objectives: setting traps in the evening and checking them the next morning is adequate for species detection, but for population estimates, more frequent checks are recommended. Funnel traps also show potential for monitoring other endangered species, such as dytiscidae beetle adults and larvae, anisopteran larvae, or aquatic gastropods (Arntzen and Zuiderwijk 2020; **Paper II**).

Other monitoring method is tracking small, protected animals like newts with passive integrated transponder tags (PIT tags) which has become a popular method for studying life history (**Paper III**). This technique is essential in conservation biology, as it helps understand movement behavior and how individuals interact with their environment and other organisms (Vojar 2007; Nathan et al. 2008). Animals move for various reasons, such as avoiding predators, acquiring resources, finding mates, or escaping high conspecific density, and studying these movements can provide insights at individual, population, and community levels (Clobert et al. 2009).

Traditional active tracking methods like coloration patterns and radio transmitters have limitations for long–term observation, especially in amphibians (Ousterhout and Semlitsch 2014). Photo–matching is a common method for individual identification in amphibians (Schmidt et al. 2005), but it can be time–consuming and often requires recapturing the animal (Drechsler et al. 2015; Mettouris et al. 2016). Radio–tracking, used for about twenty years to study amphibians (van Nuland and Claus 1981), has now been applied to European newts for the first time. This method has been valuable in understanding migration and orientation in anurans, particularly toads (Smits and Crawford 1984). However, tracking urodeles is challenging due to their smaller body mass and elongated shape, which complicates transmitter attachment (Madison 1997; Madison and Farrand, 1998).

For *T. cristatus* and T. marmoratus, relatively large newts, implanting minimum–sized transmitters is at the limit. Despite the guideline that transmitters should not exceed 10% of body mass, strict adherence is less critical for less active animals like newts, as no link was found between weight ratio and migration distance. The average transmitter to body weight ratio was under 10%, and all radio–tracked newts were included in the analysis. Recent developments in Radio Frequency Identification (RFID) and PIT tags have made it feasible to document dispersal patterns and quantify habitat use in small–bodied vertebrates, including amphibians and fishes (Bubb et al. 2002; Hamed et al. 2008; Chevalier et al. 2017; Winandy and Denoël 2011; Atkinson–Adams et al. 2016). Since their

first biological use in the mid–1980s, PIT tag studies have increased (Cooke et al. 2013). This method allows for long–term individual identification and can provide information on life history traits like diurnal activity, gender–based movement differences, philopatry, and metapopulation distributions (Langton et al. 2001; Gvoždík and Van Damme 2006; Jehle et al. 2011; Cayuela et al. 2019).

Unlike photo–matching, PIT tagging requires capturing the animal just once, without further handling (Mettouris et al. 2016). However, this method has limitations like the cost of the reader or antenna and the limited reading range of the antenna (Hill et al. 2006; Linnansaari et al. 2007; Ryan et al. 2014). The half–duplex (HDX) system offers the advantage of constructing larger antennas (up to 100 m), unlike the smaller antennas and higher cost of full duplex systems (FDX) systems, which also need stabilization in flowing waters (Atkinson–Adams et al. 2016).

Implantable tags are most suitable for radio–tagging small to medium–sized urodeles like *T. cristatus*, with passive telemetry tracking following (Dervo et al. 2010). In mark–recapture studies, understanding tag retention and failure rates, which vary by species, life stages, gender, and tag placement, is crucial (Dieterman and Hoxmeier 2009; Mamer and Meyer 2016). The placement of the transmitter in the animal's body is critical, and external attachment methods like elastic harness systems or sutures have been deemed unsuitable for *T. cristatus* due to the likelihood of tag loss (Dervo et al. 2010). However, telemetry studies with internal tags have been successful in larger species (McDonough and Paton 2007; Semlitsch et al. 2007; Peterman et al. 2008).

Concerns have been raised about the potential adverse effects of PIT tag surgery on the behaviour and growth of species (Adams et al. 1998; Bateman and Gresswell 2006; Zakęś et al. 2017). Research comparing PIT tags with other marking techniques like coloration patterns on newt species has shown no significant effects on body condition or recapture rates, especially in long–term studies on *Triturus dobrogicus* and *Pelobates fuscus*, compared to belly pattern recognition (Jehle and Hödl 1998; Arntzen et al. 1999). Given the low risk of mark misreading, PIT–tagging is considered the best method for amphibians of sufficient size (Perret and Joly 2002). PIT tag implantation thus generally does not cause high mortality (Cooke et al. 2013; **Paper III**), with 87.5% of animals surviving up to 48 days in the wild following active telemetry surgery (Trochet et al. 2017). Studies indicate that PIT tagging does not affect *T. cristatus* behaviour (**Paper III**), aligning with

observations in other amphibian species (Madison and Farrand 1998; Johnson 2006; Marcec et al. 2016; Chevalier et al. 2017; Trochet et al. 2017). The size and weight of the PIT tag are important, with a mass of around 1.5% of *T. cristatus* body mass being within recommended limits, whereas a study on active telemetry suggested a 10% limit (**Paper III**). Tags constituting up to 5–7% of body mass are deemed safe without compromising animal welfare (Jehle 2000; Dervo et al. 2010; **Paper III**). In some case expulsion rate of PIT tag observed (**Paper III**), and in T. dobrogicus research, one–tenth of individuals lost their tags (Jehle and Hödl 1998). High expulsion rates might be due to large incisions; most losses occurred within the first week post–surgery, suggesting that suturing or medical adhesives might be beneficial (Chevalier et al. 2017; Jehle and Hödl 1998). However, amphibians' regenerative abilities often result in only a scar a few days later, so suturing was opted against (Chevalier et al. 2017).Some of studies also considered the safety and efficacy of anaesthetics like clove oil, with larger–bodied individuals possibly experiencing prolonged anaesthesia (Pojman et al. 2011; Wright and Whitaker 2001). The duration of surgical depth of anaesthesia (60–90 minutes) allowed ample time for procedures, emphasizing the importance of keeping the skin moist during handling and recovery (Wright and Whitaker 2001; **Paper III**). This promising method could bring us new information about life of *T. cristatus* (Jehle et al. 2011; **Paper III**).

2. Aims and objectives

The overall aim of this thesis is to characterise and describe the migration strategy of the endangered *T. cristatus*, together with the identification of effective observation and capture methods. In four separate studies, performed in Tověř, central Moravian – Czech Republic, the movement activity of *T. cristatus* and monitoring options were examined. **Paper I** examined if gender influences immigration and emigration patterns. We also explored how the direction of migration varies with individual body size. Additionally, we investigated how climate factors like temperature, rainfall, humidity, wind, moon phase, and time of year affect migration. **Paper II** focused on assessing the effectiveness of three the most used trap (prism, umbrella, and Ortmann's trap) and various baits (chicken liver, and green and yellow glow stick chemical lights) in capturing *T. cristatus*. We specifically aimed to determine if sex and body size influence capture rates with different traps and baits. Furthermore, we investigated the most effective duration for monitoring the traps over a 12–hour period and examined the newts' capability to escape from these traps. In **Paper III**, we explored the feasibility of using PIT tags for individual identification in *T. cristatus*. We used clove oil as an aesthetic prior to the implantation of PIT. We also aimed to assess the effectiveness of detecting newts with PIT tag in their natural habitat using a passive telemetry system. In **Paper IV**, we focused on residence time of recaptured marked (photo identification) individuals of *T. cristatus* in the artificial pond and examining their movement patterns, particularly in relation to gender and body size. Our objective was to explore if there is a difference between gender in residence time, or if there is changing in body condition in the individuals between immigration and emigration. Lastly if identified newts could remember their immigration and emigration paths. Moreover, we studied the impact of meteorological factors such as temperature, humidity, and rainfall, especially considering current climate change trends, on the length of time newts spend in ponds.

3. Results

Paper I

Weber L, Růžička J, Tuf IH, Rulík M. 2023. Migration strategy of the Great crested newt (*Triturus cristatus*) in an artificial pond. *Herpetozoa*, *36*, 345–356.

3.1 Summary results derived from Paper No. 1

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. During the study, 543 male and 532 female were captured immigrating to the pond, along with 21 juveniles. Emigration saw 530 males, 386 females, and 191 juveniles captured. The overall sex ratio at the Tověř site was slightly male–dominant at 1.21:1. The majority (over 75%) of immigration occurred between March 4th and 31st, with 390 females and 433 males arriving. A smaller immigration spike was noted around late April to early May. Emigration primarily took place from June 5th to July 12th, accounting for about 40% of the total, with 336 females and 421 males leaving. Juvenile emigration occurred mainly from August 7th to September 6th. Migrations in autumn were also observed. Newts predominantly immigrated from the southwest (village area) and emigrated towards the southeast (forest area).The study identified key factors influencing *T. cristatus* migration, including time of year, temperature, humidity, and sunshine duration. No significant gender difference was noted in these preferences, though juveniles' immigration was tied to the week of the year, and males preferred cooler temperatures for immigration. The Generalized Additive Model (GAM) revealed that males typically arrived at the pond first, followed by females, with juveniles starting around mid–year. Females tended to arrive at around 10 °C, males at cooler temperatures (up to 5 °C), and juvenile numbers increased with temperatures above 10 °C. The analysis also showed a correlation between male immigration and higher average humidity, while females preferred lower humidity levels. Smaller males tended to immigrate first, followed by larger females, with the largest individuals arriving at temperatures between 10 and 15 °C. Larger newts showed decreased immigration at humidity levels up to 80%, but increased again at higher humidity. The Canonical Correspondence Analysis (CCA) on emigration factors accounted for 26.15% of variation, highlighting the importance of the week of the year, wind strength, precipitation, humidity, sunshine duration, and temperature. Males emigrated during lower rain, stronger winds, and warmer days, while females preferred sunny, warm days. Juveniles' emigration was

influenced by the time of year, higher humidity, and precipitation. The Generalized Additive Model (GAM) showed males typically emigrating by the 25th week, with a resurgence around the 35th week. Female emigration peaked around the 20th week and again in the 35th week, whereas juveniles peaked in the 35th week. Male emigration decreased with rising mean temperature, females preferred 15–20 °C, and juvenile emigration increased with temperature. Males favoured stronger winds for emigration, while females and juveniles emigrated during heavier rainfall. Optimal humidity for male emigration was around 60%, but increased humidity reduced female emigration and increased juvenile emigration. Larger individuals primarily emigrated around the 20th week, favouring 15 °C and higher wind strengths, but reduced their migration with increasing humidity and precipitation. Our study found an increase in the number of *T. cristatus* immigrating and emigrating with brighter lunar phases for all genders, but the correlation was statistically non–significant for both immigration and emigration. The study highlighted the significant impact of climatic conditions on amphibian migration, stressing the importance of continued research and robust conservation approaches in the face of global climate change. This research offers important understanding of the environmental influences on the migration of *T. cristatus*, potentially informing future conservation initiatives.

Paper II

Weber L, Botorová M, Rulík M. 2023. Comparing trap and bait efficiency to record the great crested newts (*Triturus cristatus*). *Knowledge & Management of Aquatic Ecosystems*, (424), 26.

3.2 Summary results derived from Paper No. 2

This study evaluated the efficacy of three funnel trap designs (prism, umbrella, and Ortmann's) and three baits (chicken liver, chemical light in glow sticks, and control/no bait) in capturing *Triturus cristatus*. The research also aimed to determine the ideal duration for monitoring within a 12–hour period. The umbrella–shaped trap emerged as the most efficient, capturing five times more newts than the Ortmann's and prism–shaped traps, with the latter performing surprisingly poorly. During the study, a total of 1386 *T. cristatus* were captured (867 males, 519 females). The majority of *T. cristatus* (1066 individuals) were caught in the umbrella–shaped trap, averaging 22 individuals per trap per night. Ortmann's

trap captured 239 individuals (average 4.98 per night), and the prism–shaped trap caught 81 (average 1.69 per night). The umbrella trap had the highest capture efficiency per entry (3.67 individuals). The study also tracked new arrivals in each trap type. In the non–baited traps, 87 newcomers were recorded, while the chicken liver baited traps attracted 85 newcomers, and the green chemical light traps attracted 110. This indicates a varied response to different bait types, with green chemical light showing a slightly higher attraction rate, but not statistically significant. There was also a higher capture rate of males compared to females, but no significant correlation between trap type, bait, sex, and newt length. Furthermore, the research revealed that both the type of trap and the bait used significantly affected the duration of newts' stay in the traps. Newts stayed longest in Ortmann's trap with chicken liver bait, averaging about 4.5 hours. The study also noted that newts frequently returned to the traps, particularly to the Ortmann's trap without bait. The umbrella–shaped trap had the shortest retention time for newts, with most escaping before the first 2–hour control check. Most newts in the umbrella–shaped trap were caught between 10:00 pm and 12:00 am, in the Ortmann's trap between 2:00 am and 6:00 am, and in the prism–shaped trap between 8:00 pm and 2:00 am. This data suggests that different trap designs may be more effective at different times of the night. The type of trap and bait used significantly affected the length of time newts stayed in the traps. Despite repeated trapping in various traps, the study did not confirm any trap–shy behaviour in the newts. The study's findings are essential for wildlife researchers and conservationists, as they provide insights into the most effective methods for trapping and monitoring *T. cristatus*, a species of conservation concern.

Paper III

Weber L, Šmejkal M, Bartoň D, Rulík M. 2019. Testing the applicability of tagging the Great crested newt (*Triturus cristatus*) using passive integrated transponders. *Plos One*, *14*(7), e0219069.

3.3 Summary results derived from Paper No. 3

In this research, we assessed the effectiveness of using PIT tags for individually marking Great Crested Newts (*Triturus cristatus*) and examined their detection in natural settings via a passive telemetry system. A total of 140 PIT tags (12.0 mm x 2.12 mm, 0.1 g, half duplex (HDX), from Oregon RFID in Portland, Oregon, USA) were implanted under the

skin of 140 individuals of *T. cristatus*. For the procedure, each newt was anesthetized through a 7–10 minute immersion in a solution of clove oil (0.025 ml of 100% oil extract in 400 ml of dechlorinated water at 20 °C) in a covered plastic box. Post–procedure, the survival rate was high (98.57%) with no significant injuries observed (e.g., necrosis). There were two fatalities (one male and one female) without a clear cause, as determined by a veterinarian. Following their surgery, all individuals of *T. cristatus* exhibited normal eating habits, and their movement and swimming behaviours were consistent with their pre–surgery patterns. X–ray imaging was utilized to verify the precise location of the PIT tags. Notably, about 15.71% of the tagged newts (9 males and 12 females out of 140) managed to expel the tags from their bodies. Of the 100 PIT–tagged *T. cristatus* released into the wild, 97 were detected in their aquatic habitat using four antennas connected to an HDX Reader. The highest number of detections occurred on the release date, resulting in a total of 24,106 records. The first three days saw the highest detection rates, with 47 males and 49 females detected in the first 24 hours, 32 males and 16 females in 48 hours, and 26 males and 12 females in 72 hours. Males exhibited a significantly higher detection rate than females ($F = 9.4$, df = 1, $P = 0.003$, $R2 = 8\%$). On average, 6.5 more males were detected per hour than females (95% confidence interval = 5.6 to 7.4, $t = 14.6$, df = 71, $P < 0.001$). Analysis of two individuals with high detection rates (one female with 714 records and one male with 712 records) allowed for the creation of a graph showing their diurnal activity over 72 hours. No significant difference in male and female detections between day and night was observed over the first three days. The movement analysis revealed that a male *T. cristatus* in a breeding pond could travel up to 20 meters in 78 seconds. Our study demonstrates that using PIT tag for *T. cristatus*, despite some tag loss and minimal mortality, is a promising method for the automated tracking of newts in various habitats, providing valuable insights into their movement, including activity patterns, and dispersal. This technique, which employs clove oil as an anaesthetic, shows negligible impact on newt welfare and allows for reliable data collection in both aquatic and terrestrial environments, although further research is needed to refine mortality and tag loss estimates.

Manuscript IV

Weber L, Růžička J, Tuf IH, Rulík M. 2024. Should I stay or should I go? Movement strategy of the Great crested newt (*Triturus cristatus*) – submitted to Amphibian and Reptile Conservation

3.4 Summary results derived from Paper No. 4

In this study we investigated the migration activity of *T. cristatus*, examining the impact of body size and weather on their movements. Using pitfall traps, we captured and recaptured 59 males, 78 females, and 7 juveniles. The sex ratio was nearly balanced during immigration (1.02:1 male to female) but skewed towards males during emigration (1.37:1). Females were generally larger than males by 4.5 mm. A notable size decrease was observed during emigration, with 31.94% of females and 18.64% of males shrinking by an average of 6 mm and 6.4 mm, respectively. These changes could show the different physical demands of aquatic and terrestrial environments. Migration patterns indicated females primarily arrived from the southwest and departed towards the southeast, with males following a similar route. However, there was no significant evidence of memorized migration paths for either sex, indicating that climatic conditions significantly influence their migration behaviours. Redundancy Analysis (RDA) showed that meteorological factors explained 26.07% of the variation in the size of immigrating female *T. cristatus*. Key factors included maximum night temperature (9.4% variance, F=7.3, p=0.004), duration in pond (5.1%, F=4.1, p=0.048), and minimum day temperature (4.6%, F=3.8, p=0.054). Generalized Linear Models (GLM) further confirmed significant links between size and variables like pond duration, precipitation, and day/night temperatures, indicating that larger females migrate on warmer, drier days and spend less time in the pond. For male *T. cristatus*, RDA revealed that 18.37% of the variation is explained by environmental factors, with maximum night temperature being the most significant contributor (7.6% variance, F=4.7, p=0.046). Generalized Linear Models (GLM) also found statistical significance in average and maximum night temperatures. Larger males, in contrast to females, tend to migrate on warmer nights. In terms of emigration for male, RDA showed that environmental factors account for 19.30% of the variation, with maximum day temperature (F=6.6, p=0.008) and mean day temperature (F=5.0, p=0.028, 8%) being the most influential. GLM results were significant for average and maximum day temperatures, indicating that larger males leave the pond on warmer days compared to smaller males.

These findings provide insights into the environmental factors influencing the movement activity of *T. cristatus*, which may guide future conservation efforts.

4. Conclusion and future prospects

The comprehensive research undertaken in this PhD thesis on the Great Crested Newt (*Triturus cristatus*) provides valuable insights into the species' migration patterns and behaviour, with a focus on understanding the influence of various environmental factors and the impact of human–modified habitats. The research emphasizes the significant role of temperature in migration, with distinct preferences observed across genders and sizes, and notes that rainfall and humidity also considerably affect migratory behaviour. No substantial correlation was found between moonlight and migration, suggesting the need for further research in this area. Additionally, the study presents detailed findings on the movement of newts within their habitats, and showed that *T. cristatus* can adapt to human–altered environments. Analysis of sex ratios, body size changes, and environmental conditions during migration periods revealed several patterns. Protandry, with males reaching breeding grounds before females, was observed, indicating potential mate selection advantages. Females either remained in the pond or emigrated later than males. The research also found that larger individuals migrated during warmer nights and smaller females preferred rainy weather. Autumn migration with overwintering within water habitats was also confirmed. These findings offer a deeper understanding of how environmental factors in a changing climate can impact the migratory behaviours of *T. cristatus*.

Furthermore, the thesis focusses on monitoring of *T. cristatus* and discusses the effectiveness of various trapping methods and the implementation of Passive Integrated Transponder (PIT) tags for long–term monitoring and study of *T. cristatus*. Umbrella–shaped funnel traps were identified as the most efficient for monitoring newts in ponds. The study recommends specific strategies for different research goals, such as determining species occurrence or estimating population size. The research underscores the importance of considering PIT tagging mortality and tag loss in population estimates and highlights the potential of PIT tags in studying the dispersal, activity, and behavioural patterns of small amphibians in both aquatic and terrestrial habitats. In conclusion, this thesis advances our understanding of the migratory behaviour and environmental adaptations of the Great Crested Newt but also provides practical recommendations for their conservation and monitoring. It underscores the need for continuous research and adaptive management strategies to protect this species, particularly in the face of global climate change and habitat alteration.

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Paper I

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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.

PENSOFT.

Key Words

Schlüsselwörter

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 bombina*), the European tree frog (*Hyla arborea*), the common toad (*Bufo bufo*), the European green toad (*Bufotes 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
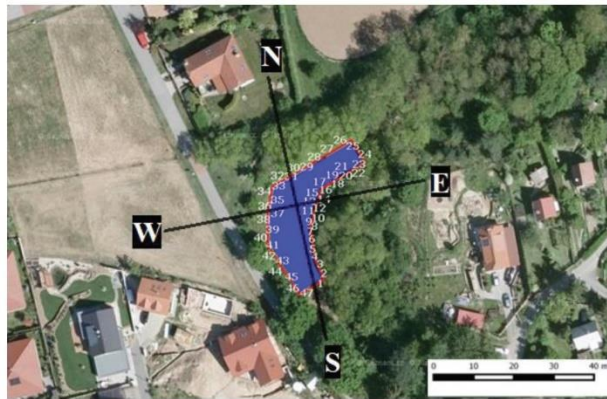

Figure 1. Map of the site with marked water area (blue), drift fence (red), individual trapping containers (white numbers) and distribution of cardinal directions.

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 uses 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 Tovéř 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 ± IC95 is μ=215.111±11.27°; 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; μ=148.598±8.84°; r=0.265; p<0.0001) (Fig. 2).
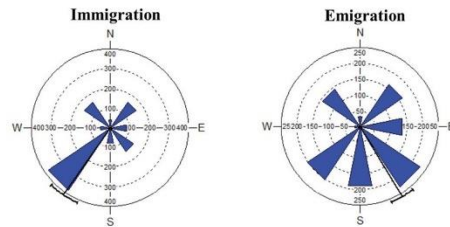

Figure 2. Directional rosettes of immigration and emigration for all individuals of *T. cristatus*. The black section shows the mean angle of migration, and the arcs extending to either side represent the 95% confidence intervals of the mean.

When examining the direction of immigration separately for each sex, we find that for females (Rayleigh test; μ=209.735±17.43°; r=0.196; p=0.510) and juveniles (Rayleigh test; μ=39.639±67.54°; 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; μ=219.5±13.94°; 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).
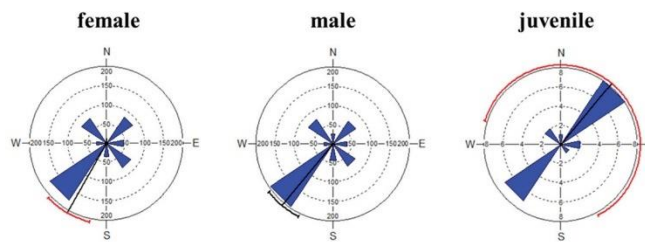

Figure 3. Directional rosettes in immigration, by gender. The black section shows the mean angle of migration, and the arcs extending to either side represent the 95% confidence intervals of the mean. Red colour sings nonsignificant results.

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).
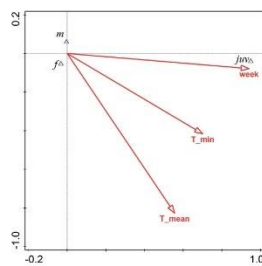

Figure 4. CCA model for immigration for sex with the environmental factors (the week in year (week), average temperature (T_mean), minimum temperature (T_min). Only significant variables are shown.

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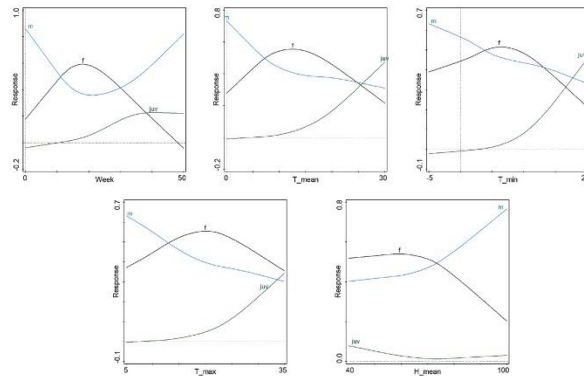
Figure 5. GAM of immigration acitivity for the week (Week), average temperature (T_mean), minimum temperature (T_min), maximum temperature (T_max), average humidity (H_mean)). Only significant variables are shown.
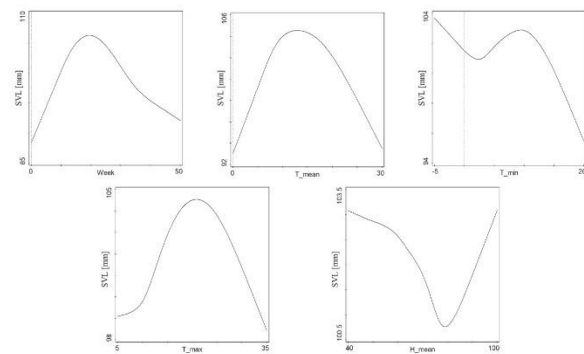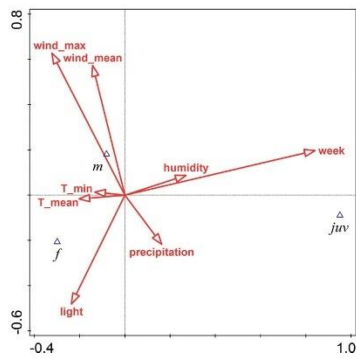

Figure 6. GAM of size of the newts of immigration activity for the week (Week), average temperature (T_mean), minimum temperature (T_min), maximum temperature (T_max), average humidity (H_mean). Only significant variables are shown.

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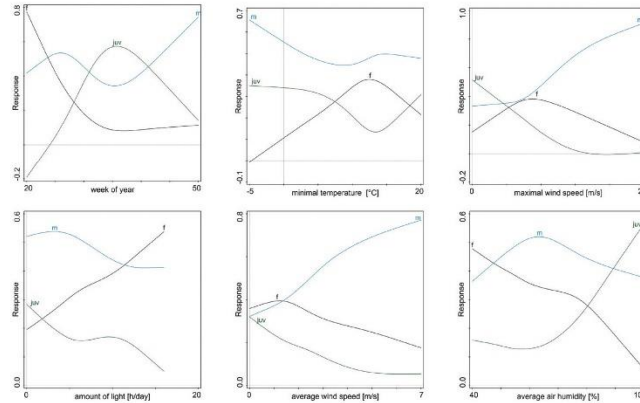
Figure 8. GAM of emigration acitivity for the week of year, minimum temperature, maximum wind speed, amount of light, average wind speed, average humidity. Only significant variables are shown.
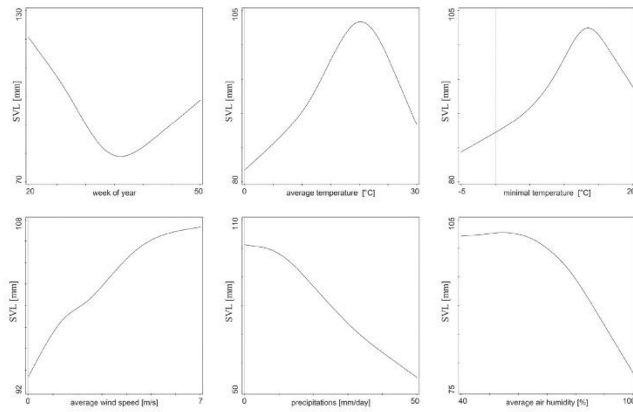

Figure 9. GAM of size of the newts of emigration activity for the week of year, average temperature, minimum temperature, average wind speed, precipitations, average humidity. Only significant variables are shown.
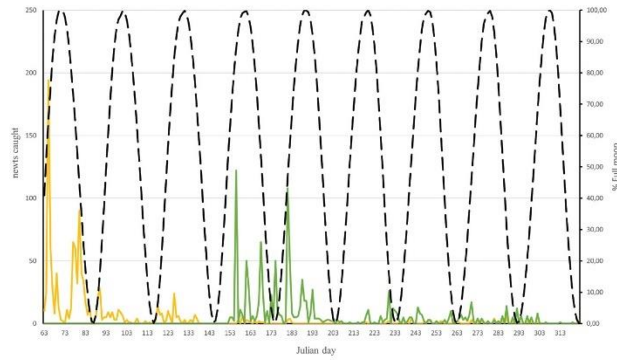

Figure 10. The number of newts (orange line for immigration, green line for emigration) caught plotted against the phase of the moon (dashed line).

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 dispersal, 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-Viellot 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 decreases 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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Paper II

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Comparing trap and bait efficiency to record the great crested newts (*Triturus cristatus*)

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Abstract − A crucial aspect of conservation management for endangered newt species is the establishment of a monitoring methodology and the evaluation of trap efficacy to ensure the accuracy of data collection. In this study, we assessed three funnel trap types (prism shape, umbrella shape, and Ortmann's trap) to capture great crested newts (*Triturus cristatus*). We also tested three baits (chicken liver, chemical lights in glow sticks, and control traps without bait) and determined the optimal trap control time within a 12 h period. Our findings showed that the umbrella shape trap was most effective, catching five times more newts than the Ortmann's and prism shape traps. Surprisingly, the commonly used prism shape trap performed poorly. Bait type did not significantly impact newt captures compared to control traps. During the 12 h experiment, newts spent the longest time in the chicken liver-baited Ortmann's trap (averaging 4.5 h), while the umbrella shape trap with chicken liver bait had the highest turnover of individuals. We observed no behavioural response from "trap-shy" individuals. This study emphasizes the importance of selecting appropriate traps, considering bait choice, and trap control time for effective monitoring of endangered newt populations.

Keywords: Conservation management / funnel trap / Ortmann's trap / great crested newt (*Triturus cristatus*) / trap-shy response

1 Introduction

The evaluation of various sampling techniques is vital for successful amphibian monitoring (Antonishak *et al.*, 2017*).* Breeding season is a focal period for monitoring, due to the visibility of migrating adults or egg masses (Miller and Grant, 2015; Davis *et al.*, 2017). Capture success depends on factors such as body size, home range, activity patterns, trap avoidance, and weather conditions (Crosswhite *et al.*, 1999). Numerous techniques, including drift fences with pitfall traps, aquatic funnel traps, visual encounter surveys, and dip-net surveys, are employed in amphibian monitoring (Heyer *et al.*, 1994; Hutchens and DePerno, 2009; Willson and Gibbons, 2009). Notably, dip-netting is frequently used for capturing breeding newts in Europe (Malmgren *et al.*, 2005; Briggs *et al.*, 2006; Goverse *et al.*, 2006; NARRS, 2021; Skei *et al.*, 2006; Denoël *et al.*, 2013). However, studies have pointed out the effectiveness of fish traps over drift fences (Baker, 1999), and the benefits of funnel traps like Ortmann's trap for cost-effectiveness and efficiency (Ortmann, 2009; Willson and Gibbons, 2009; Drechler *et al.*, 2010). Most surveys to detect newts were performed at night, to maximise

the detectability of target species (Halliday, 2006; Manenti *et al.*, 2019). The study and conservation of newts, many of which are endangered, heavily rely on effective surveying and monitoring (Kålås *et al.*, 2010; Arntzen and Zuiderwijk, 2020).

Our model species, the great crested newt (T. cristatus), falls under annex II and IV of the Habitats Directive (92/43/ EEC), and is, as a result, stringently protected in Europe (Bock *et al.*, 2009). The effective conservation of great crested newt necessitates population monitoring, a task that has grown in significance (Graeter *et al.*, 2013). Given the species' amphibious nature—alternating between aquatic and terrestrial environments—it poses a challenge to secure representative samples for monitoring (Dervo *et al.*, 2014). Accurate determination of species abundance and composition might demand several short sampling periods throughout their active phase (Vogt and Hine, 1982). The capture-mark-recapture (CMR) technique, which employs the use of unique pattern mapping photography, can provide critical demographic parameter estimates, such as survival rates and abundance, hence supporting more effective conservation decision-making (Williams *et al.*, 2002; Nichols, 2014). Studying abundance dynamics can pose difficulties due to the need for strategic long-term sampling planning and employing suitable models to analyse the gathered data. For instance, population growth at a specific moment can be influenced by the density (Cayuela *et al.*,

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Fig. 1. Three types of traps used throughout this study. Prism shape (left), umbrella shape (middle) and Ortman's trap (right).

2019). Moreover, the likelihood of detecting individuals might be low, necessitating multiple surveys at each location during each sampling season to secure reliable abundance measures (Kellner & Swihart, 2014; Ficetola *et al.*, 2018; Falaschi *et al.* 2021; Falaschi *et al.*, 2022).

Aquatic funnel trapping is often used for surveying and monitoring pond-breeding amphibians (Adams *et al.*, 1997). The first studies using aquatic traps were conducted in 1973 (Calef, 1973; van Gelder, 1973). A variety of funnel traps have been tried and tested, including lightweight, collapsible funnel traps designed for crayfish that are furnished with smaller mesh (Arntzen and Zuiderwijk, 2020). Commercially available cylindrical traps constructed of 6 to 4 mm mesh size galvanized wire, box funnel traps made of 3 mm mesh size galvanized wire, traps made from plastic beverage bottles (Calef, 1973; Richter, 1995), collapsible nylon mesh traps, and traps constructed with acrylic plastic sheet have also been used (Adams *et al.*, 1997). Most studies use funnel traps without bait to capture caudate amphibians, while others have used shrimp or salmon eggs as baits (Adams *et al.*, 1997). Commonly used baits include chicken liver, other entrails, parts of fish, salami, dog granules, or bits of raw beef (Jeřábková and Boukal, 2011; Baker, 2013; Sannolo and Gatti, 2017).

However, there are some shortcomings to the funnel trapping method. One study in France showed that in 95 out of 171 experiments (56%), the probability for an individual to go undetected was <1%, but the numbers captured decreased over time suggesting "trap shyness" (Arntzen and Zuiderwijk, 2020). The other risk could be transfer of agent of chytridiomycosis, but this problem would be solved by disinfecting with a 1% weight/volume (w/v) solution of Virkon® and drying the traps after every use (Johnson *et al.*, 2003; Dejean *et al.*, 2010). Light traps and light sticks are commonly used in studies of fish, particularly larvae (Marchetti *et al.*, 2004), but they have not been widely used to capture amphibians (Grayson and Row, 2007).

In the Czech Republic, by national guidelines a combination of funnel trap with chicken liver bait and dip netting methods are used for capturing newts (Jeřábková and Boukal, 2011). The main objectives of our study were to compare the sampling efficiency of three commonly used funnel trap shapes (prism, umbrella, and Ortmann's trap) and different baits (chicken liver, green, and yellow chemical lights in glow sticks) for capturing newts. Specifically, we aimed to analyse the effect of sex and body size on the trapping success using different traps and baits. Additionally, we evaluated the optimal trap control time during a 12 h experiment and assessed the ability of newts to escape from the traps.

2 Materials and methods

The study was carried out during the main breeding season (April-May) in 2018 and 2019 at a retention pond located in Tovéř, Czech Republic (49.6405478N, 17.3281758E, altitude 235 m). This site supports breeding populations of the great crested newt (*T. cristatus*), the smooth newt (*Lissotriton vulgaris*), and the alpine newt (*Ichthyosaura alpestris*). The pond has a surface area of 500 m² during the spring and a maximum water depth of approximately 1.9 m, which completely dries up in warm summers. The littoral zone is dominated by submerged grasses while the water surface layer is usually covered by a pondweed (*Lemna minor*). According to the Habitat Suitability Index (Oldham *et al.*, 2000; ARG UK, 2010), the Tovéř locality is categorized as good (with score 0,73) for T. cristatus occurrence. Based on our previous research, four places in the pond near the shore with depth from 25–50 cm with plenty of vegetation and high probability of occurrence of newts were selected. All traps were placed so that there was minimal space between the bottom and each trap. Woody sticks approx. two meters long were inserted into the bottom sediment and three traps, one of each type — the prism shape, the umbrella shape and the Ortmann's trap (Fig. 1) were attached around stick. The nylon prism funnel traps had a metal frame size of 45 × 22 × 22 cm covered with a green 5 mm mesh size nylon webbing and 3 cm holes on one side and 2 cm on the opposite side; elastic bands were secured between the entrance holes to maintain a funnel shape. The umbrella shape type has a hexagonal base with outer radius 52.5 cm with 6 entrances. Ensure constant air access, the net was placed or secured with polystyrene so that small part remains at the water surface (Jehle et al., 2011). The Ortmann's funnel trap was made of an empty 15 L bucket with four distinct openings in which half-cut inverted 1.5 L plastic bottles were inserted acting as funnels (Drechler et al., 2010). Counter-sunk in the respective habitat (e.g., pond), aquatic amphibians (adults and larvae) can easily enter the bucket through the funnels, but cannot leave it. The bottom of the bucket as well as the lower part of the bucket walls was perforated with little holes (smaller than 4 mm in diameter) to allow free movement of the larvae. The accompanying lid of the bucket is riddled with small holes to allow oxygen exchange and it is used as a cover for the bucket during an exposure. Two plastic bottles (0.5 L) placed at the upper part of the bucket wall fixed with a robust plastic string supported floating of the traps, so the caught newts were able to breathe (Drechler *et al.*, 2010).

Table 1. Summary of the linear mixed-effects model testing the effect of trap and bait on the number of caught newts. Test statistics for fixed effects and standard deviations for random effects are presented. Marginal R^2 indicates explained variability by fixed effects, conditional R^2 indicates explained variability by fixed and random effects together (Nakagawa and Schielzeth, 2013).

Fixed	DF	F-value	P-value
Trap	(2,94)	123.9	<0.001
Bait	(3,8)	0.6	0.660
Model R^2	Marginal = 0.57	Condition = 0.67	
Random	**SD**		
Day	0.35		
Day/Location	0.20		

Trap installation occurred typically at 6–8 pm, and traps were emptied the following day between 7–10 am. This process was repeated for 2–4 consecutive days (29.4, 1.5., 3.5, 5.5, 7.5., 9.5., 13.5, 15.5., 17.5, 20.5, 23.5, 27.5 in 2018) after which traps were removed from the pond to allow time for animal regeneration and to avoid a trap-shy response. Three types of baits were used simultaneously (chicken liver, yellow chemical light — 15 cm length, Lightstick powder, green chemical light — 15 cm length, Lightstick powder), or traps were left without bait on each trapping night. Following the application of chicken liver, a one-week pause was included to prevent confounding effects of scent residuals in the water (Adams *et al.*, 1997). All traps were cleaned and dried before reuse. For each captured newt, sex, body length snout-to-vent length (SVL), and belly patterns were recorded (Arntzen *et al.*, 2003; Jehle *et al.*, 2011). The effectiveness of different trap types and baits was evaluated using a linear model (lm function), and data were logarithmically transformed to meet statistical test requirements. Additionally, the relationship between trap preference based on sex or body size was evaluated using a linear model.

To assess the optimal trap control time, we conducted an experiment where 10 individuals (5 males and 5 females) of *T. cristatus* were placed in each trap and monitored for 12 h. The traps were checked every 2 h, starting at 6:00 pm and ending at 6:00 am the next morning. To avoid any influence from previous experiments, new individuals were used for each test. The experiment was conducted in three series in 2019, the first without any bait (9.-10.4, 24-25.4), the second using chicken liver as bait (14.-15.4, 29.4-1.5.), and the third using green chemical light as bait (19.-20.4, 5.-6.5). To ensure the correct identification of individuals, we obtained belly and side pattern maps for each captured newt, including the newly arrived individuals, and returned them to the same type of trap. To avoid excessive stress on the individuals from trapping, ten newts captured from another part of the pond were used for each capture night.

The data from the 12 h control time experiment was analysed using a generalized linear model assuming a Poisson distribution with the logarithmic link function. All analyses were performed using the statistical software R version 3.4.3 (R Core Team, 2014). We evaluated the efficiency, *i.e.*, the number of caught newts in a trap, the different types of traps and baits using a generalized linear model (the glm function in R). We included four explanatory variables (trap, bait, day of sampling, and location) in the model comparison process. We used day of sampling and location as confounding covariates

since these variables were not of direct interest and performed forward selection as a model building procedure. After examining the data, we applied a conservative approach using a quasipoisson error structure due to the high overdispersion of the number of caught newts (estimated dispersion parameter of the model including day, trap type, and bait type was 6.5; for a Poisson error structure, it should be around 1 to meet model assumptions).

3 Results

In total, we captured 1386 individuals of *T. cristatus* (867 males and 519 females) and we also caught 87 individuals of *L. vulgaris* (47 males and 40 females) and 5 individuals of *I. alpestris* (4 males and 1 females) during 12 trapping nights. Due to the low numbers of those newt species, we further analysed only data for *T. cristatus*. Most of *T. cristatus* (1066 individuals) were found in the umbrella shape funnel trap, with an average of 22 individuals (± 2.07) per a trap and night. A total of 239 individuals were trapped in Ortmann's trap, with an average of 4.98 individuals (± 0.59) per a trap and night and 81 newts were captured in the prism shape trap, with an average of 1.69 individuals (± 0.21) per a trap and night. The average number of individuals captured per trap entry is 3.67 individuals for the umbrella funnel trap, 1.49 individuals for the Ortmann trap, and 0.85 individuals for the prism trap (umbrella shape > Ortmann's trap > prism shape trap; Tab. 1, Fig. 2a).

We observed no significant effect of using bait as traps with a bait showed similar efficiency as those without (Fig. 2b). In terms of bait performance, we found only a slight difference between green chemical light and chicken liver, with traps using green chemical light catching an average of 14 (± 2.93) newts, compared to 10 (± 1.64) with yellow chemical light, 9 (± 0.81) with no bait, and 7 (± 1.72) with chicken liver. The only significant difference was between chicken liver and green chemical light (Fig. 2b; $p < 0.05$). We observed a higher capture rate of males than females, but no statistically significant differences were found between the different types of traps or baits and sex or newt body size ($p > 0.05$).

Our study revealed that both the type of trap and bait significantly impacted trapping time (Fig. 3). We found that *T. cristatus* captured in Ortmann's trap type with chicken liver as bait remained significantly longer in the trap compared to other trap types, with an average time of about 4.5 h. Interestingly, we also recorded individuals who repeatedly returned to the
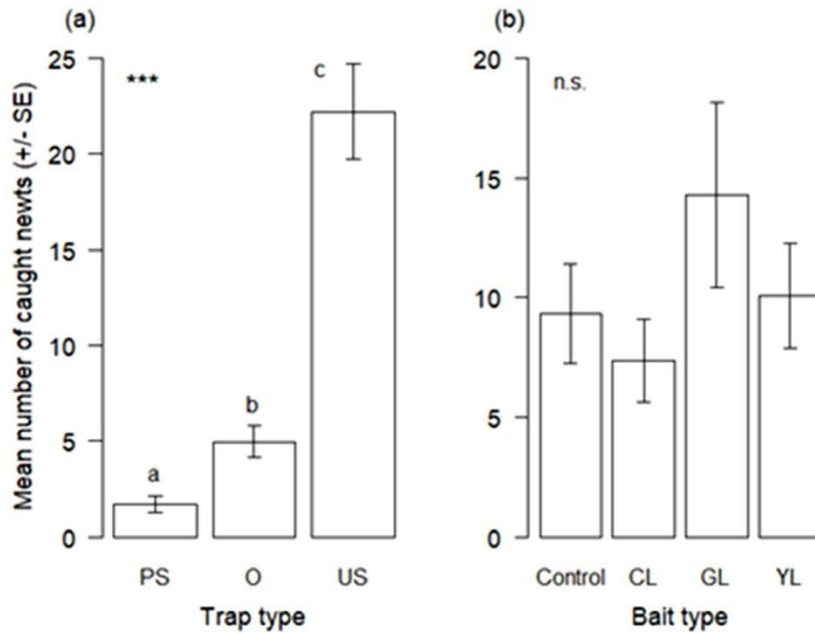
Fig. 2. Efficiency of a) three traps and b) three baits in terms of caught newts. Letters indicate the Abbreviations: PS = prism shape trap, O = Ortman's trap, US = umbrella shape trap, CL = chicken liver, GL = green light, YL = yellow light.
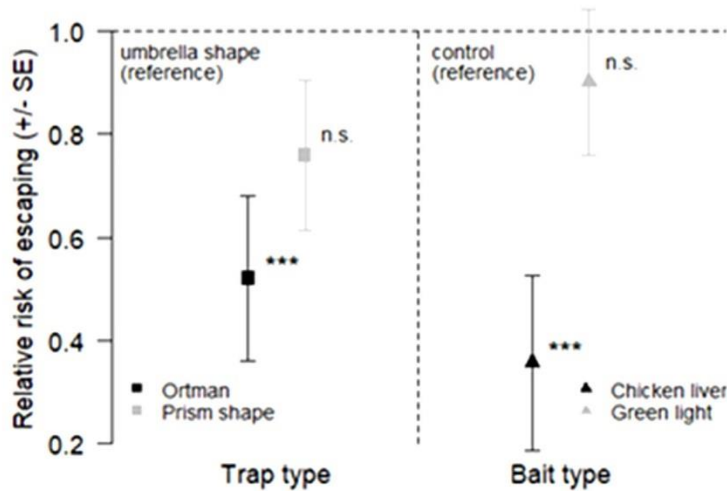

Fig. 3. Comparison between traps and baits in terms of relative risks of escaping during the 12 h monitoring experiments. Umbrella shape trap and control traps (without a bait) were used as the reference levels for the trap and bait comparison, respectively.
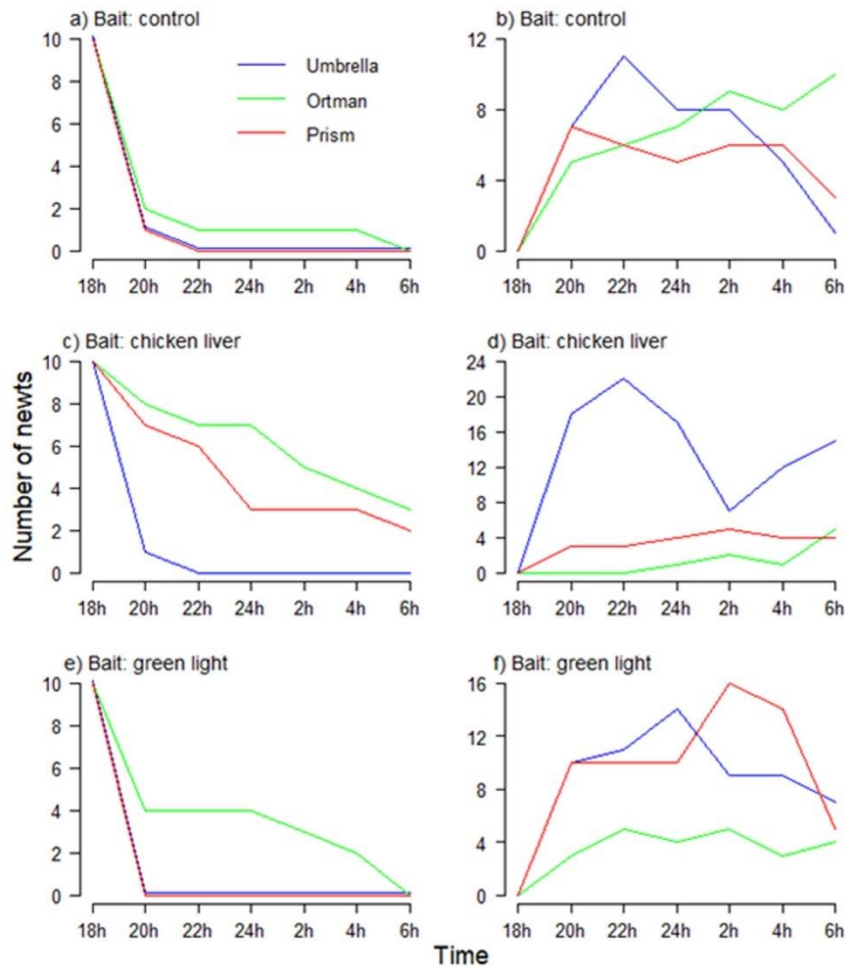
Fig. 4. Changes in the numbers of newts during the 12 h monitoring experiments in different kind of traps. a), c), e) denote newts putted at the beginning of the experiment; b), d), f) denote newcomers.

traps, with most newts returning to the Ortmann's trap without bait. Out of ten individuals placed in any of the three trap types at the beginning of the experiment, almost all were able to escape during the night.

Newts remained the longest in the Ortmann's trap and the shortest in the umbrella shape trap, where most individuals escaped before the first control 2 h after the start of the experiment (Fig. 4a). We also recorded the number of newcomers in each trap type. A total of 87 newcomers were recorded in the non-bait trap, 85 in the chicken liver bait trap,

and 110 in the green chemical light trap (Fig. 4b). Regardless of the bait type, most newts in the umbrella shape trap were captured between 10:00 pm and 12:00 pm, in the Ortmann's trap between 2:00 am and 6:00 am, and in the prism shape trap between 8:00 pm and 2:00 am. We did not find a statistically significant relationship between sex and trapping time ($p > 0.05$). However, we did find that trap type and bait significantly affected trapping time ($p < 0.05$). Despite trapping the newts repeatedly and in different types of traps, we cannot confirm a trap-shy response.

4 Discussion

Monitoring of amphibians will become increasingly important for conservation decision-making due to population declines (Anderson *et al.*,2015; Davis *et al.*,2017). In this study, we found that the umbrella shape funnel trap was the most efficient at capturing T. cristatus compared to the Ortmann's trap and the commonly used prism shape trap (Fig. 2a) (Drechler *et al.*, 2010; Pellet *et al.*, 2010; Baker, 2013). The larger size and openings of the umbrella shape trap likely explain its higher efficiency. Conversely, the prism shape trap, despite being widely used for monitoring caudate amphibians, had the lowest efficiency (Bock *et al.*, 2009; Pellet *et al.*, 2010; Baker, 2013). Studies using prism traps to detect T. cristatus without a combination of CMR methods may underestimate the true population abundance. The low efficiency of the prism shape trap may be due to its small entrance, transparency, and size.

Studies on the use of baits in trapping amphibians have yielded contradictory results (Grayson and Row, 2007; Pellet *et al.*, 2010;Antonishak *et al.*, 2017; Sannolo and Gatti, 2017). For example, Pellet et al. (2010) found no difference between traps with or without bait, and Sannolo and Gatti (2017) suggest that the presence of bait can reduce capture efficiency by attracting amphibian predators. However, the impact of predators on capture probability is unknown (Adams *et al.*, 1997). Since T. cristatus has been shown to have color vision (Williams, 2014), the color of the bait and trap may also play a role. Antonishak et al. (2017) suggested that glow sticks could increase captures by providing a visual stimulus that attracts adult amphibians to the trap, which may explain the higher capture probability observed in this study.

The results of this study suggest that further investigation is needed to determine the difference between the efficiency of green and yellow light in capturing T. cristatus. The diminished effectiveness of chicken liver bait might stem from an unpublished study carried out at the same site, where newts were captured using prism-shaped traps baited with chicken liver and then subjected to gastric lavages. This experience could have led the newts to develop a bait aversion, which may continue to influence their behaviour over time. Males were found more frequently in the traps, possibly due to caution that drives females to stay deeper in the pond, as confirmed by Baker (2013), where traps were placed further from the shore and completely immersed in the water, resulting in a sex ratio opposite to the open water catch. Another possible explanation for the sex ratio could be the day of the year, as males tend to arrive at the site first during the migration from terrestrial to aquatic habitats (Langton et al., 2001; Gustafson, 2011) However, in this study, the difference in sex was not statistically significant. The Ortmann's trap combined with chicken liver bait was found to be the most effective in terms of trapping time and the ability of individuals to escape. The trapping time and escape ability were dependent on the type of trap and bait used. Drechsler *et al.* (2010) found that the newts remained the longest in the Ortmann's trap, which is consistent with the current study. Animals may seek traps as a safe place to hide, and the opaque Ortmann's trap may be particularly attractive for this reason (Griffiths, 1985). In contrast, newts were found to easily escape from the umbrella shape trap

within 2 h of installation, possibly due to the large entries (Baker, 2013).

Funnel trapping is an effective technique for conducting amphibian inventories and monitoring trends (Adams *et al.*, 1997). The use of traps allows for standardized experiments and more comparable results than dipnets .(Arntzen and Zuiderwijk, 2020). Aquatic funnel traps are non-destructive and suitable for surveying amphibians in lentic habitats, as opposed to dip-net surveys which may disturb aquatic vegetation and affect the water column through increased turbidity. Funnel trapping is recommended for sites where dense vegetation or woody debris limits visibility and inhibits dip-netting (Adams et al., 1997). Captured newts in aquatic funnel traps have been found to linearly scale with adult amphibian population density, suggesting captures as a reasonable estimate of adult population size (Wilson and Pearman, 2010). In the experiment during the year, the numbers of captured newts were higher at early sessions compared to late sessions (Arntzen and Zuiderwijk, 2020), irrespective of marking status. Consistently lower capture numbers at later sessions may indicate 'trap shyness,' where an animal's behaviour is altered after being caught for the first time, or conversely 'trap addiction' (Seber, 1982).

5 Conclusions

Based on our findings, we recommend using umbrella shape funnel traps for efficient monitoring of newts in ponds. The choice of monitoring strategy depends on the goal of the study. For determining the occurrence of newt species, traps dipped in the pond in the evening (22:00 pm) and checked the next morning (6:00 am) would suffice. However, for estimating population size, we suggest counting newts in traps continuously every 2 h during the night, as their numbers display high fluctuations with a peak at midnight. We did not find evidence of a trap-shy response in newts, as they were captured repeatedly in different types of traps. The use of funnel traps could also be effective for monitoring other endangered species, such as dytiscidae beetle adults and larvae, anisopteran larvae, or aquatic gastropods.

Supplementary Material

Table S1. Turnover of newts during the 12 h monitoring experiments. Ratios of total cumulative numbers of newts and numbers of newts recorded at the end of the experiment are presented for each trap and bait (total number of captured newts/numbers of remaining newts in parentheses).

The Supplementary Material is available at https://www.kmae-journal.org/10.1051/kmae/2023022/olm.

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Paper III

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Testing the applicability of tagging the Great crested newt (*Triturus cristatus*) using passive integrated transponders

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Abstract

Tracking individual animals with small-sized passive integrated transponder tags (PIT tags) has become a popular and widespread method, one which can be used for investigating life history traits, including dispersal patterns of small protected animals such as newts. In this study, we tested the applicability of PIT tag usage for individual marking with the Great crested newt (*Triturus cristatus*) as a model amphibian species, and to test the detection of the newts in nature using a passive telemetry system. Clove oil was used as an anaesthetic before surgery. We implanted PIT tags under the skin of 140 newts. The survival rate of newts was 98.57%. X-ray images were taken to check the exact positions of the PIT tags. Since approximately 15.71% of the newts were capable of expelling the tag from their bodies, tag loss has to be accounted for in future behavioural studies dealing with newts and other amphibians potentially capable of frequent tag expulsion. Lastly, we detected by passive telemetry 97 individuals out of 100 released into a natural breeding pond. Males had higher activity (13 detected males vs 7 females per hour) than females, thus males could be detected if present with more certainty. The result of the movement behaviour showed that e.g. the male of *T. cristatus* in a breeding pond can travel up to 20 m in 78 seconds. In summary, this promising method could allow the automatic data collection of marked newts in aquatic as well as in terrestrial biotopes, providing data on their dispersal, diurnal activity and movement behaviour.

Introduction

Amphibian populations have been in fact declining for several decades [1]. In our study we took the Great Crested Newt (*Triturus cristatus*), as a model amphibian species, which shows a significant decline in populations [2, 3, 4]. One of the critical components of conservation biology is movement behaviour, affecting how individuals interact spatially with other organisms and their environment [5, 6]. Animals may move to avoid predators, acquire resources, find mates, or to escape high conspecific density [7]. Movement studies are unique in their capacity

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to investigate processes at a variety of levels, including individual, population, and community [8]. Movement behaviour such as dispersal, foraging, and migration is poorly understood in many taxa (e.g. amphibian) due to the incompatibility of traditional active tracking methods (colouration patterns, radio transmitters) with long-term observations [9]. Photo-matching is popular and largely used method for individual identification in amphibian species [10, 11]. However, this method can be time-consuming, even using automatic processes for photo-graphic re-identification. It is necessary to recapture the animal and handle it again [12, 13]. Recent developments in radio-frequency identification (RFID) and passive integrated transponder (PIT) tags have introduced a method suitable for documenting dispersal patterns and also quantifying habitat use of many small-bodied vertebrates, including amphibians and fishes [11, 14, 15, 16, 17].

RFID passive telemetry automatically recording PIT tag presence is today an available and increasingly popular option for investigating life histories, including the above-mentioned dispersal patterns of small animals [18, 19]. PIT tags have been widely used in ornithological research [20], including studies providing data of nestling diet [21], possible differences in the incubation behaviour of adults at successful and unsuccessful nests [22], hypotheses (better option, incompatibility or asynchronous arrival) best explaining divorce in the common tern [23], investigation of prospecting behaviour of pied flycatchers (*Ficedula hypoleuca*) at conspecific nests within a short time period following a simulated predator visit [24] and if seasonal date of initial arrival at breeding grounds predicts the individual age at first reproduction of the common tern [25], etc. Since PIT tags' first usage in biology in the mid-1980s, the numbers of studies using them has continually increased [26]. Passive telemetry could provide amazing and new opportunities to study amphibians, because of their ability to identify an individually marked animal for a long time and could bring us many of information about life history (e.g. diurnal activity and differences in movement between male and female, filopatry, metapopulation distributions, etc.) [27, 28, 29, 30]. In this contribution, we want to apply a method, which newly used subdermally implanted PIT tags in the Great crested newt (*T. cristatus*) as is threatened and declining species in the Europe [29]. One of the problems of tagging could be the choice of appropriate anaesthetics. A variety of anaesthetics have been used in amphibian studies with varying effectiveness and duration of anaesthesia, including zolazepam, methoxyflurane, isoflurane, propofol, tricaine methanesulfonate, barbiturates and clove oil [31]. We decided to use clove oil as an anaesthetic. We also want to determine the survival rate of *T. cristatus* individuals carrying PIT tags for 48 h in the lab and in the pond. The other aim was to answer whether some PIT tags can be expelled. This could be a problem for future studies aiming to estimate population parameters of given species, potentially leading to overestimation of population size in mark-recapture models. Lastly, we tested tracking of *T. cristatus* with passive telemetry in a natural breeding pond; we tested whether males differ from females in their activity and whether the newts are more active during the day or night.

Methods

The Great crested newts (*T. cristatus*) used in this study were obtained in a breeding pond located in Tovéř (49.6405478N, 17.3281758E, altitude 235 m), 7 km northeast of Olomouc in the eastern part of the Czech Republic. This locality hosts breeding populations of both *T. cristatus* and *Lissotriton vulgaris*, and its surface area reaches 500 m^2 during the spring, with a maximum water depth of approximately 1.9 m; sometimes in warm summers it completely dries up. The littoral zone is dominated by pondweed (*Lemna minor*) and submerged grasses are present around the pond. According to the Habitat Suitability Index (HSI) [32] assessing the suitability habitat for GCN occurrence, the Tovéř locality falls into the category "good".

The experiment started at the end of the breeding season; however the pond surprisingly dried up, because of low precipitation and higher temperature that year. In May 2018, we caught 140 individuals of *T. cristatus*, 64 females and 76 males, by using 10 standard funnel prism shaped traps commonly used for capturing amphibians [33, 34, 35]. We took photos of the captured *T. cristatus* with their characteristic patterns on the belly (for double marking), then they were placed into several separate aquariums (80 l, water temperature 18 °C, submerged vegetation, gravel and sand at the bottom) in an air-conditioned room (20 °C) for 10 days. The daylight/dark pattern was set to 14/10 h according to local natural summer sunrise and sunset. The *T. cristatus* individuals were fed by frozen blocks of bloodworms (*Chironomus plumosus*) thawed one hour prior to feeding. *T. cristatus* were left to acclimate for 10 days before the experiment started. This study was carried out in strict accordance with the recommendations by the preamble to Act No 246/1992 Czech Law Coll., on the protection of animals against cruelty, the basic law related to animal protection governing the activities of all the state authorities of animal protection in the Czech Republic, such as the Ministry of Agriculture, including the Central Commission for Animal Welfare, and the veterinary administration authorities. The protocol was approved by the Ministry of Agriculture (protocol no. 23/2016). All surgery was performed under clove oil anaesthesia, and all efforts (short time of manipulation in a sterile environment, etc.) were made to minimize suffering. The phenolic compound eugenol, the active component of clove oil, is an effective anaesthetic for amphibians, and can be applied by immersion, potentially making it suitable for work in the field with species that are difficult to handle [36]. After consulting a veterinarian, by protocol (23/2016 –see above), the basic criterion for humane endpoints were impaired ambulation, which prevents animals from reaching food or water, excessive weight loss and extreme emaciation, lack of physical or mental alertness, difficult laboured breathing, or prolonged inability to remain upright [37].

In this study, we implanted 140 PIT tags (12.0 mm x 2.12 mm, 0.1 g half duplex (HDX), Oregon RFID; Portland, Oregon, USA) under the skin of 140 *T. cristatus*. Each individual was anaesthetised by a 7–10 minute immersion in a clove oil solution prepared by adding 0.025 ml of 100% oil extract into 400 ml of dechlorinated water at 20 °C, in a small plastic box with cover [38]. Finally, anaesthetic depth was based on our previous experiment with the Alpine bullhead (*Cottus poecilopus*) and Smooth newt (*Lissotriton vulgaris*). The weight of *T. cristatus* falls in the range between those two species. Anaesthesia was achieved after 5–10 minutes. In the clove oil solution, *T. cristatus* tended to behave normally during the first 5 minutes, without any signs of stress (e.g. accelerated breath), until they started to turn upside-down. We did not observe any prolapse or respiratory depression. After removal from the plastic box, *T. cristatus* were gently put on one side and a short (2 mm) lateral subdermal incision with a sterile scalpel was performed in the side of the body, half-way between the belly and the back, approximately 5 mm before the hind legs. A sterile needle with a blunt end was inserted into the incision to create space for the PIT tag, which was gently inserted into the cavity (Fig 1). We did not use a medical adhesive to seal the site of injection because of risk of rupture [11]. The surgical procedure took less than 3 minutes; afterwards the *T. cristatus* were laid onto a wet substrate. The anaesthetized individuals of *T. cristatus* awoke after 60–90 minutes. After that, *T. cristatus* were left under control (48 h) by an internet protocol (IP) camera, and in case of abnormal behaviour, the PIT tag was removed from the body. The presence of the PIT tag was checked individually by an HDX hand reader (Portland, Oregon, USA). One week later, X-ray (79 kV and 0.8m As) images were taken to check the exact positions of the PIT tags (Fig 2). During the X-ray the *T. cristatus* were once again anaesthetised using the clove oil solution by the procedure described above.

In order to explore the feasibility of studying *T. cristatus* in its aquatic phase using a passive telemetry system, we tracked the presence of 100 randomly selected of 140 PIT tagged
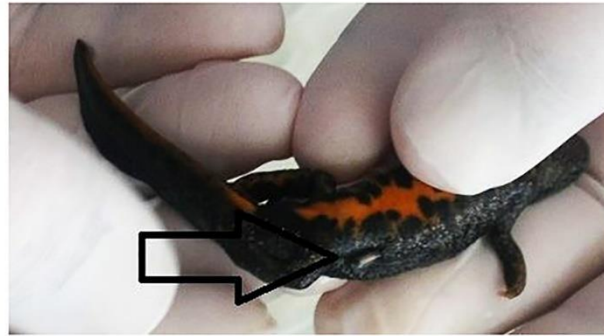
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Fig 1. Position of PIT tag. Insertion position of a PIT tag into the body cavity of the *T. cristatus*.

individuals at the place where the newts were originally caught via a passive telemetry system (Oregon RFID, Multi-Antenna HDX Reader). Of the remaining 40 individuals, 21 expulsed the PIT tags and another 19 marked individuals were used for other behavioural experiments. Four antennas with length 4 m and height 0.4 m were situated in the pond approximately 5 m apart (Fig 3). If *T. cristatus* was moving in the longitudinal profile of the pond, it was guided to pass through the 4 m wide antennas using plastic barriers on the pond edges, which prevented movement of *T. cristatus* out of the tracking corridor (Fig 3). The antennas were periodically emitting a magnetic field that charges a PIT tag when present in the magnetic field. Subsequently, the charged PIT tag emits an individual code that is recorded and stored together with the date and time in the HDX Reader memory. The reader recording frequency was set to 10 energize and receive cycles s^{-1}.

Since the experiment with releasing *T. cristatus* was started at the end of the breeding season, telemetry data captured the switch from aquatic to terrestrial phase. In a 72 h period we also tested differences of movement activity between males and females during day (5:00–21:00) and night (21:00–5:00). For each hour, we subtracted the number of detected females from the number of detected males and applied one sample t-test on these values. Prior to the analysis, we visually checked data for normality. Day and night settings were based on meteorological data from the Czech Hydrometeorological Institute. We also evaluated the differences in frequency of detections between males and females using the binominal general linear model (GLM) between males and females in their day/night activity. To do so, we compared
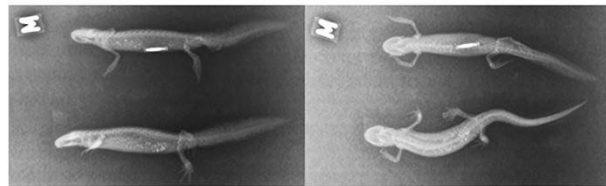

Fig 2. X-ray images. X-ray images of two *T. cristatus* in lateral (left picture) and in dorsal (right) position. The upper newt is a male with a PIT tag, the lower newt is a female without PIT tag.
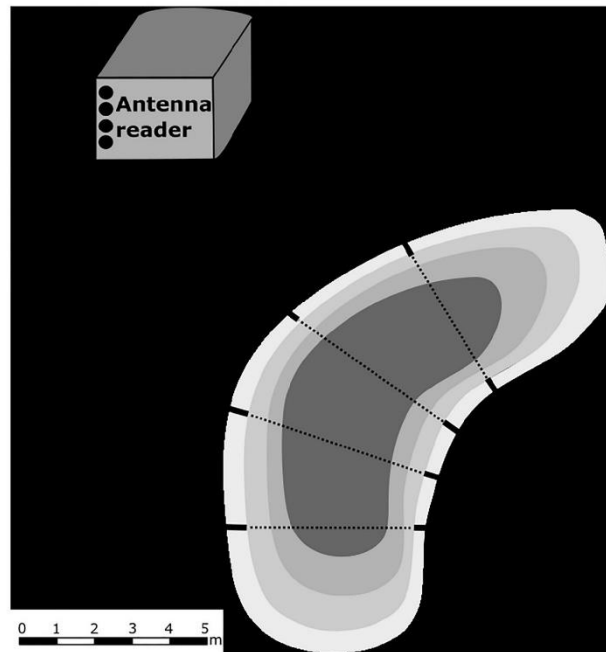
79

Fig 3. Passive telemetry system. Position of the passive telemetry system with four antennas and reader in the Tověř breeding pond. In order to guide *T. cristatus* through antennas, we used plastic barriers on the edges of the pond.

detections (yes/no) of all newts between night and the following day. We had three comparable day-night sets in total, for each we tested the differences between males and females using the generalized linear model (GLM) assuming a binomial error structure, all in the statistical software R, version 3.4.3. [39].

Results

The majority of *T. cristatus* survived the anaesthetics and surgery (98.57%) without any apparent bodily injuries (necrosis). Only two *T. cristatus* (one male and one female) died without euthanasia. They died without apparent cause of death (evaluated by the veterinarian) 40 hours after surgery from which they recovered well. After recovery from the surgery, all *T. cristatus* ate normally; movement and swimming behaviour was congruent with their behaviour before surgery without pathological signs (with only one exception).

When verifying the presence of PIT tag in the tagged *T. cristatus*, we discovered that 9 males and 12 females of all 140 PIT tagged individuals had been able to dislodge their PIT tags within three days after surgery. From the 100 PIT tagged *T. cristatus* released in the wild, we detected 97 individuals in the aquatic habitat by using four antennas connected with HDX Reader. The maximum number of recorded *T. cristatus* was on the date of release and we still registered a few individuals over the next next9 days. Altogether 24 106 records were obtained.
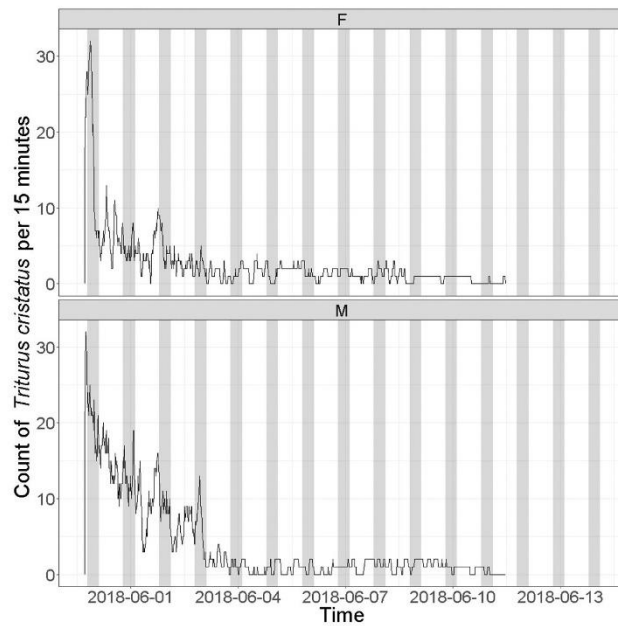
80

Fig 4. Detection rates. Detection rates in *T. cristatus* tracked by the passive telemetry system in the breeding pond. Upper panel shows counts of female newts and lower panel counts of male newts. White and grey stripes represent day and night periods.

Higher numbers of counts (detection rates) were recorded during the first 3 days of the experiment (Fig 4). In first 24 h, we detected 47 males and 49 females, in 48 h we had 32 detections of males and 16 of females, in 72 h we recorded 26 males and 12 females. Males had a significantly higher detection rate (F = 9.4, df = 1, P = 0.003, R2 = 8%) than females (Fig 5). On
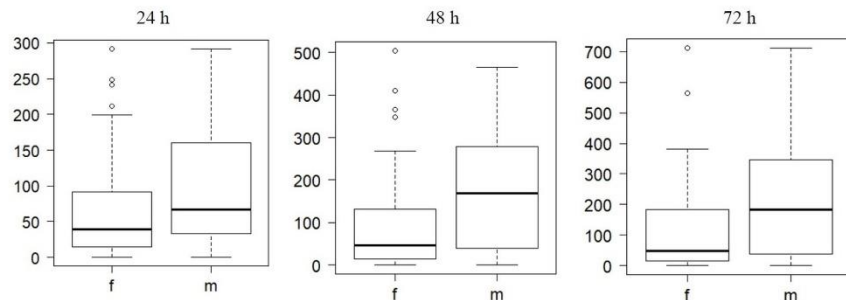

Fig 5. 72 h experiment. Differences in detection during 72 h experiment, males (m) had significantly higher detection (F = 9.4, df = 1, P = 0.003) than females (f).
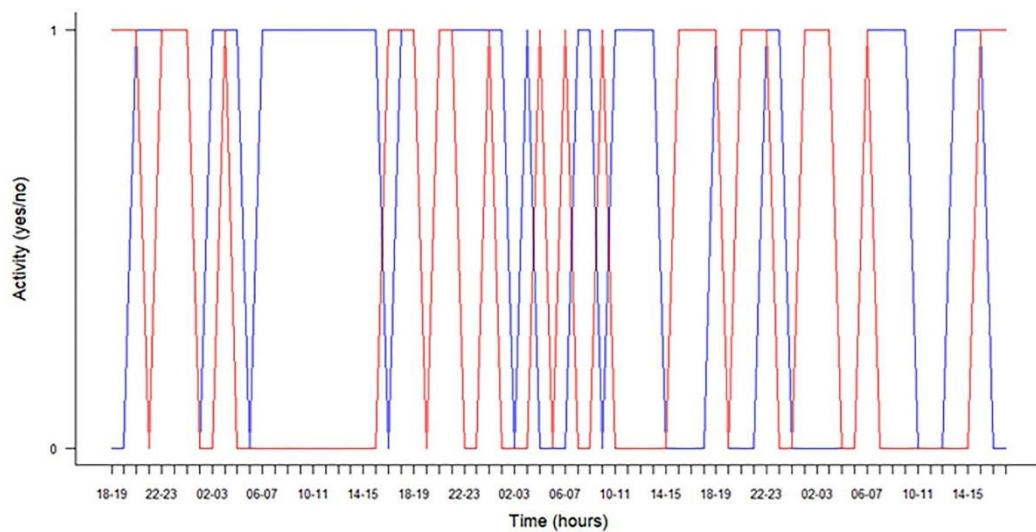
81

Fig 6. Diurnal activity. Diurnal activity during 72 h observation of the two most-detected individuals (Blue – male, red – female). Activity 1 (yes) means detection in one of the four antennas, 0 (no) means without detection.

average, we captured 6.5 (95% confidence interval = 5.6 to 7.4, using t test R function, which assumes normal distribution) more males than females each hour (t = 14.6, df = 71, P <0.001). In two individuals that were more frequently detected (one female with 714 records and one male with 712 records), it was possible to create a graph of their diurnal activity during the 72 h after release (Fig 6) There was no significant difference in detection for males and females between day and night: first day (Dev = 0.32, df = 198, P = 0.57; binominal GLM), second day (Dev = 0.55, df = 198, P = 0.46; binominal GLM), third day (Dev = 1.59, df = 198, P = 0.21; binominal GLM). Other days were not tested, because lower detection rates.

Discussion

Passive telemetry can bring wealth of information about life history of species under scrutiny. Depending on the study design, research can focus on diurnal activity or differences in movement between males and females. Another possibility is to tag individuals year prior to telemetry study and quantify arrivals and departures on the reproductive ground. Compared to the non-invasive photo-matching method, the PIT tag method requires catching the animal only once, with no further manipulation required [13]. The limitations of this method could be the high price of the reader or antenna and the reading range of the antenna [40, 41, 42]. The advantage of the HDX system is the ability to build an antenna of large size (up to 100 m), in comparison with the limited size of full duplex systems (FDX) antennas. In addition, FDX systems are more expensive, and in case of installation in flowing waters, they have to be fixed to prevent vibrations [19].

There are serious concerns about the possible negative impact of PIT tag surgery on species' behaviour and growth [43, 44, 45]. Several studies investigated the possible negative effects on the body condition of different species of newts, or which compare PITs versus colouration

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patterns or other marking techniques [46, 47]. No significant effects of PIT-tagging on body condition and recapture rates were detected in long-term studies on *Triturus dobrogicus* and *Pelobates fuscus* by comparison with belly pattern recognition [46]. Because of high accuracy with regard to mark misreading risk, PIT-tagging appears to be the best available marking technique in amphibians, provided that the body size is sufficiently large for sheltering the transponder [48]. An implantable tag seems to be the best method for radio-tagging small and medium sized urodeles species such as *T. cristatus* [49] and subsequent tracking with passive telemetry.

For mark-recapture studies aiming at assessing dispersal, migration or survival, information regarding tag retention and failure rates is important for interpretation of results. PIT tag retention rates have been shown to vary among species, and even within species, depending on life stage, sex or location of tag placement [50, 51]. The position of the transmitters in the animal body is an important factor in determining the success of the study [46]. Methods using external tag attachment by elastic harness system or sutured to the skin seem unsuitable for telemetry studies of *T. cristatus*, because they could be easily lost [49]. On the other hand, telemetry studies with the tag positioned inside the body have previously been conducted on several species; however, most of them were larger than our model for amphibian species, *T. cristatus*–e.g. *Ambystoma maculatum* [52, 53], *A. tigrinum* [54] and *Desmognathus quadramaculatus* [55]. However, there might be several problems, e.g. with using the holding pen. In a study on the Bluehead sucker (*Catostomus discobolus*) one bluehead sucker died in the holding pen [56]. This fish was dissected and neither sign of internal damage nor puncture of internal organs was evident. The fish did have a lesion near its anal opening and a fungal infection which covered the anal opening and anal fin. The fungal infection in combination with the stress of being held in the holding pen may have contributed to its death.

The first aim of this study was to determine the survival rate of *T. cristatus* individuals carrying PIT tags for 48 h in the lab. In our study we implanted PIT tags under the skin of 140 *T. cristatus*; the survival rate of tagged *T. cristatus* was 98.57%. Such low mortality is common in PIT tagging studies, since it seems implantation of PIT tags into animal bodies does not usually cause high mortality [26]. Handling may indirectly lead to mortality [57], stress in e.g. fishes has been shown to have cumulative negative effects, including reduced growth and condition [58, 59]. Therefore, it is possible that in our study, the two dead individuals may be the result of a combination of several factors and not caused solely by surgery. If we compared it with an active telemetry, 87.5% of animals survived up to 48 days in the wild for successful radio-tracking surveys [60] post-surgery, until the battery life expired. By our results PIT tag implantation seemed to not impact the behaviour of *T. cristatus*, as already observed in other amphibian species [11, 60, 61, 62, 63, 64].

The survival rate can be also influenced mainly by the size and weight of the PIT tag [65]. Active (transmitters) and passive (PIT) tags differ in size due to presence or absence of battery, therefore PIT tags may be used for smaller organisms that transmitters. We calculated that the mass of the tag was around the 1.5% of the body mass of the *T. cristatus*, which is well within the recommended limits; for example study for active telemetry recommended a 10% limit [66]. In our study, the smallest (95 mm total length) male *T. cristatus* after 24h started to turn sideways, biting its skin; hence we decided to remove the PIT tag, euthanasia was not needed. Other newts (99.29%) were bigger (on average 102 mm) and the surgery did not affect their behaviour. In one study, the surgically implanted tags [67] in *T. cristatus* and *T. marmoratus* were 7.0–14.3% of the body mass. In another, the tags were 3% of the body mass of *T. cristatus* [49] in that study the authors also suggested that surgically implanted tags in *T. cristatus* may be up to 5–7% of the body mass without compromising neither animal welfare issues, nor the need for unbiased behavioural data. Although our sample size is small to make a conclusion

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about minimal body length, a 12 mm PIT tag may become a problem especially for small newts with standard length (tip of snout to posterior margin of cloacal lips) under 50 mm. The miniaturization process of PIT-tags and similar marking techniques has improved in recent years, being less invasive, and the size should continue to decrease in the future [26, 68].

The second aim of the study was to answer whether some PIT tags can be expelled. We observed a higher PIT tag expulsion rate value (15.71%). However, in a study of using PIT tags in *T. dobrogicus*, one-tenth of the individuals lost their tags [46]. One of the causes for such a high expulsion rate may be an overly large incision; the glass cover of the PIT tag is very smooth and it allows a sliding movement of the tags when incisions are not yet healed. The loss of the tags happened within the first week after surgery, before the X-ray was taken. This occurrence leads us to the consideration that future incisions could be sutured. Another option is to use a medical adhesive [11] or to insert the PIT tag more deeply into the body cavity [46]. However, amphibians have great regenerative abilities; a few days later only a scar is seen, therefore we decided to omit this procedure. Moreover, in fish, it was observed that sutures lead actually to an unnecessary increase in mortality [69]. This was the same in a study [11] where the newts had ruptured their sutures due to the solidified surgical adhesive. PIT tag expulsion has been described in other species, like fish, birds and rodents [50,70]. Results from the studies of long- and short-term retention rates and experiences from other types of surgically implanted transmitters [71] have led to the assumption that tag loss mainly occurs shortly after tagging for juvenile fish and during spawning for adults. That experiment started with 2 986 fish, and during the entire period PIT tags were not detected in 191 fish. Observed tag retention rates of 12.5 mm PIT tags implanted in the body cavity of Atlantic salmon over a 533 day period was 91% [72]. Low PIT tag retention rates of larger fish in studies of other Salmonidae species have been ascribed to tag loss during spawning [51, 73, 74]. In addition to tag expulsion with eggs, there are several ways tags can exit the fish: through the incision, through the body wall, and through the intestine [71]. Visual inspection of fish without tags from the fourth and fifth scanning did not reveal any obvious signs of tags having exited through the body wall [72]. In a study on birds, the overall PIT tag retention was 77.2% (N = 102); 12% (N = 6) of male and 29% (N = 24) of female tags were lost during the study period. Successful PIT tag retention depends on implanter's experience and the attachment method [70]. In their study, once the implanter's experience improved, retention increased from 69% (in the first five trapping sessions) to 88% (the last five trapping sessions). The percentage retention in study [70] of birds (~77%) was higher than in previous studies in non-passerines species: 30% for Adélie Penguins (*Pygoscelis adeliae*) [75] and 59% for Common Terns (*Sterna hirundo*) [76]. The loss rates of PIT tags vary, depending on the species of rodents, from 3.6 to 7.2% [77].

Finally we tested the reliability and possibility of using passive telemetry by detection of *T. cristatus* with PIT tags in a natural breeding pond. When we focused on practical use in the field by using four antennas in the breeding pond, we detected 97% of individuals in natural conditions. This is a similar number as in other studies [9, 17].*T. cristatus* are predominantly nocturnal [29, 78, 79]. Males may show additional daytime activity during the peak of the breeding season [29]. Our results of activity showed that major detections were between 18:00–24:00 and lower records between 10:00–14:00, however, when we look at individuals, there is great variability and clearly there is no hour without detection (same for males and females). Generally, both sexes showed great variability in their activity. In our experiment, we observed that males had a higher detection rate than females. The result of movement behaviour showed that e.g. male of *T. cristatus* in a breeding pond can travel up to 20 m between antennas in 78 seconds (see data set).

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Ease and safety of application of anaesthetics are additional criteria [36]. Isoflurane is considered effective, but it is expensive, difficult to apply (particularly in the field) and its vapours are toxic for the investigator [80]. Application of other anaesthetics by injection may not be possible in subjects that are difficult to capture and hold without damage (e.g., salamanders). Phenolic compounds, such as eugenol, an active component of clove oil, is an effective anaesthetic for treating amphibians that can be applied by immersion, potentially making it suitable for work in the field with species that are difficult to handle [81]. However, in a study on African clawed frogs (*Xenopus laevis*), it has been documented that the duration of clove oil anaesthesia lasted longer in larger bodied individuals [38]. In our study, we did not observe any problems with the anaesthetic. The duration of the surgical depth of anaesthesia (60–90 minutes) gives plenty of time for surgical procedures. It is necessary to keep the skin moist during handling and the recovery time, as dermal respiration is assumed to be sufficient to oxygenate the circulatory system and prevent clinical hypoxemia [81]. The newts can be removed from the anaesthetic bath before the cessation of gular respiration, because there is a time lag of two–three minutes between induction of anaesthesia, i.e. loss of righting reflex and abdominal respiration, and subsequent apnoea [50]. This could reduce the recovery period, which offers an important recommendation for field studies.

To sum up, our study reports the partially successful use using of PIT tags in the body of *T. cristatus*, as a small amphibian species using clove oil as anaesthetic. Although we report small mortality and substantial PIT tag loss, we conclude that this promising method could facilitate the detection of recaptured individuals in long-term studies. We cannot exclude that there may be later expulsion of PIT tags; however, thanks to the double mark approach the possibility of identification of individuals can be made on the comparison of photos in a database, provided that the individual occurs at the same site. If the number of lost tags is stable for a certain period and can be quantified, it can be accounted for, and thus the mark-recapture or telemetry study does not have to be unsuccessful. PIT tag usage allows the observation of marked small animals of different species in aquatic as well as in terrestrial habitats, providing data on their dispersal, diurnal activity, movement behaviour and generally behavioural patterns. This promising method had no significant effect on welfare of newts, no signs of stress and pathological changes in behaviour were observed. However, it is important to assess estimates of PIT tagging mortality and PIT tag loss before making population estimates based on acquired data. Moreover, it is necessary to note that our data were affected by the short time of observation, because the breeding pond completely dried up.

Supporting information

S1 Table. Supporting dataset. Field survey data.
(XLS)

Acknowledgments

Author Contributions

Conceptualization: Lukáš Weber.

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Manuscript IV

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Should I stay or should I go? Movement strategy of the Great crested newt (*Triturus cristatus*)

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Abstract

The dual habitat reliance of the Great Crested Newt (*Triturus cristatus*), encompassing aquatic environments for breeding and terrestrial settings post–breeding, underscores the importance of understanding their movement patterns. Our research, conducted over 259 days in 2017, analysed migration behaviours in relation to body size and the potential influence of meteorological conditions. Using pitfall traps around the pond, we captured and recaptured 59 males, 78 females, and 7 juveniles. Results indicated size variations during migration, with 31.94% of females and 18.64% of males reducing in body size, averaging 6 mm and 6.4 mm, respectively. While there was no significant evidence that newts memorize migration paths, climatic conditions played a discernible role in their migration patterns. Specifically, larger females preferred drier, warmer days for immigration, and humid days for emigration, whereas large males exhibited higher activity at higher temperatures. Furthermore, the duration of pond stays was influenced by length of females and night temperature during emigration. The observed body length differences shed light on potential trade–offs between aquatic and terrestrial locomotion, suggesting that physical adaptations beneficial in one environment might be detrimental in another. These findings provide insights into the environmental factors influencing the movement activity of *T. cristatus*, which may guide future conservation efforts.

Keywords: Triturus cristatus, movement, migration, body size

Introduction

Amphibian activity, ranging from movement patterns to reproductive tendencies, are deeply influenced by external climatic variables (Martof, 1953; Bellis, 1962; Palis, 1997). Amphibians, as ectothermic animals, regulate their body temperatures using external heat sources. This makes their life cycles intrinsically linked to environmental factors, particularly the climate (Morris, 1992). Amphibians provide a unique lens for climate study due to their diverse life spans, ranging from short–lived species to ones that can live up to a century, and reproductive capabilities that can span from just a few eggs (or new–borns) to prodigious clutches exceeding 25,000 (Wells, 2010). Disturbances in their habitats, particularly those caused by human activities, can intensify their vulnerability to climatic shifts. This is because such habitats, e.g. clear–cuts or fields, offer little to no buffer against the changing climate. Moreover, factors like human–induced habitat discontinuities can significantly influence their movement behaviours (Raymond and Hardy, 1991). Navigation towards breeding ponds sees amphibians employing a suite of techniques, encompassing celestial cues to conspecific vocalizations and magnetic fields (Griffiths, 1996; Hayward et al., 2000). Newts, for instance, exhibit directional tendencies, relying on pond odour (Joly & Miaud, 1993) and consistent habitat preferences like deciduous woodlands (Jehle & Arntzen, 2000). These consistent movements are pivotal for conservation efforts, directing habitat preservation strategies (Dodd & Cade, 1998).

Elevated temperatures pose risks, such as increased amphibian mortality, changing their activity and reduced female fecundity. Reading (2007) linked reduced female conditions of the common toad (*Bufo bufo*) with dwindling annual survival, attributing it to milder winters affecting body size and egg production. Similarly, Griffiths et al. (2010) observed reduced survival rates in male great crested newts (*Triturus cristatus*) following winter temperature surges. The repercussions also extend to amphibian larvae, with accelerated pond drying potentially curtailing their metamorphic phases (Rowe & Dunson, 1995). Fluctuations in pond dynamics might disrupt larval growth (Boone et al., 2002), and predation dynamics could alter due to size–dependent vulnerabilities. The risks associated with premature breeding, like exposure to erratic spring weather, are contrasted by potential benefits such as extended growth periods for larvae (Corn & Muths, 2002). On the other hand, study Reading & Clarke showed that larger amphibians generally showcase better over–winter survival and fitness. . In disturbed terrains, amphibians tend to be larger, given

their heightened resistance to desiccation (Thorson, 1955; Ray, 1958). The aquatic phase sees varied weight changes due to reproduction–related activities, with females generally gaining and males losing weight (Jehle et al., 2011; Sinsch et al., 2003). Yet, these patterns have notable individual–specific variations (Mullner, 1991).

Movement behaviour is pivotal in conservation biology since it determines how organisms engage with both other species and their environment (Vojar, 2007; Nathan et al., 2008). The Great crested newt (*Triturus cristatus*), our model species, like many pond–breeding amphibians, relies on dual habitats: the aquatic environment for breeding and the land–based habitat for activities after breeding and during their juvenile stage. A functional connection between these habitats is essential for effective dispersal and seasonal migration (Gustafson, 2011). In this research, we centred our attention on movement patterns related to body size. We aimed to determine if newts recall the paths of both incoming and outgoing migrations. Additionally, we investigated how meteorological factors (due to ongoing climate change) like temperature, humidity, and rainfall might influence duration stay in pond in the pond.

Materials and Methods

The study took place at an artificial pond in Tovéř, a village in the Czech Republic (49°38.433'N; 17°19.691'E). This pond, northeast of Olomouc town and 227 meters above sea level, spans roughly 500 m^2. Lacking continuous water input, its levels fluctuate with rainfall. While its depth in spring is around 1.8 meters, it can dry out in hot summers, but in monitoring period the pond didn't dry up. Algae prominently grows on its eutrophic surface. The southern and northeastern edges slope gently. The pond's littoral zone predominantly features pondweed (*Lemna minor*) and submerged grasses in the vicinity. The Habitat Suitability Index (HSI) rates Tovéř as a "good" (score 0.7) habitat for *T. cristatus*. There are no fish in the pond, but mallards (*Anas platyrhynchos*) frequently visit the area. Based on monitoring and the use of photo traps, only grass snakes (*Natrix natrix*) and cats (*Felis catus*) occur as potential amphibian predators. Other amphibians despite the great crested newt, include common newt (*Lissotriton vulgaris*), alpine newt (*Ichthyosaura alpestris*), fire salamander (*Salamandra salamandra*) as well as European fire–bellied toad (*Bombina bombina*), European tree frog (*Hyla arborea*), common toad (*Bufo bufo*), European green toad (*Bufotes viridis*), and agile frog (*Rana dalmatina*).

The monitoring period spanned 259 days, from March 4 to November 18, 2017. Throughout the study, amphibians were trapped using drift barrier equipped with pitfall traps (n=47) encircling the pond. A 75 cm tall, UV–resistant polyethylene (PE) half–sheet served as a guidance drift fence, with about 10 cm embedded in the soil to protect against undermining. White plastic buckets, 30 cm tall and 25 cm in diameter, were buried around the pond's perimeter as traps, each set about 3 meters apart and level with the ground surface (Crosswhite, 1999). Buckets were placed on both sides of the drift fence (inside n=24, outside n=23) to capture amphibians during both emigration and immigration phases. Each bucket contained a damp sponge and several leaves to maintain humidity and offer shelter to the captured animals. The drop traps, numbered 1 to 47, formed a directional rosette pattern to track migration. Traps were sectioned into two based on proximate environments symbolizing potential hibernation sites: traps 1–25 were allocated to the forest section, and 26–47 to the section adjacent to the village (Fig. 1).

Each morning, the sex, length (measured from snout to vent – SVL), and the specific trap number of every captured *T. cristatus* were documented. Those displaying ambiguous adult sexual traits were labelled as juveniles within SVL size to 80 mm. A belly photograph was taken of every captured newt for identification using capture–mark–recapture method. The newts were then released in the direction they were migrating. It was presumed that they would travel straight from the pond to the fence, falling into one of the closest two traps, a typical assumption in drift fence research. All traps were deemed equally adept at trapping newts, ensuring a statistically meaningful sample of migrating newts from every direction (Malmgren, 2002). The meteorological data for this research were gathered at a DAVIS Vantage PRO weather station. Measurements included air temperature (°C) and humidity (%) at 2 m above the ground level and rainfall (mm) at 1 m level. Daily and nightly (according to sunshine) means averages were taken for temperature, and humidity, also minimal and maximal temperature for day and night separately, while cumulative rainfall of 24h was recorded for precipitation.

The minimum number alive (MNA) method was used to calculate the total population size. The method is commonly used to estimate population size from data obtained using the CMR method. MNA is defined as the number of individuals captured at the time of capture plus those that were not captured at that time but were captured both previously and subsequently (Pocock et al., 2004). Because MNA uses information from previous and subsequent captures, it is sensitive to the effects of temporary emigration or mortality,

which increases error in population estimates using MNA (Pocock et al., 2004). The error due to emigration was eliminated in our study because of the inability to free emigrate from the study pond.

The influence of meteorological factors and duration stay in pond on the migration patterns was assessed using Redundancy Analysis (RDA) in the Canoco for Windows 5.0 software. Models were established for both the immigration and emigration activities of the newts. Size groups and genders were treated as species data, while the duration stay in pond and environmental parameters (average day and night temperature, lowest day and night temperature, highest day and night temperature, precipitation, and average humidity) were used as explaining variables. Significant environmental factors affecting newt activity or duration stay in pond were used to calculate predictive Generalized Linear Models (GLM).

Migration directions, encompassing both inward and outward movements, were depicted using the Oriana for Windows software, incorporating the Rayleigh–Test. A t–test with inequality of variances was used to determine differences in duration stay in pond between sexes, and correlation was used to analyse if there is the effect of body size on duration stay in pond on sexes separately. To evaluate memorizing the migration path, the CHITEST method was chosen by selecting the 10 smallest and 10 largest individuals divided by sex into the following categories: immigrating from the forest and emigrating to the forest, immigrating from the forest and emigrating to the urban area, immigrating from the urban area and emigrating to the urban area, immigrating from the urban area and emigrating to the forest. These analyses were conducted using the statistical software R, version 3.4.3.

Results

The total population size using the MNA method is 1016 males, 840 females and 204 juveniles located at the study site. The sex ratio of *T. cristatus* individuals was 1.21 males per 1 female. Of this number, only 59 males, 72 females and 7 juveniles were recaptured during the migration. In immigration, the sex ratio for recaptured newts was 1.02 : 1 (males : females), but in emigration it was 1.37 : 1 (males : females). Analysing recaptured individuals, females were larger than males by an average of 4.5 mm (Tab. 1). During emigration, individuals were recorded to have reduced body size (SVL). Among the females captured, 23 (i.e., 31.94%) had a smaller body size during emigration than during immigration, with an average decrease of 6 mm. For males, 11 (18.64%) individuals were found to be reduced in size by an average of 6.4 mm. In females that increased in the aquatic

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phase, the average growth was 10.63 mm, while in females that reduced in size after the move to the terrestrial phase, the mean length loss was –5.93 mm. For males that increased in the aquatic phase the mean growth rate was 8.08 mm and for males that reduced in size the mean length loss was –6.36 mm.

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

sex	immigration					emigration				
	max	min	med	Q1	Q3	max	min	med	Q1	Q3
female	127.00	81.00	104.50	97.00	114.25	126.00	90.00	110.50	105.00	115.25
male	119.00	86.00	100.00	94.00	107.00	123.00	92.00	106.00	100.00	110.00
juvenile	70.00	57.00	62.00	61.50	69.50	68.00	59.00	63.00	62.50	66.00

Females of *T. cristatus* were observed immigrating to the pond from the different directions, but mainly from the southwest, i.e. area near the village (Rayleigh test; $\mu=166.604\pm36.73°$; $r=0.349$; $p>0.05$). On the contrary, females predominantly departed to the southeast during emigration, where the forest is situated (Rayleigh test; $\mu=166.604\pm36.73°$; $r=0.349$; $p<0.0001$; Fig.2). For males the situation is similar, they preferred to come from the southwest (Rayleigh test; $\mu=160.65\pm69.947°$; $r=0.207$; $p>0.05$) and emigrated in a southeastern direction (Rayleigh test; $\mu=160.65\pm69.947°$; $r=0.207$; $p<0.0001$; Fig.2). The effect of memorizing the migration path was not statically significant for both females and males (CHITEST, $p>0.05$).

Redundancy Analysis (RDA) applied to individual meteorological factors during immigration for females accounts for 26.07% of the variation, when the most important factors contributing to prediction of size of immigrating females are maximum night temperature ($F=7.3$, $p=0.004$, explained 9.4%), days in pond ($F=4.1$, $p=0.048$, 5.1%), minimum day temperature ($F=3.8$, $p=0.054$, 4.6%). Generalized linear models (GLM) were statistically significant for days in pond ($F=10.1$, $p=0.002$), precipitation ($F=5.3$, $p=0.024$), maximum day temperature ($F=6.3$, $p=0.014$) and maximum night temperature ($F=7.3$, $p=0.009$). Larger females immigrate to the pond on drier days, which are warmer (maximum day and night temperature) and stay in the pond for a shorter time than smaller females (Fig. 3).

The variation accounted for by applying RDA to individual environmental factors during female emigration is 16.12% and just humidity was significant for predicting emigration of females (F=4.4, p=0.036, explain 5.5%). Larger females leave on more humid days than small females (GLM, F=4.1, p=0.04741; Fig. 3).

The variation explained by RDA when applied to individual environmental factors during male immigration is 18.37% and the only factor significantly contributing in this model to predictability of length of immigrating males is maximum night temperature (F=4.7, p=0.046, explains 7.6%). GLM were statistically significant for average night temperature (F=4.4, p=0.04004) and maximum night temperature (F=4.7, p=0.03406). Larger males, compare to females, immigrate in warmer nights (Fig. 4). In the emigration of males, RDA of effect of environmental factors explains 19.30% of the data variation and maximum day temperature (F=6.6, p=0.008) and mean day temperature (F=5.0, p=0.028, 8%) are the only factors significantly contributing to predictions of size pattern of emigrating male newts. GLM were statistically significant for average day temperature (F=5.0, p=0.03004) and maximum day temperature (F=6.6, p=0.01269). Results shows that larger males leave the pond on warmer days than small males (Fig. 4).

There is a significant difference in the duration of time spent in ponds for each sex for recaptured individuals (ANOVA, F=11.52, p<0.001). Males stay in the pond the longest time (med= 98.75), followed by females (med= 91), whereas juveniles leave the pond in a shorter time (med=35) (Tab. 2). The correlation between duration stay in the pond and body size (SVL of immigrating individuals) was significant (r=–0.32, p<0.001) when larger newts leaved the pond sooner than smaller ones, this correlation was significant for females (r=–0.36, p=0.002), but not for males alone (r=–0.24, p=0.07).

Table 2: Duration stay in pond in days (Q1 = lower quartile, Q3 = upper quartile, med = median).

sex	max	min	med	Q1	Q3
female	133.00	14.00	91.00	79.00	104.00
male	223.00	30.00	98.75	89.00	113.50
juvenile	149.00	2.00	35.00	6.00	67.50

Redundancy Analysis (RDA) applied to duration of the stay in pond influenced by meteorological conditions at the newt emigration explained 14.15% of the data variation. The only significant predictor in this model was minimum night temperature (F=8.8,

p=0.006, explains 6.4%). GLM relating number of days spent in ponds and minimum night temperature (F=8.8, p=0.00365) shows, that the longest–staying animals leaving the pond at warmer nights (Fig. 5).

Discussion

The population size count by MNA method in the monitored pond is 2060 individuals of which only 138 individuals were recaptured. On the other hand, research using mark–recapture data to estimate population sizes has shown significant variations across different locations (Jehle et al., 2011). For instance, Baker (1999) reported an average population size of 113 (SD ± 59) for a metapopulation in Buckinghamshire. In contrast, Arntzen et al. (1999) found a considerably larger average population size of 1408 (SD ± 73) in Leicestershire. Within Europe, the average size of metapopulations varies widely: from as few as 29 (SD ± 6) in Western Germany (Wenzel et al., 1995) to as many as 1229 (SD ± 919) in Eastern Germany (Meyer & Grosse, 2007). However, studies in similar regions using count data, such as those by Feldmann (1981) and Veith (1996), often yield lower average population size estimates. This suggests that simple counts might not provide as insightful estimates compared to mark–recapture methods (Jehle et al., 2011).

The sex ratio of *T. cristatus* individuals was 1.21:1 towards males. For recaptured individuals, the sex ratio was balanced 1.02 : 1 (males : females) at immigration, but for emigration it was dominated by males 1.37 : 1 (males : females). For breeding amphibians, balanced sex ratios are generally observed, though some populations have slightly more males, especially early in the breeding season when males typically reach breeding ponds before females (Arntzen, 2002). Proper sex ratios impact population dynamics and shape mate competition intensity, a skewed ratio can intensify mate competition in the predominant sex, driving stronger sexual selection for advantageous traits (Grayson et al., 2012). Males in the *Triturus* genus can mate with multiple females, but there are constraints like spermatophore supply (Halliday, 1987). Optimal mating chances for *T. cristatus* occur mainly during evenings (Griffiths, 1985), underscoring the need for balanced breeding ratios to ensure successful reproduction and population growth. The sex ratio in favour of males was probably due to greater capture of males during immigration and may also indicate that females remain in the pond for wintering. Females lay about 250 eggs per season, with half failing due to chromosome issues (Langton et al., 2001). The hatched larvae grow by consuming aquatic invertebrates. They undergo metamorphosis, evolving from gill–bearing larvae to juvenile newts. If conditions aren't right, some may delay

metamorphosis, overwintering in ponds. Upon reaching 2–3 years, they achieve sexual maturity and start reproducing (Jehle & Arntzen, 2000). Our results show, that on 840 females, only 204 juveniles were recorded in traps during migration. It seems to be underestimated number, however, most of the juveniles remain in the pond. It is important to mention, that adverse impacts on population sizes often stem from density–dependent processes during the larval and juvenile phases. In larger populations, high larval counts can hinder larval growth, survival, and post–metamorphic outcomes like decreased size at metamorphosis (Scott, 1994; Cayuela et al., 2020). This can subsequently diminish juvenile recruitment and overall population size (Ousterhout & Semlitsch, 2016). Some of the studies show annual survival rates for newts vary between 25–100% based on location and year (Baker, 1999; Griffiths et al., 2010). Adults generally survive more than juveniles, but consistent patterns aren't clear. High adult counts don't guarantee juvenile numbers, and low juvenile rates don't predict adult decreases (Jehle et al., 2011). Newt populations are influenced by factors like predation, climate, and resources, complicating generalizations and necessitating further research (Griffiths et al., 2010).

Our results also show that during emigration, some of individuals have reduced their body size. Great crested newts, with their indeterminate growth, suggest a correlation between body size and age (Duellman, 1989). This leads to potential evolutionary research, such as body size's role in mate selection (Halliday & Verrell, 1988). If larger, older males are preferred, females might select mates with heritable longevity traits (Howard, 1978). Still, amphibians often grow quickly before maturing, slowing afterward (Marvin, 2001). Thus, adult size may reflect juvenile growth more than age (Halliday & Tejedo, 1995). While body size varies in mature adults (Arntzen, 2000), natural selection may favour earlier reproduction, impacting growth and overall reproductive success. Body condition scores indicate an individual's fat reserves, reflecting health, vulnerability to diseases, and overall population quality (Janin et al., 2011). It provides insights into foraging success, adaptability to environmental stress, and consequent reproductive outcomes (Jakob et al., 1996). Amphibians typically start the breeding season with a higher body condition, which depletes due to reproductive energy costs (Arntzen et al., 1999). Factors like breeding pond temperature can affect condition at metamorphosis (Reading, 2007). For *T. cristatus*, milder winters result in lower body conditions possibly due to increased metabolism (Reading, 2007). Moreover, condition score differences between genders can hint at reproductive potential in females and energy reserves in males, reflecting varied habitat use (Jarvis,

2015). The difference in body length in our study touches on the trade–off between movement in water and on land. The demands for effective movement in both aquatic and terrestrial settings might hinder the overall performance of semi–aquatic creatures (Gillis & Blob, 2001). In other words, physical adaptations for efficient swimming could potentially hamper land–based movement capabilities, and the opposite is true as well with body elongation as a significant factor (Gvoždík & Damme, 2006). However, Gvoždík & Damme (2006), didn't find any indication of a compromise between relative swimming (longer body favourited) and running speeds (shorter rigid body favourited) at the interspecific level. According to Warwick (2021), male newts had SVL measurements between 53.4–91.1 mm and females between 51.4–93.2 mm and males were shorter (70.7 mm) than females (74.4 mm). Linear mixed effects models indicated ordinal day significantly influenced SVL for both sexes over the years. As the season progressed, females' SVL decreased, yet they still finished the season longer than males, who grew in length. However, neither gender nor ordinal day significantly impacted the SVL and newt age relationship. Males initially had higher SVLs than females but, by 12 years of age, female SVL growth outpaced males. Males peaked in SVL growth around 16–17 years, then declined. Female SVL growth peaked closer to 18 years before it too started to decrease.

Evidence indicates that *T. cristatus* might not always show a directional preference in pond movement (Verrell & Halliday, 1985), which we confirmed in our study. This variation could be due to distinct environmental conditions at study locations. Several studies propose that upon leaving a breeding pond, newts move directly towards suitable habitats, emphasizing efficient space utilization (Verrell, 1987; Sinsch, 1991; Jehle et al., 2011; Jehle & Arntzen, 2000). This we confirmed in our study, but there was no significant evidence that *T. cristatus* remembered their way to and from the pond in a body size–dependent manner. Most amphibians have a movement range too limited to utilize Earth's magnetic field for navigation (Sinsch, 2014). Dispersal, or one–way movements without return, involves random–walk strategies rather than goal–directed actions (Brown et al., 2014). Experiments to alter the homeward orientation in the European common toad using magnetic fields were unsuccessful (Sinsch, 1987; Landler & Gollmann, 2011). However, movements within routine areas often rely on visual and olfactory landmarks (e.g., Joly & Miaud, 1993; Hayward et al., 2000). Displaced individuals might not return home, either due to an inadequate spatial map or inverse relations between dispersal distance and return

motivation. Overall, navigation skills seem of limited fitness value for modern amphibians. It is important to use this knowledge when planning new ponds. While studies on the colonization of newly created ponds by great crested newts exist, it remains uncertain if juveniles are the initial colonizers. For instance, in a study on the Danube crested newt, individuals colonized ponds 200m and 700m away from their original habitat (Gressler, 1997). In Vienna, new ponds were colonized after two years, in a British study, farm ponds were colonized from up to 400m away (Baker & Halliday, 1999). Moreover, Lenders (1996) documented adult great crested newts colonizing newly built ponds in the Netherlands within 100m in the first year.

In our study, key factors influencing migration include night temperatures and precipitation. Larger female newts migrate to ponds on warmer, drier days and stay shorter than smaller ones, larger males migrate on warmer nights. While some studies link rainfall with amphibian breeding, others, including Verrell and Halliday (1985), found no connection. Rainfall at night can influence amphibian migrations by reducing desiccation risks. However, when it comes to understanding the precise spatial orientation mechanisms that *T. cristatus* employs during these movements, our knowledge is somewhat lacking (Jehle et al., 2011). Intriguingly, there's evidence suggesting that these newts might utilize syntopic amphibian species as reference points for orientation, a notion proposed by Diego–Rasilla & Luengo (2007). Newts *T. cristatus* migrate on wet or humid nights, which limits their spreading ability (Jehle et al., 2011). Older individuals of *T. cristatus* arrive at a pond earlier, while the younger counterparts tend to exhibit a proclivity for prolonged stays within ponds (Sinsch et al., 2003). Duration of stay in pond could be between 58 days to 176 day (Stoefer & Schneeweiss, 2001), which is similar to our study, where for male is median 99 days, for female 91 days and 35 for juveniles. The difference in residence time between the sexes in our study results from the observation that males are the first to enter the pond and juveniles are among the first to leave the pond. Water column height, presence of predators and food supply are also factors that determine residence time (Jehle et al., 2011, Gustafson, 2011).

Conclusions

We measured 139 newts trapped during its immigration to the pond and recaptured later during emigration. Analysing circumstances among sex and body size, its length of stay in pond and environmental factors during its immigration and emigration, we can conclude

that: 1) Both females and males departure ponds predominantly toward neighbouring forest, whilst its return to the pond is not directionally synchronised. 2) In females that increased in the aquatic phase, the average growth was 10.63 mm, while in females that reduced in size after the move to the terrestrial phase, the mean length loss was –5.93 mm. For males that increased in the aquatic phase the mean growth rate was 8.08 mm and for males that reduced in size the mean length loss was –6.36 mm. 3) In immigration, the sex ratio for recaptured newts was 1.02 : 1 (males : females), but in emigration it was 1.37 : 1 (males : females). Males predominated during emigration, suggesting that females remained in the pond or migrated later. 4) Probability of immigration of both males and females were affected by their size and climatic conditions – larger individuals immigrated during warmer nights; smaller females preferred rainy weather. 5) Emigration of males was affected by size and temperature – larger males emigrated from ponds after warmer days, larger females preferred humid nights. 6) Shorter females stayed in ponds for longer time and, despite its sex, newts staying in ponds for longer time, emigrated during warmer nights.

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Figures

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

Fig. 2. Directional rosettes in immigration, by gender. The black line indicates the mean and standard deviation, the red line the nonsignificant result.

Fig. 3. GLM female immigration and emigration for duration stay in pond (days in pond), precipitation, maximum day temperature (T–day max), maximum night temperature (T–night max) and humidity. Only significant variables are shown.

Fig. 4. GLM male immigration and emigration for average night temperature (T–night mean), maximum night temperature (T–night max), average day temperature (T–day mean) and maximum day temperature (T–day max). Only significant variables are shown.

Fig. 5. GLM duration stay in pond for minimum night temperature (night min). Only significant variables are shown.

Tables

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

Table 2: Duration stay in pond in days (Q1 = lower quartile, Q3 = upper quartile, med = median).
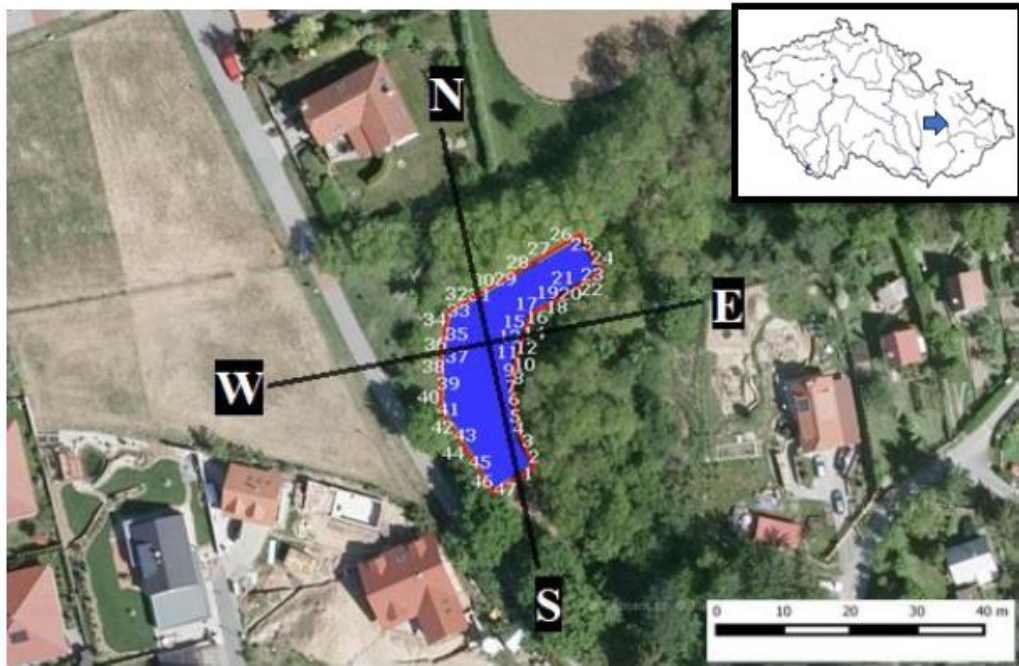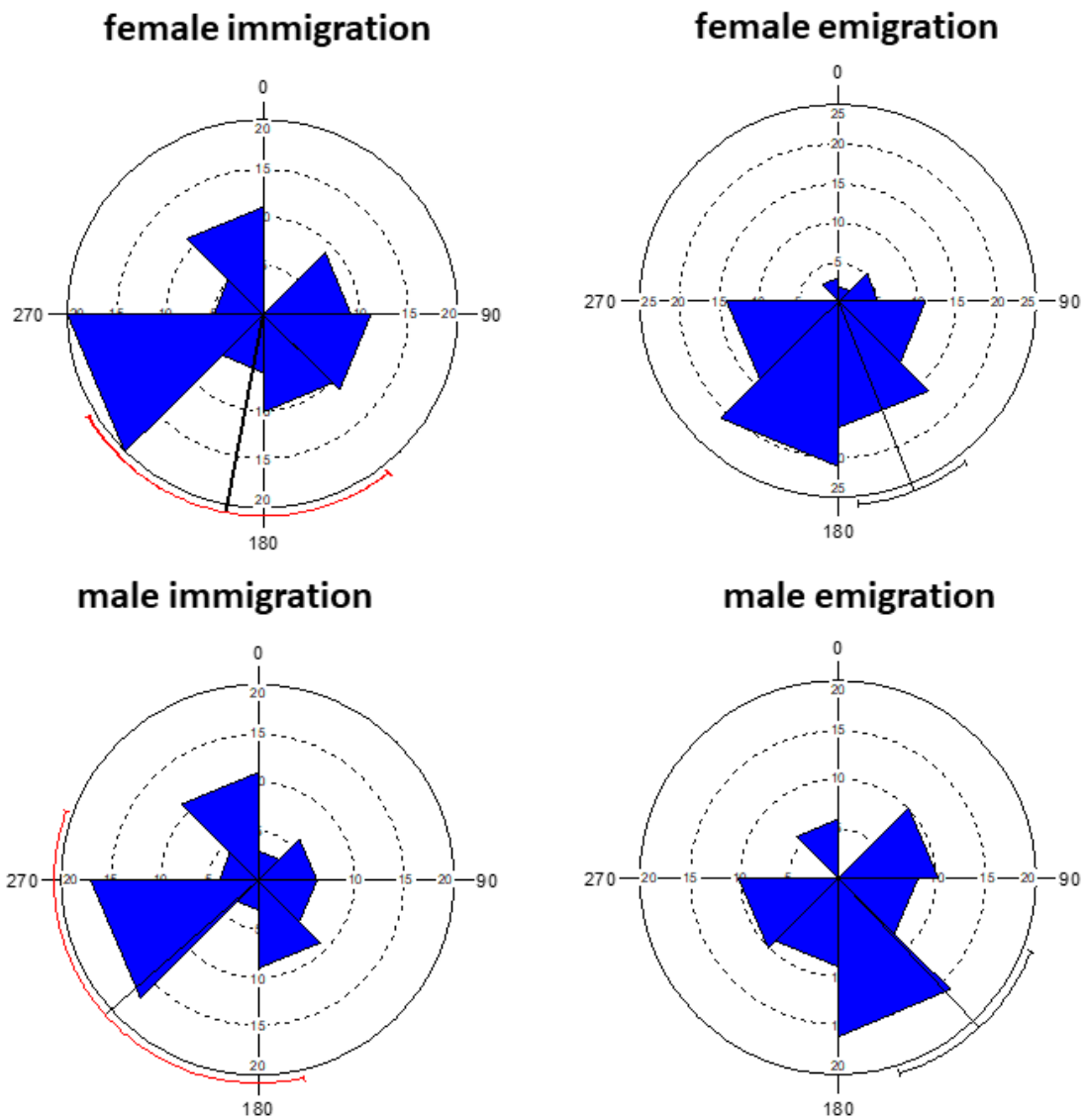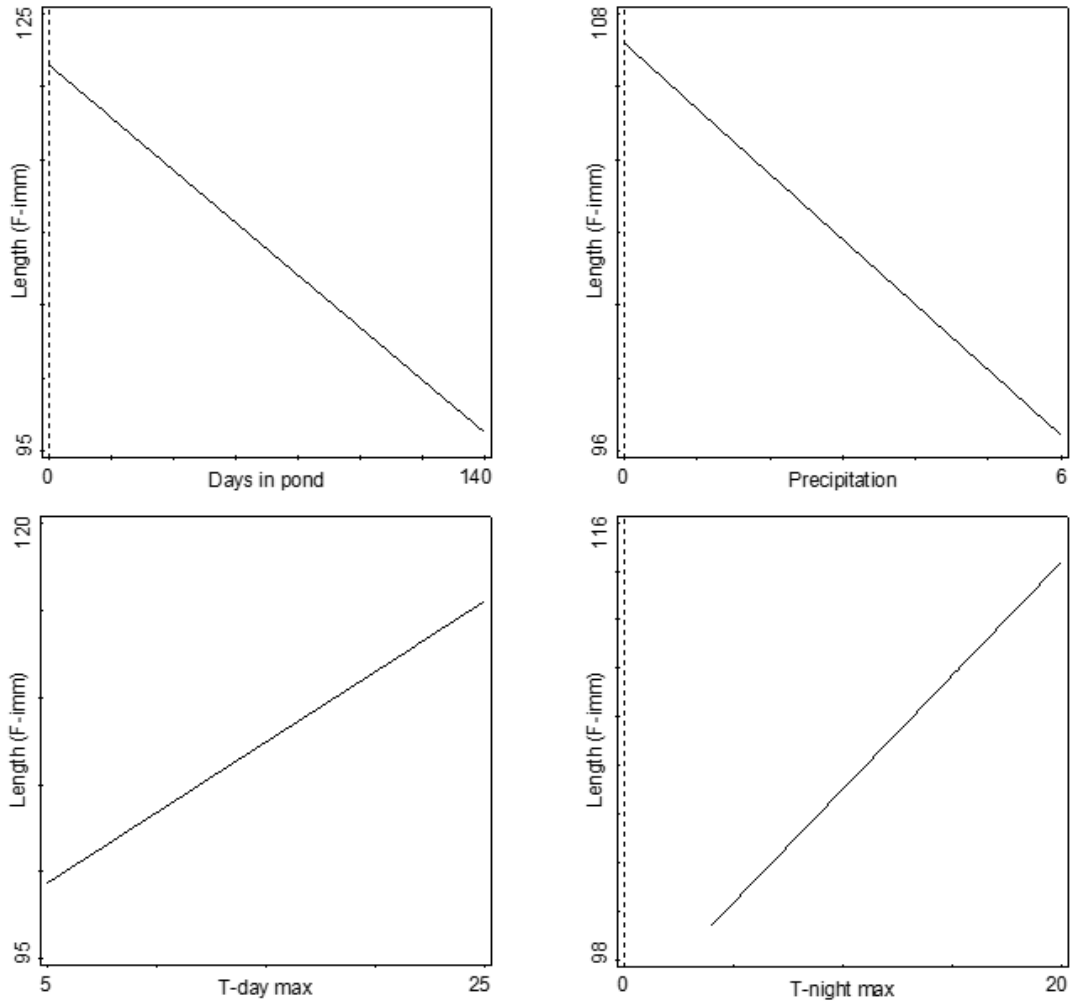
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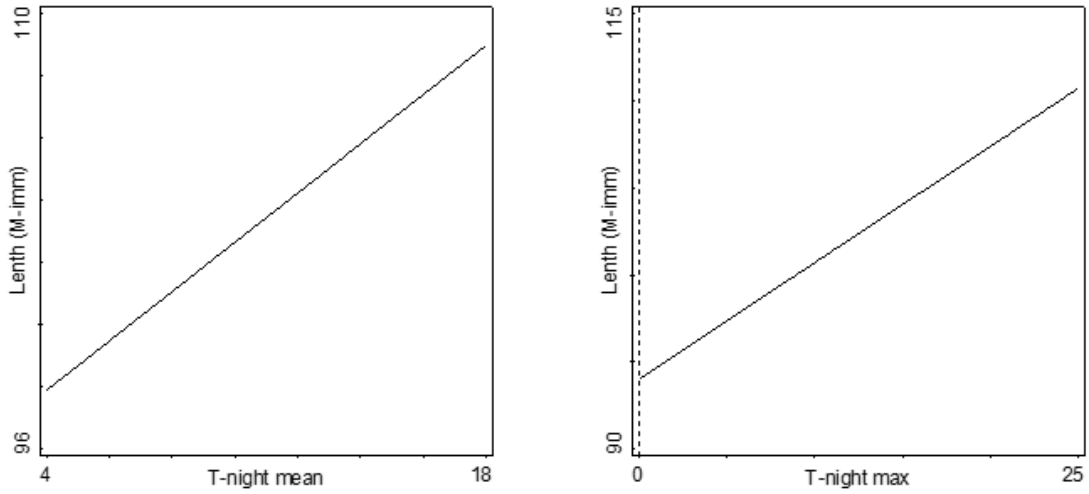
Female immigration

Female emigration

Fig. 3. GLM female immigration and emigration for residence time (days in pond), precipitation, maximum day temperature (T-day max), maximum night temperature (T-night max) and humidity. Only significant variables are shown.
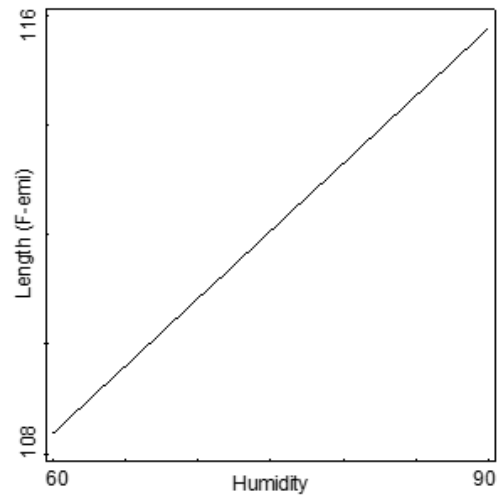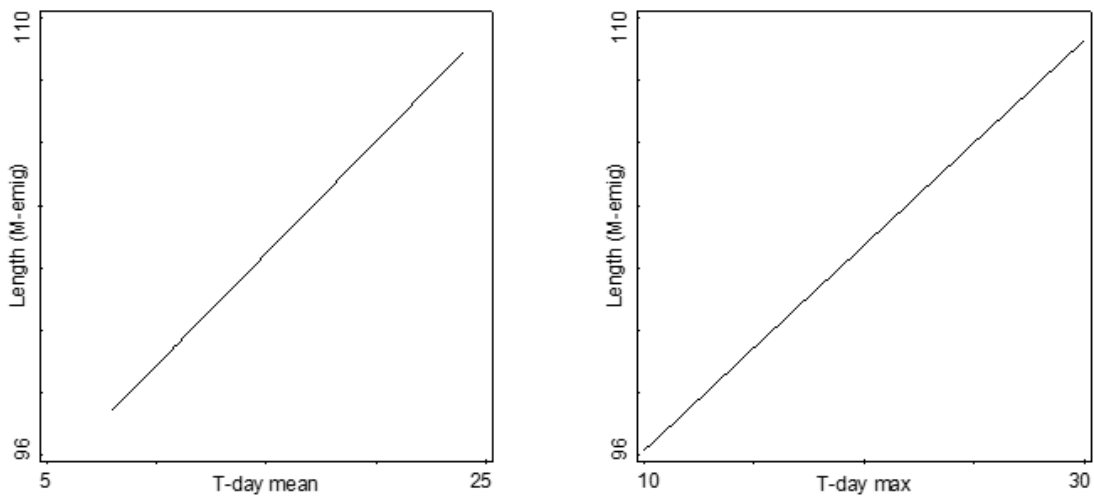
Male immigration

Male emigration

Fig. 4. GLM male immigration and emigration for average night temperature (T-night mean), maximum night temperature (T-night max), average day temperature (T-day mean) and maximum day temperature (T-day max). Only significant variables are shown.
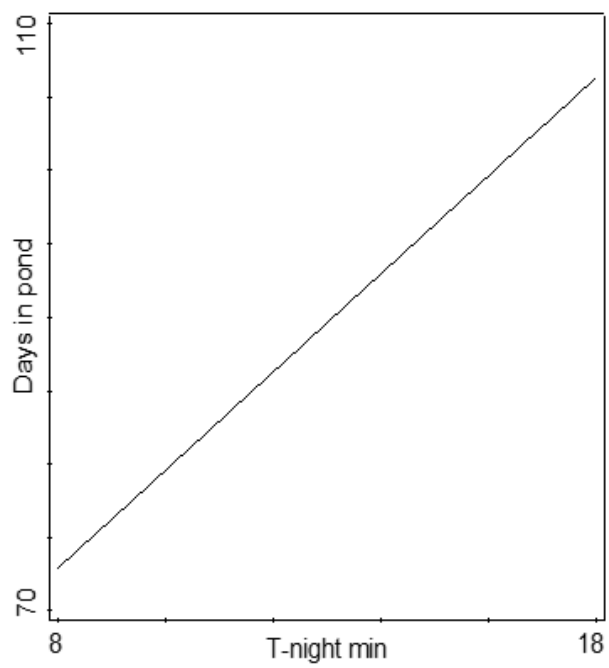
Fig. 5. GLM residence time for minimum night temperature (night min). Only significant variables are shown.