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Photo-Recapture of Great Crested Newts Reveals Extent of Pond Fidelity and Movement Within and Between Ponds

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Ecology

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Abstract

1. Expanding the current knowledge of great crested newts' (*Triturus cristatus*) pond fidelity and movements between ponds is crucial for effective conservation planning and habitat management. Individual differences in great crested newts' pond usage and tendency to enter traps (trappability) may affect research results, hence it is important to understand and quantify the variation within populations.
2. Over a period of three years, differing pond usage and fidelity were examined through a capture-photo-recapture study of 347 newts in three ponds. The ponds were located eight, 48 and 58 meters apart. In this system, individual newts displayed varying degrees of pond fidelity as some individuals returned to the same pond for two consecutive years whereas others switched ponds between breeding seasons. Some also moved between ponds during the breeding seasons. The majority (73.8 %) of the newts were only observed in one pond. However, about a quarter of the newts moved between two or three ponds.
3. A total of 132 pond switches were recorded. Fifty-nine of them were observed within a breeding season, and 73 between breeding seasons. The highest number of pond switches by an individual was three within a season, and the highest number within and between breeding seasons combined was five. I found a significant positive relationship between weight and the number of pond switches, and the newts that moved between the ponds were generally larger than those that stayed put in one pond.
4. I observed substantial differences in individuals' susceptibility to being trapped: of the 347 individuals identified in this study, 99 were only caught once, whereas 32 were trapped eight or more times over the three-season period. The mean number of catches per individual was 3.3, and the highest was 16. I found that heavier individuals were trapped more often than small ones.
5. If frequent trapping induces trap shy (individuals avoiding traps) and trap happy individuals (individuals seeking out traps), this can in turn affect great crested newt population and mortality rate estimates. My results suggest that there is indeed substantial individual variation in the susceptibility to being trapped. I therefore recommend capture-mark-recapture research on great crested newts to avoid excessive trapping, and to consider their differing pond usages by releasing the individuals back into the same area as they were caught.
6. My finding that many newt individuals switch ponds both within and between breeding seasons also highlights the importance of protecting the land surrounding ponds and the corridors between them in addition to the ponds themselves.

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1. Introduction

The great crested newt (*Triturus cristatus*) is a species of conservation concern in Europe, facing habitat fragmentation and loss due to human activities. The species is one six native amphibian species in Norway (Dervo et al., 2021). Since 1980, its habitat has been lost at a rate of 1% per year (Dervo & van der Kooij, 2020), and it is listed as near threatened on the Norwegian red list due to its declining population (Artsdatabanken, 2021).

Akershus county has the highest number of known great crested newt localities in Norway (Dervo et al., 2013). However, many pond habitats disappear, particularly in the agricultural setting, and others become unsuitable due to stocking of fish that eat newt eggs (Dervo et al., 2017; Vedum et al., 2004). Furthermore, the discovery of the chytrid fungus (*Batrachochytrium dendrobatidis*) during surveys in Akershus in 2017 poses a new and potentially grave threat to the great crested newt population (Dervo, 2018) (Info box 1).

As the newt populations decline, fragmentation becomes an additional challenge. In fact, connectivity between populations is so essential that even big populations of great crested newts risk extinction in 50 years if isolated due to demographic or environmental stochasticity (Griffiths & Williams, 2000). Access to multiple ponds is important for feeding, but also for recruitment and genetic exchange between

Info box 1: Amphibian Decline Worldwide

Amphibians are a highly diverse animal group, and the lineage of the modern amphibian spans back at least 250 million years. Despite being one of the oldest animal groups alive, surviving since a time before the first dinosaurs, they are now undergoing worldwide decline (Kolbert, 2014). The IUCN has in recent years found that two in five amphibian species are threatened with extinction (Luedtke et al., 2023). This means that they are the most threatened vertebrate class.

Habitat destruction, both aquatic and terrestrial, are strong drivers of decline. This has been particularly demonstrated in relation to agricultural intensification and arable farming experienced in Europe in the twentieth century (Beebee & Griffiths, 2005). Furthermore, roads separating breeding sites can cause fragmentation and high mortality rates amongst migrating individuals (Beebee, 2013). Chemical contamination further impacts amphibians. For instance, the herbicide atrazine has been found to cause feminization and an unbalanced sex ratio in leopard frogs (*Rana pipiens*) (Hayes et al., 2002).

Species and populations in remote locations are also declining. Though shielded from certain threats, some still face the consequences of climate change, higher UV-B radiation due to the depletion of the ozone layer, disease and the introduction of non-native species (Blaustein & Wake, 1995). The chytrid fungus, which has spread across the globe, has also killed entire species and populations in several instances. Though extremely deadly to some, other species are able to live with it (Beebee & Griffiths, 2005).

The causes of decline are often complex, and each threatened species requires careful attention to reverse its current negative (or declining) trajectory.

populations. Having a network of ponds serves as a safety net in the event of drought, overgrowing (vegetation on the water surface) or environmental pollution in individual ponds (Langton et al., 2001).

Ponds play crucial roles in the great crested newts' life: this is where they breed, their eggs develop, and the hatchlings spend the first few months of their lives before metamorphizing. Newts need permanent fish-free ponds with good sun exposure, ideally near forests. In Eastern Norway, the size of ponds with great crested newts tend to be between 100 and 6000 m^2, with an average water surface area of 1000 m^2 (Dervo & van der Kooij, 2020).

Great crested newts head to the ponds to breed in the spring. The migration is initiated by mean temperatures close to or above four degrees Celsius for three consecutive days and generally happens between March and April (Dervo et al., 2016). There is some variation however, and some individuals arrive as late as mid-May. The migration period generally spans a longer period of time if the population is large and if there are not good overwintering habitats in the near vicinity (Dervo et al., 2016). During the summer, the newts may move onto land at night to feed or to switch ponds, but they generally stay in the pond for the duration of the breeding season before they migrate to land habitats in the late summer (Langton et al., 2001).

Great crested newts depend not only on ponds, but also on suitable land habitats surrounding them. In their terrestrial habitat the newts need areas for long term shelter (in times of drought or for hibernation), daytime refuges, good foraging opportunities and dispersal opportunities (Langton et al., 2001). They often prefer old growth forests with some open patches in the forest canopy as well as a moist herbal understory with a height of 10 - 20 centimeters (Dervo & van der Kooij, 2020). After metamorphization, the juveniles spend their first two or three years on land. These land-dwelling juveniles may walk long distances and are important for dispersal to new ponds (Dervo & van der Kooij, 2020). As mature adults they also spend the late summer and fall foraging on land. Then they seek out places such as wood piles, rock fences or underground tunnels for hibernation. They will however stay relatively close to their breeding pond. Their functional area is set to 300-meter radius around their breeding pond as well as the path to their hibernation spot (Dervo & van der Kooij, 2020). This is not a fixed radius, however. The distance they must travel varies depending on the resource availability and land habitat surrounding their ponds. Seventy percent of the newts overwinter within a hundred meters of their pond, but some may wander as far as 800 meters (Dervo & van der Kooij, 2020).

The great crested newts have been found to display high pond fidelity in several instances. A German study spanning six years, found that 99 % of recaptured adults returned to the pond of first capture (Kupfer & Kneitz, 2000). A study evaluating the success of great crested newt translocation also found a strong tendency for adult great crested newts to leave their new site and head towards their old homes (Oldham &

Humphries, 2000). Yet, there is more to learn about their pond fidelity and several more recent papers point out exceptions to the previously held belief in consistent high pond fidelity. A German study found that several of the 33 identified individuals moved between ponds and out of their open-air laboratory across the span of the studied field season (Haubrock & Altrichter, 2016). They focused on habitat suitability and the effect of decreasing water levels, but a Belgian study explored some of the characteristics of adult individuals with pond infidelity. The authors studied 946 newts across a network of 73 ponds, providing further evidence of two different site fidelity phenotypes: One of high pond fidelity individuals and another of dispersing individuals. They found that individuals with low pond fidelity occupied bigger ponds on average, and that males and bigger individuals were more likely to disperse (Denoël et al., 2018). To the best of my knowledge, there are no studies looking at how the newts move between ponds within the breeding season, nor of the individual characteristics of newts that move between ponds in a Norwegian context. Understanding the movement dynamics of individuals between ponds is crucial for effective conservation planning and habitat management.

The research presented in this thesis provides a rare opportunity to enhance our understanding of individual-based movements and pond fidelity in the great crested newt, particularly in a region at the northern edge of the species' geographic range, where the breeding and growth seasons are shorter than in more southerly populations. The system has been monitored over a three-year period and contains extensive individual-specific data. Individual-based information can be obtained through capture-mark-recapture methodology, which is widespread in wildlife research (Info box 2). Information about individual ID, time and location can be used to investigate the movements and site fidelity of individuals, and to understand the extent of individual variation in movements. Individual-based data can also provide insight into individuals' tendency

Info box 2: Capture – Mark - Recapture

To monitor population trends as well as the effectiveness of mitigation measures, one needs to estimate the population size. A common method to quantify the size of wildlife populations is through capture-mark-recapture studies, which allow us to calculate how many individuals are in a population based on how often the same individuals are recaptured. There are different forms of capture-mark-recapture studies, but the overall premise is the same: to trap and mark the animal, which allows for accurate identification upon recapture.

However, one needs to be careful that these studies do not negatively affect the animals. Tags must not be too heavy or make individuals more visible to predators. Trapping animals too frequently can also negatively impact them by causing stress or interrupting their search for food or mates. The impact on larger animals such as birds or mammals, can be limited by only catching them once to tag them, then "recapturing" them through binoculars, GPS or camera traps.

However, for smaller animals like the great crested newt, physical recapture is required for accurate identification. Fortunately, adult great crested newts have patterns on their abdomens unique to the individual (Hagström, 1973). This means that photo-identification mark-recapture method can be applied, making it unnecessary to attach a physical tag or mark the individuals.

to (re)enter the traps (trappability), and to determine whether susceptibility to being trapped is related to factors such as sex, age, and body condition. This type of information is important both to understand to what extent the newts show fidelity to their pond – and even to their own part of the pond – but also for its implications for conservation and mitigation measures. With individual-level data one can also estimate population size and return rates, a good proxy for survival in the system.

In this study, I used a photo-identification mark-recapture method to investigate the dynamics of great crested newt movement within and between three neighboring ponds over multiple seasons. I also investigated whether movement patterns were influenced by biotic factors like sex, age, and body size. My research questions were as follows:

(1) What is the extent of – and variation in – individual movements (a) between and (b) within ponds?
(2) What is the extent of – and variation in – individual trappability?
    a. Is trappability affected by trapping frequency?
(3) To what degree is individual variation in (a) movement and (b) trappability related to year, sex, maturity level or body size?

The ponds of the study site were in close proximity, within the typical functional area of newts, so I expected some movement between the ponds. I predicted that most individuals would show strong fidelity towards one pond as demonstrated in previous research (Kupfer & Kneitz, 2000), but that some individuals would be more likely to move between ponds. I expected some of the variation to be explained by body size as seen in the study by Denoël et al. (2018), who argued that big adults can afford to spend more energy and have better locomotor capacities. They also found males to be more likely to belong to the low site fidelity phenotype, I therefore expected the same for my research. I predicted that there would be a significant difference between adults and juveniles due to the juveniles' lower body weight. I expected that within-pond site fidelity (trap location) would be weaker than between ponds, as it is easier to move around within the ponds and as newts likely need to utilize different parts of the pond for feeding and breeding. I expected some individual differences in the number of times an individual were captured in a trap, and I predicted that this variation would be related to body size and maturity level as bigger individuals are more active.

2. Methodology

2.1 Study Area

The study area is located in Ås, Norway. The area has a temperate climate, and for the last five years, the municipality experienced a yearly average temperature from 6.2 – 8.2 degrees Celsius and a yearly average precipitation of 648 – 1171 mm (Norsk Klimaservicesenter, 2024). The mean temperature was -1.2 degrees Celsius during the fall and winter months of October to March 2023 and 12.8 degrees Celsius from April to September 2024 (Norsk Klimaservicesenter, 2024).

The precise study area is within the Dyster-Eldor catchment and consists of three ponds (figure 1). Nylenna Gammel is an old 34 m^2 watering pond belonging to a farmstead. The pond is partly shaded and borders a mixed boreal forest. Nylenna Ny is part of the same property and was created in 2016. The 42 m^2 pond is located within a fruit and vegetable garden with good sun exposure and minimal shade. These ponds are eight meters apart, separated by a low-trafficked path. Nylenna Ny and Nylenna Gammel sit at an elevation of 107 and 109 meters above sea-level, respectively (Statens kartverk, 2024). A compensation pond of 677 m^2 at maximal water level was also created by the developers on request from the municipality (the planning authority) in connection with the building of a neighborhood which involved the destruction of forested land habitats (Oslo Tingrett, 2012). The creation of the compensation pond started in 2022 and was completed in March 2024. This new pond, from now on referred to as Triturus, is roughly 48 meters away from Nylenna Gammel and 58 meters away from Nylenna Ny. It sits at an elevation of 131 meters (Statens kartverk, 2024).

During the spring of 2024, the housing developers did work on the circumference of the pond to fix drainage issues. This resulted in high turbidity levels in the water in the beginning of the field season. There was no vegetation in the pond then, but vegetative matter from the Nylenna ponds were transferred to speed up the process and in June the vegetation had started to establish. By the end of the season, there was a solid circumference of vegetation in the shallower areas of the pond as can be seen in figure 4. Species of which included bulrush (*Typha latifolia*), marsh cinquefoil (*Comarum palustre*) and wood club-rush (*Scirpus sylvaticus*).

There are great crested newts and smooth newts (*Lissotriton vulgaris*) in all the ponds. Additionally, common frogs (*Rana temporaria*) have been observed in and by the water. Common frogs have laid eggs in the Nylenna ponds before, but not in recent years. In 2024, they laid a few egg clusters in Triturus. Common toads (*Bufo bufo*) are also in the area, but they are not known to lay eggs in the ponds in this study system.

Various insects are present in the ponds, for instance dragonfly larvae, water striders (Gerridae), backswimmers (Notonectidae) and water beetles (Dytiscidae). Some of these serve as food sources for the newts, but others, such as the water beetles, may hunt adult smooth newts and the newt larvae of both newt species (Langton et al., 2001). There are also leeches (Arhynchobdellida) in the Nylenna ponds.

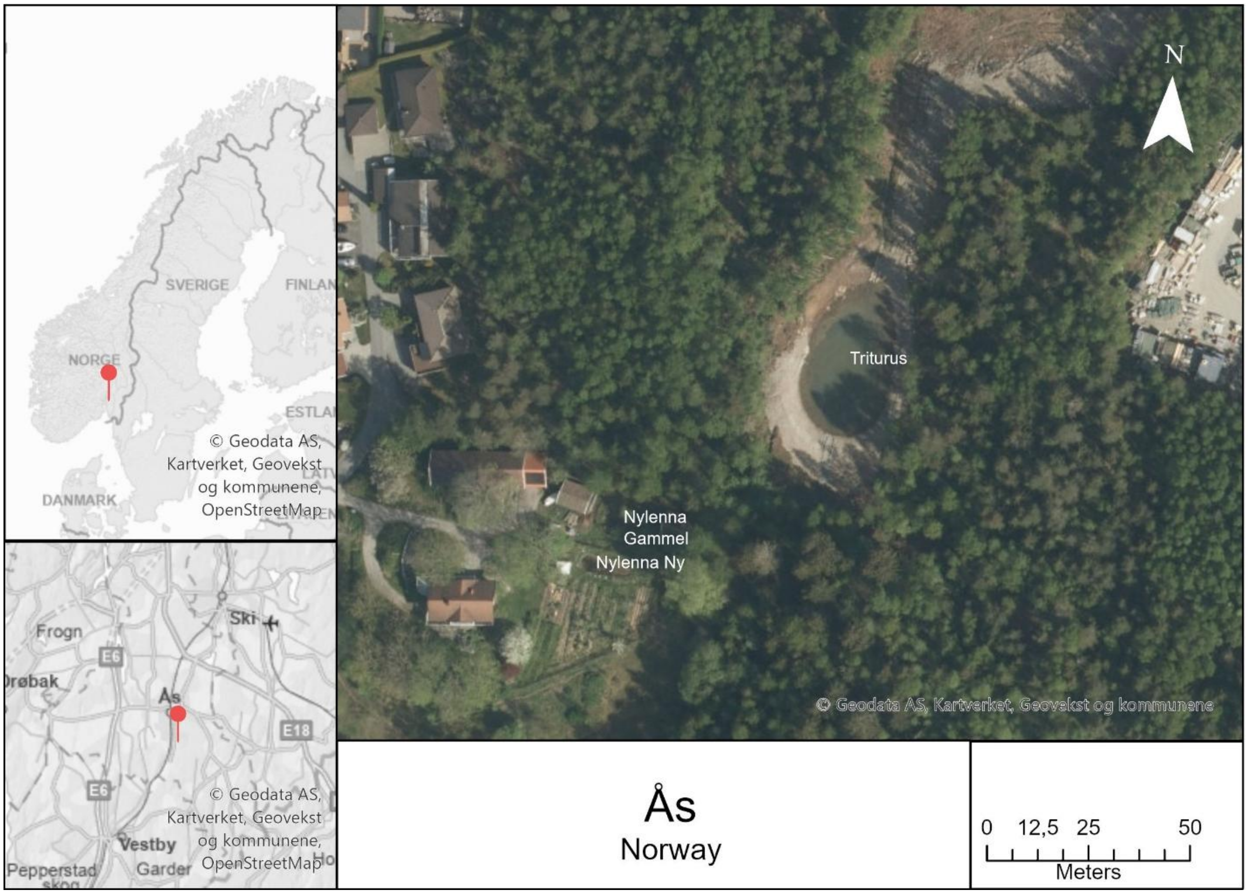

Figure 1: Maps showing where the study site is located and arial photo with the Nylenna ponds to the left and the compensation pond, Triturus, in center with construction work to its right. The map is created in ArcGIS Pro 3.1.0 (Esri, 2023).

Bordering Nylenna Gammel and separating Triturus from the other ponds is a mixed boreal forest with species such as Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), birch (*Betula* sp.), rowan (*Sorbus aucuparia*), goat willow (*Salix caprea*), oak (*Quercus robur*) and common hazel (*Corylus avellana*). An outlet runs out of Triturus in its southern end, providing moist terrain for newts to wander on.

2.2 Data Collection in the Ponds

2.2.1 Investigation of Breeding Activity in Compensation Pond

To determine if there was breeding activity in Triturus, six plastic egg strips imitating vegetation were placed in the pond on 17. April 2024. Some newts were observed in Triturus during the 2023-field season, but whether they used the pond for breeding was not examined at the time. The egg strips were cut from black plastic bags using the procedure described by Freshwater Habitats Trust and weighed down with rocks so they would not drift away (Williams, 2013). The egg strips were removed at the end of the season.

2.2.2 Investigation of Individual Differences in Pond Usage and Site Fidelity

To investigate individual differences in site fidelity and movements amongst the great crested newts, and to quantify the number of unique individuals and return rates in the three ponds, I carried out photo-identification mark-recapture surveys. Thus, the newts were not physically marked but identified through photographs of their unique belly patterns. Capture-recapture surveys were conducted using floating Ortmann's funnel traps (Drechsler et al., 2010).

The traps in Nylenna Gammel and Nylenna Ny were made of 15-liter buckets (figure 2A), whereas the ones in Triturus were made of 10-liter buckets (figure 2B). The funnel openings were from the tops of 1.5-liter soda and spray bottles. The 15-liter traps had five openings, and the 10 liter-traps had three openings. The traps all had drainage holes and floating objects for the safety of the newts and potential mammal bycatch. There were five traps in each Nylenna pond (figure 3) and 14 traps in Triturus (figure 4).

Figure 2A and 2B: Ortmann's funnel traps used in the Nylenna pond (A) and Triturus (B). Illustration made by Judith Aarseth Tunstad and edited in Adobe Photoshop 26.4.1 (Adobe, 2025).

The ponds were surveyed weekly from 14. April 2024 to 13. June 2024. Data collection of Nylenna Gammel and Nylenna Ny was done on Mondays, and Triturus on Thursdays. The traps were placed into the pond at around 17:00 or 18:00 the evening before and recollected the morning after starting at 09:00 or 10:00. The capture-recapture data of the Nylenna ponds were supplemented with data collected twice a week from 23. April 2022 to 12. June 2022 and weekly from 23. April 2023 to 13. June 2023 (unpublished data provided by Katrine Eldegard). These data were collected by Katrine Eldegard and other students.

Figure 3: Trap placements for Nylenna Ny (left) and Nylenna Gammel (right). Figure made in Adobe Photoshop 26.4.1 by Judith Aarseth Tunstad (Adobe, 2025). Drone photo by Anders Gunnar Helle (2024).

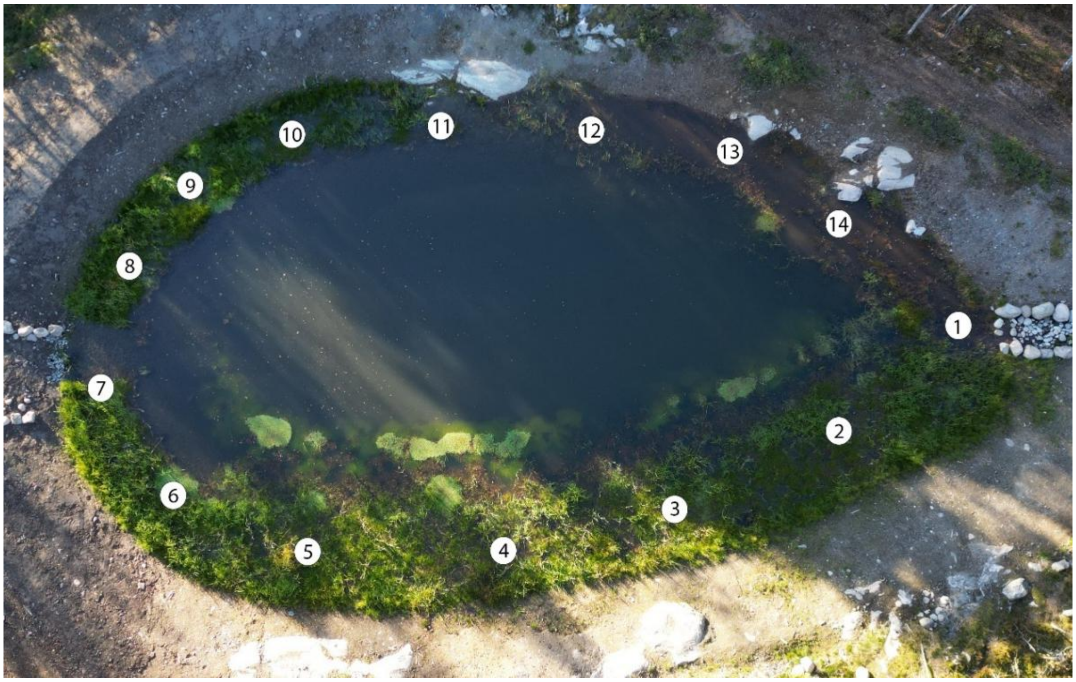

Figure 4: Trap placements for Triturus. Figure made in Adobe Photoshop 26.4.1 by Judith Aarseth Tunstad (Adobe, 2025). Drone photo by Anders Gunnar Helle (2024).

The traps were processed one by one, so the newts could be released back into the water quickly. The smooth newts were counted by sex and released, but smooth newt data is not presented in this thesis. The great crested newts were also sorted by sex. Then, to avoid overheating, processing was carried out in a shaded gazebo. VWR Nitrile gloves were worn as the newts are vulnerable to contamination (Langton et al., 2001). These were also wet with pond water to not damage their skin. Females were processed first, one newt at the time.

The newts were placed on a sieve with a cloth beneath so excess water would run off. Afterwards, they were moved to a plastic container and weighed with a New Horizon professional-mini digital scale, rounded to the nearest 0.1 decimal. The newts were placed in a see-through container filled with filtered pond water. The containers were not filled up all the way up as this could put too much pressure on the newts and cause them to throw up. Photos of the newt abdomens were captured using an Olympus Tough TG-6 camera from approximately 30-centimeter distance. Then the newts were released back into the pond at place of capture.

The ponds had HOBO Pendant Temperature data loggers (UA-001-64) recording the water temperature every ten minutes throughout the season. They had an uncertainty of ± 0.53 degrees Celsius (Onset, 2025). There were two loggers in each pond. The loggers floated at 30-centimeter depth, which is where the newts are the most active (Dervo & van der Kooij, 2020; Dolmen, 2008). Unfortunately, the loggers in Triturus were lost, likely due to a slight current by the outflow of the pond. Weather parameters such as temperature, cloud cover and wind speed, using the Beaufort scale, were noted on site. Nylenna Ny and Nylenna Gammel both had measuring sticks placed into the pond bottom with its top in line with the pond surface at spring levels. The water levels monitored across the season by measuring how many centimeters from the top the water surface was. The water levels in Nylenna Ny are not fully natural as the landowners add dechlorinated water if the summer is hot and dry.

2.2.3 Investigation of Trappability and Trapping Methods

To assess whether trapping itself might influence newt behavior, I looked at trapping frequencies and individual newt catches. The data collection methods in 2022 and 2023 were mostly similar to 2024, but with a few key differences. In 2022 the newts were surveyed twice a week, whereas in 2023 and 2024 they were surveyed once a week. In 2022 and 2023 the newts were processed by trap but thereafter gathered in one big container and released in the same spot regardless of trap capture location, but in 2024 they were released by their specific capture location. I only used data from the Nylenna ponds when comparing yearly differences, because the Triturus pond was not monitored consistently until 2024.

On 14. May 2022 six individuals captured in Nylenna Ny were released in Nylenna Gammel by mistake. In 2024, the newts were released where their traps had been except for on 20. May 2024 when researchers from Norwegian Institute for Nature Research (NINA) stopped by to take tissue samples of the newts and gathered all the Nylenna Ny individuals trapped that day in one container.

2.3 Data Collection in Terrestrial Habitat

2.3.1 Investigation of Juvenile Migration and Late Summer Pond Usage

To gain better understanding of how the newts use the ponds after the breeding season and to learn more about juvenile recruitment and migration, I installed drift fences and pitfall traps within two meters of the water surface. Pitfall traps were present between 17. July 2024 and 07. October 2024 by Nylenna Ny and Nylenna Gammel. Triturus was not surveyed as there were concerns of impacting the newly established pond circumference when digging in the fences.

Most adults were expected to have left the pond already, and the pitfall traps were placed in time to investigate the number of juveniles that hatched, survived the summer season and migrated to land in late summer-fall. The first larvae were observed in the ponds on 20. May 2024. The larvae spend 2.5 months in the pond before metamorphizing (Dervo & van der Kooij, 2020). Hence, the start of the pitfall trap data collection on 17. July 2024 would catch all migrating juveniles, also early developing individuals. However, the data collection operates with the assumption that the juveniles do not overwinter in the pond or on land inside of the fences.

The drift fences leaned towards the ponds so that the newts could not climb over them when leaving the pond, but also so they could return to the ponds if they wished to. The bottom sections of the fences were dug 10 - 20 centimeters into the ground, and in places where the ground did not allow digging, stones and dirt covered the fences to prevent the newts from escaping. As seen in the figure below, four pitfall traps were placed around Nylenna Gammel and Nylenna Ny, each with less than ten meters between each trap.

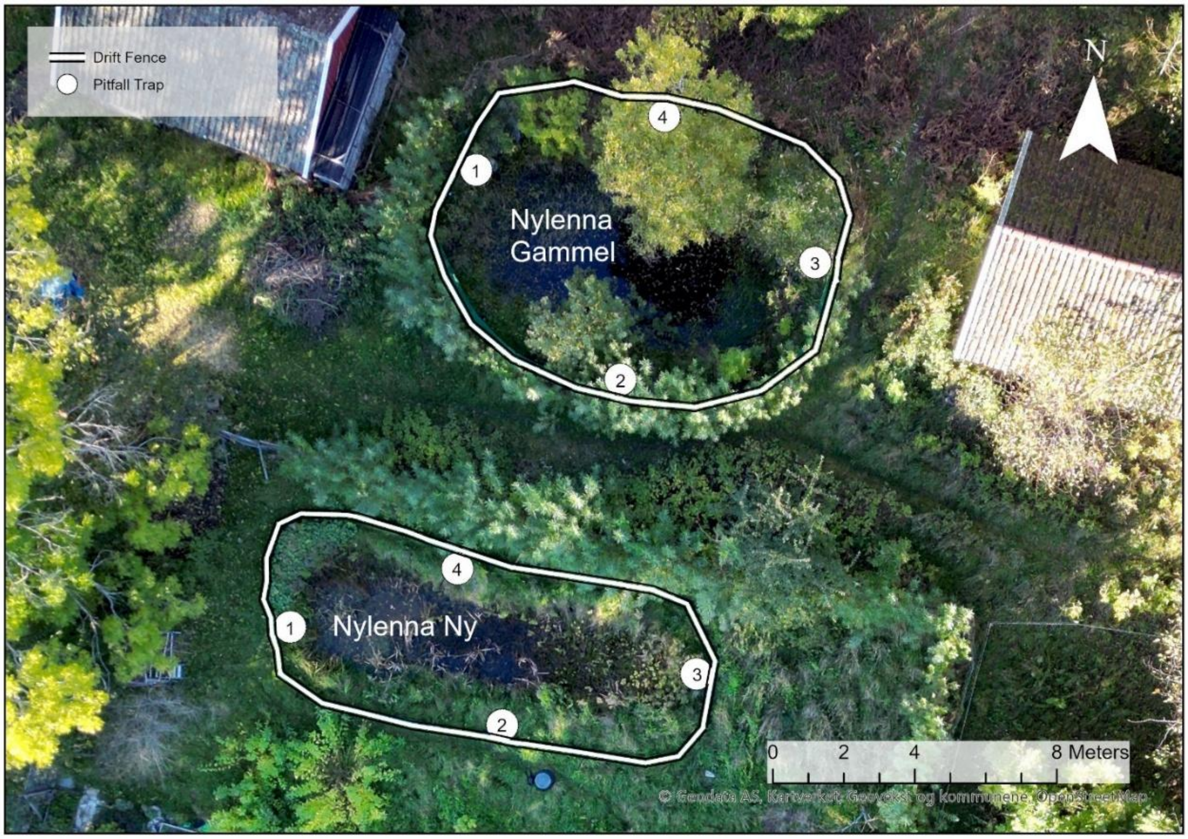

Figure 5: Pitfall trap locations and drift fences. The figure is made in combination of Adobe Photoshop 26.4.1 and ArcGIS Pro version 3.1.0 by Judith Aarseth Tunstad (Adobe, 2025; Esri, 2023). Drone photo by Anders Gunnar Helle (2024).

The pitfall traps were made of empty 3-liter plastic containers dug into the ground. The lids had a hole in the center so the newts would fall into the trap but could not climb out. The trap was filled with water from the pond and equipped with a floating object, which ensured that small mammals could jump out if they were trapped and the newts could rest if they wanted to. A roof covered the trap to prevent avian predation (figure 6). The traps were checked every morning, and if a great crested newt was caught it was weighed and photographed as previously described. It was then released on the other side of the fence so it could continue its migration.

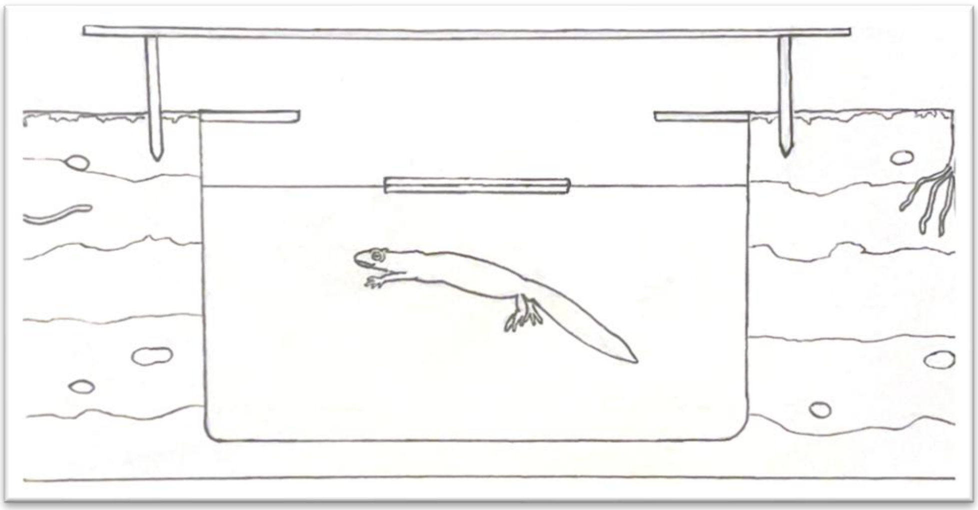

Figure 6: The design of the pitfall traps. Illustration by Judith Aarseth Tunstad.

2.4 Digital Data Collection and Processing

2.4.1 Identification of Individuals

Adult great crested newts have yellow abdomens with black spots in a pattern that is unique for each individual (figure 7). Additional small spots may appear over several year periods, but the patterns do not change much over time. Photos of the abdomen patterns can therefore be used to visually identify recaptured newts or to determine if it is a new individual (Hagström, 1973). Hence, no tags or marks were needed or used for this capture-photo-recapture study.

Figure 7A and 7B: The newt, Narcissa, captured on two different occasions. Pictures by Vera Gano Mønnich and Judith Aarseth Tunstad (2024).

For each sampling day, the most legible photo of each newt was compared to photos of previously caught newts. These were sorted by pond and date in an excel sheet, which made it possible to determine if a newt was caught for the first time or not. Each newt was assigned a unique name and ID number the first time it was caught.

2.4.2 Statistical Analysis

Data wrangling and statistical analyses were done with R Markdown in RStudio version 2023.06.1 (R Core Team, 2023). I troubleshot code using AI (ChatGPT), but any use of AI was always based on my thoughts and I did not use it to guide the direction of my thesis.

I compiled each individual's capture history, and I did an open system Jolly Seber model in R using the FSA package for a simple estimation of the population sizes in 2024 (Ogle et al., 2025).

I did one-way ANOVAs and Tukey post-hoc tests to examine the differences in weights of individuals present in different ponds. For statistical analysis of the relationships between different factors, I used the MASS (Venables & Ripley, 2002) and glmmTMB packages (Brooks et al., 2017). I did model validation with the DHARMa package (Hartig, 2024) with visual examination of the residual distribution, Q-Q plots and fitted values versus residuals. I fitted generalized linear models (glm), with log link function, assuming a Poisson error distribution, to analyze a) the number of traps individuals were caught in by sex, b) the number of traps individuals were caught in by maturity level and c) the influence of weight and sex on the number of observed trap switches per individual newt within a season.

Due to overdispersion, I fitted a negative binomial model instead of Poisson for the relationship between number of catches and the newt individual's mean weight, sex and year of capture. The residual diagnostics through DHARMa still indicated some significant overdispersion, but attempts at more complex alternative models (e.g., zero-inflated or interaction terms) did not improve the fit. Hence, I stuck with the original while mindful of its limitations. It was not possible to add individual newt IDs as random variables due to the high number of single captures.

When looking at the newts' weight and movement patterns, the response variable was a count variable, but due to few cases of three pond switches per season, I divided the newts into three categories: 0, 1 and ≥ 2 pond switches and performed ordinal logistic regression of the influence of weight, sex and year on the number of pond switches. I used a binomial logistic regression to examine how pond and year influenced the probability of a newt's return.

Finally, I did a Wilcoxon signed rank exact test to compare the total number of unique newts caught on the first versus second days of weekly data collection events of 2022.

3. Results

Over the three-year period, a total of 347 unique individuals were caught in the floating Ortmann's funnel traps. 161 were females and 171 were males. There were 18 juveniles, but three of these were recaptured as adults in 2023 or 2024. An additional 11 new juveniles were caught in the pitfall traps in the late 2024-summer season.

As seen in table 1, the highest catch of great crested newts was in Nylenna Ny with 146 unique individuals in 2024. Nylenna Gammel had its highest catch in 2022 with 85 unique newts, followed by a decline in 2023 and a resurgence of individuals in 2024. Triturus had the lowest catch of them all.

Table 1: The number of unique great crested newt individuals caught in the different ponds and regardless of pond by year. The table only includes catch from the floating Ortmann's funnel traps, and not the pitfall traps.

	Nylenna Gammel	*Nylenna Ny*	*Triturus*	*All ponds*
2022	85	100	NA	158
2023	49	131	NA	168
2024	76	146	48	251
All years	150	244	48	347

The population size for the Nylenna ponds (both ponds combined) was estimated to be at 201 individuals with a standard error of 24 on 06. May 2024. This was the second highest population estimate of the 2024 season, but a more cautious estimate than the highest of 270 individuals with a large associated standard error of 64 (Figure S1, Supplementary Material). There were not enough recaptures in Triturus to get a good population size estimate (Figure S2, Supplementary Material).

The return rates for Nylenna Ny were higher than for Nylenna Gammel (table 2). The number of returns regardless of pond was higher than the pond-specific return rates added together. In 2023, twenty individuals returned from the previous year but were only observed in the other pond (17 of which moved from Nylenna Gammel to Nylenna Ny). Two individuals present in both ponds in 2022 were also present in both ponds in 2023. In 2024, the overall return rate was also higher than the pond-specific return rate as twenty individuals had switched ponds for the season: six moved from Nylenna Gammel to Nylenna Ny, eight the other way around, and a further six individuals returned for the season but had moved to Triturus. One individual present in both Nylenna ponds in 2023 was also present in both of them in 2024. For individuals present in 2022, not captured in 2023, but recaptured in 2024, the overall return rate was higher than the pond-specific return rates as three individuals switched from Nylenna Gammel to Nylenna Ny and nine had switched from a Nylenna pond to Triturus. One individual was captured in both Nylenna ponds in both 2022 and 2024.

Table 2: The return rates of the newts in Nylenna Ny and Nylenna Gammel as well as the return rates regardless of pond.

	Nylenna Gammel	*Nylenna Ny*	*Regardless of Pond*
Return Rate 2023	23.5 % (20/85)	51.0 % (51/100)	56.3 % (89/158)
Return Rate 2024	44.9 % (22/49)	50.4 % (66/131)	63.7 % (107/168)
Newts returning 2023, also returning 2024	40.0 % (8/20)	54.9 % (28/51)	68.5 % (61/89)
Present 2022, absent 2023, returning 2024	12.9 % (11/85)	12.0 % (12/100)	21.5 % (34/158)

Between the Nylenna ponds, a newt was more likely to return to Nylenna Ny than a newt was to return to Nylenna Gammel (table 3).

Table 3: The results of a binomial logistic regression of the influence of pond and year on return rates in the Nylenna ponds. Nylenna Gammel and the return rates of 2023 were the reference levels.

Explanatory variable	*Value*	*Std. Error*	*Z*	*P*
Pond (Nylenna Ny)	1.498	0.189	7.931	<0.001
Return Rate (2024)	-0.150	0.188	-0.794	0.427

3.1 Movements by Individuals *between* Ponds

Of the 347 individuals caught over the three-year period, 256 (73.8 %) were only caught in one pond (figure 8).

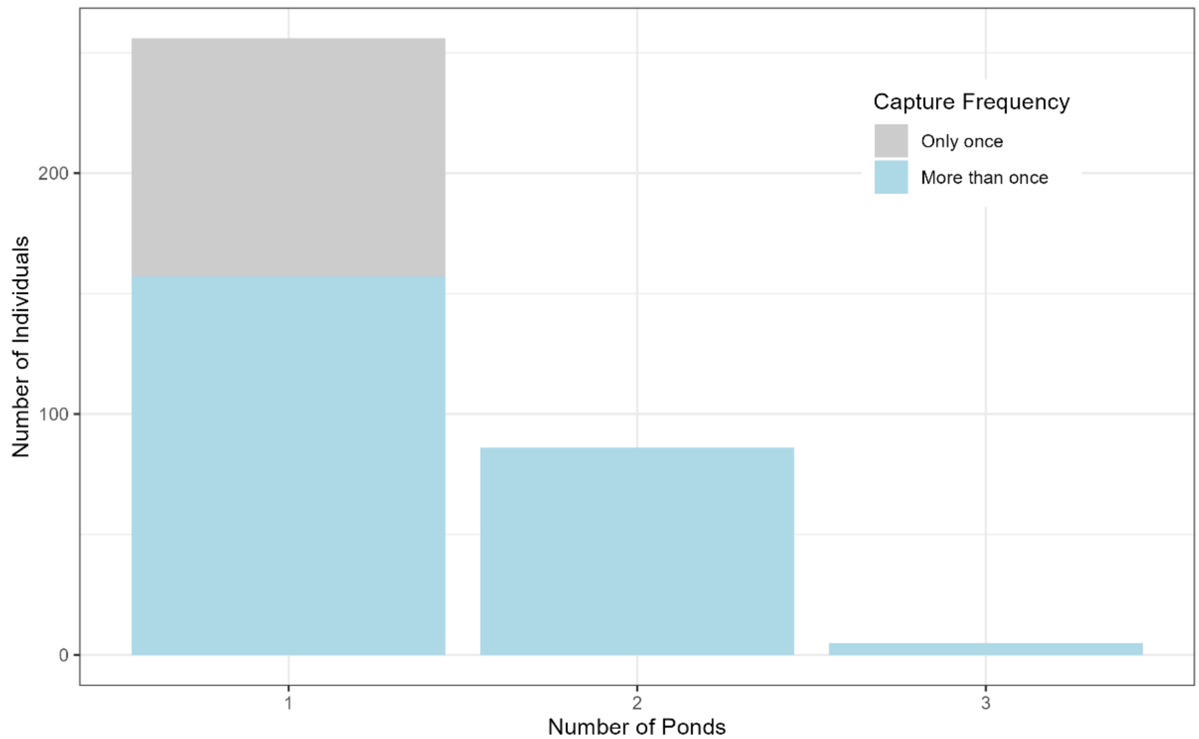

Figure 8: The number of ponds individual newts were caught in across field seasons. The grey portion of the first bar represents the individuals that were only caught once.

Ninety-nine of the individuals caught in one pond were only trapped once. The majority of the newts stayed in one pond across seasons, but 86 (24.8 %) were caught in two ponds and five (1.4 %) in all ponds.

Figure 9 shows that most of the overlap in newt individuals was between Nylenna Gammel and Nylenna Ny. In fact, there were more individuals appearing in both these two ponds than there were individuals solely staying in Nylenna Gammel.

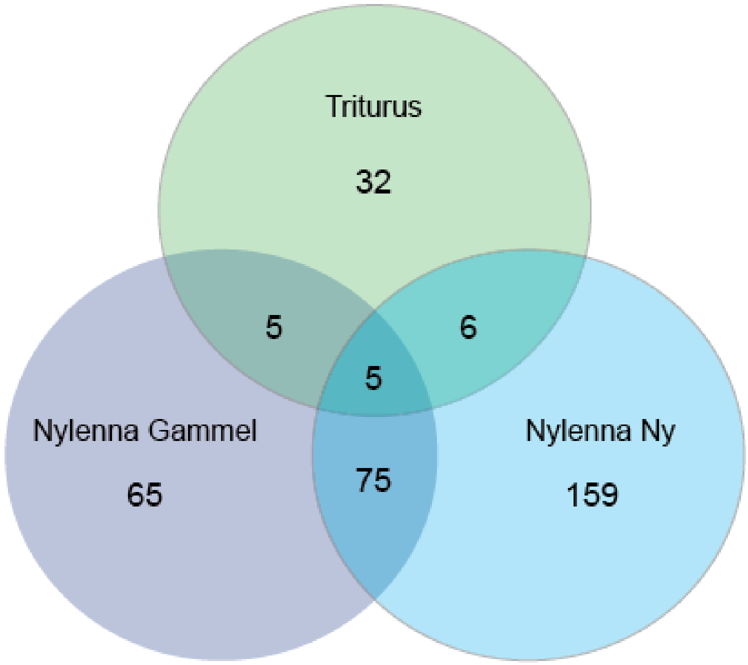

Figure 9: Venn diagram of the newt individuals' pond presence showing the overlap in certain individuals between ponds.

Of the individuals caught in more than one pond, 51 were females and 40 were males. No juveniles were caught in multiple ponds (figure 10).

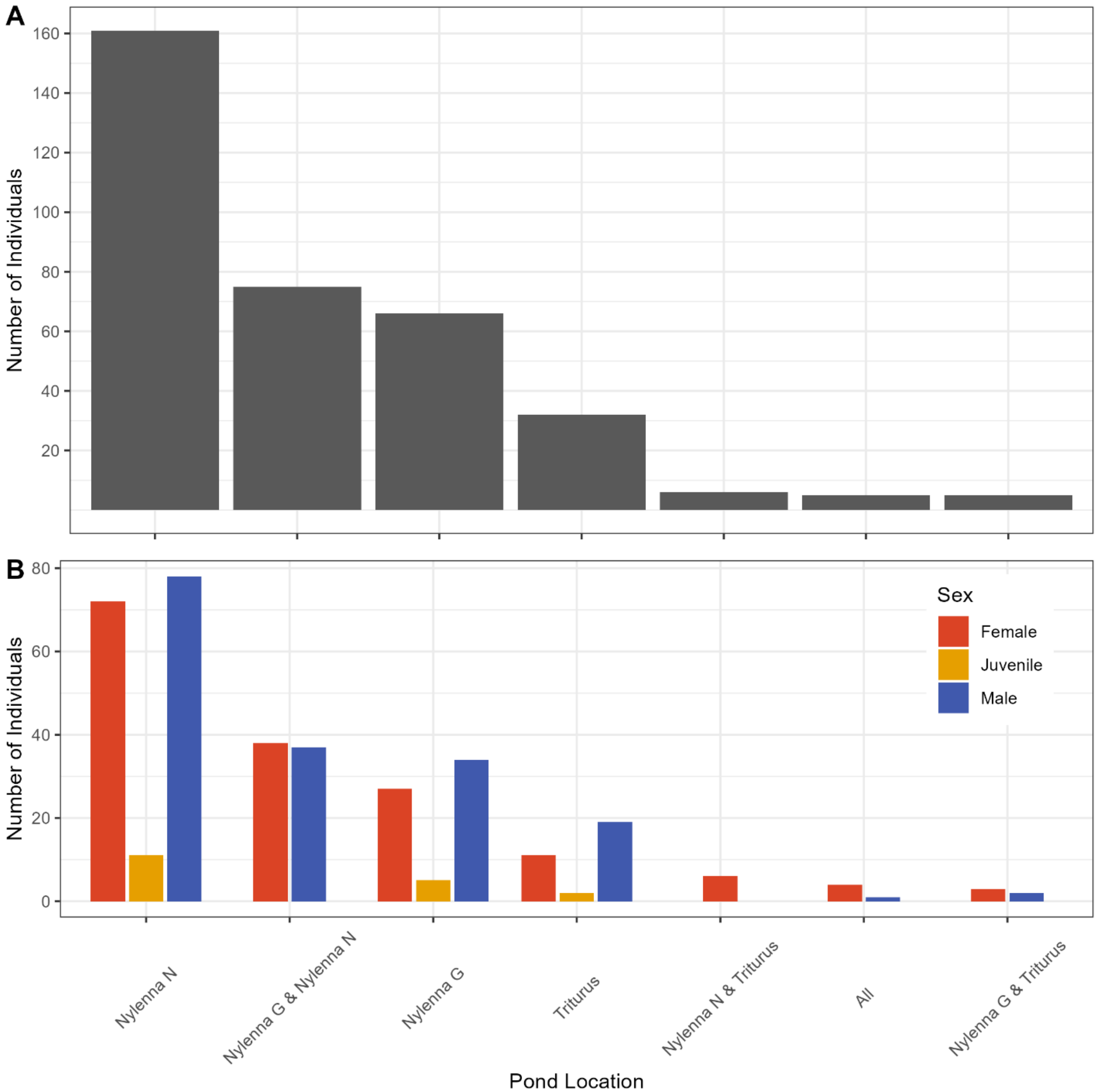

Figure 10: The pond or ponds individuals were caught in across the three years where (A) displays all individuals combined (B) displays individuals divided by sex and maturity level.

A total of 132 pond switches were observed: 59 of these were within a field season (figure 11) and 73 were between seasons (figure 12). The number of pond switches between Nylenna Ny and Nylenna Gammel was equal within (58) and between (58) seasons. However, the observed pond switches from the Nylenna ponds to Triturus all happened prior to the start of data collection there, except one that happened during the 2024-field season.

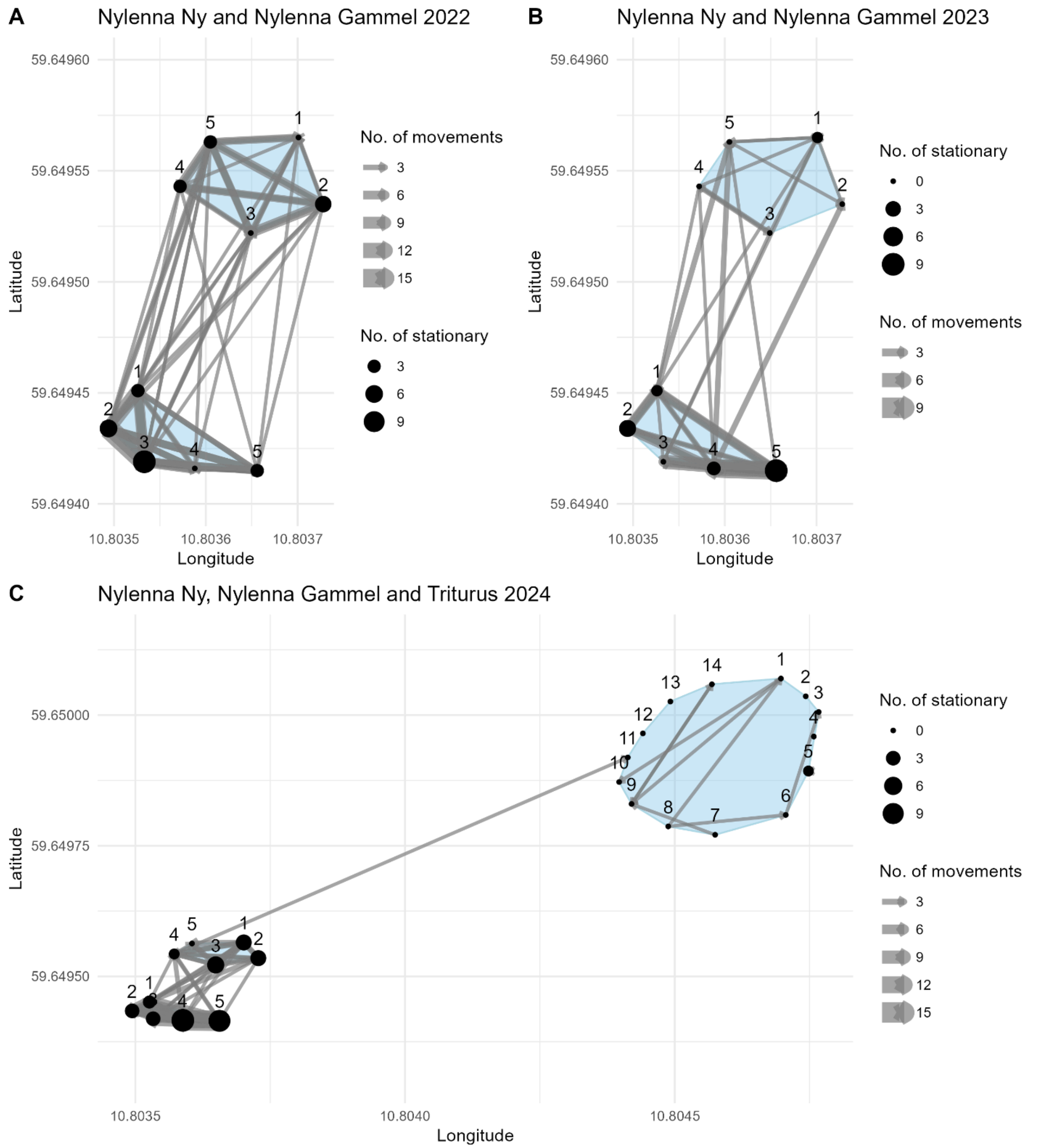

Figure 11: Visualization of within-season movements between ponds and traps in (A) 2022, (B) 2023 and (C) 2024. Line width is proportional to the number of movements observed. Larger points indicate recaptures of newts that did not move between traps, with point size proportional to the number of such recaptures. From the bottom left and up the ponds are Nylenna Ny, Nylenna Gammel and Triturus.

Although a few individuals were found in all three ponds, individuals did not move between more than two unique ponds within a single season. Some individuals moved between the Nylenna ponds multiple times though.

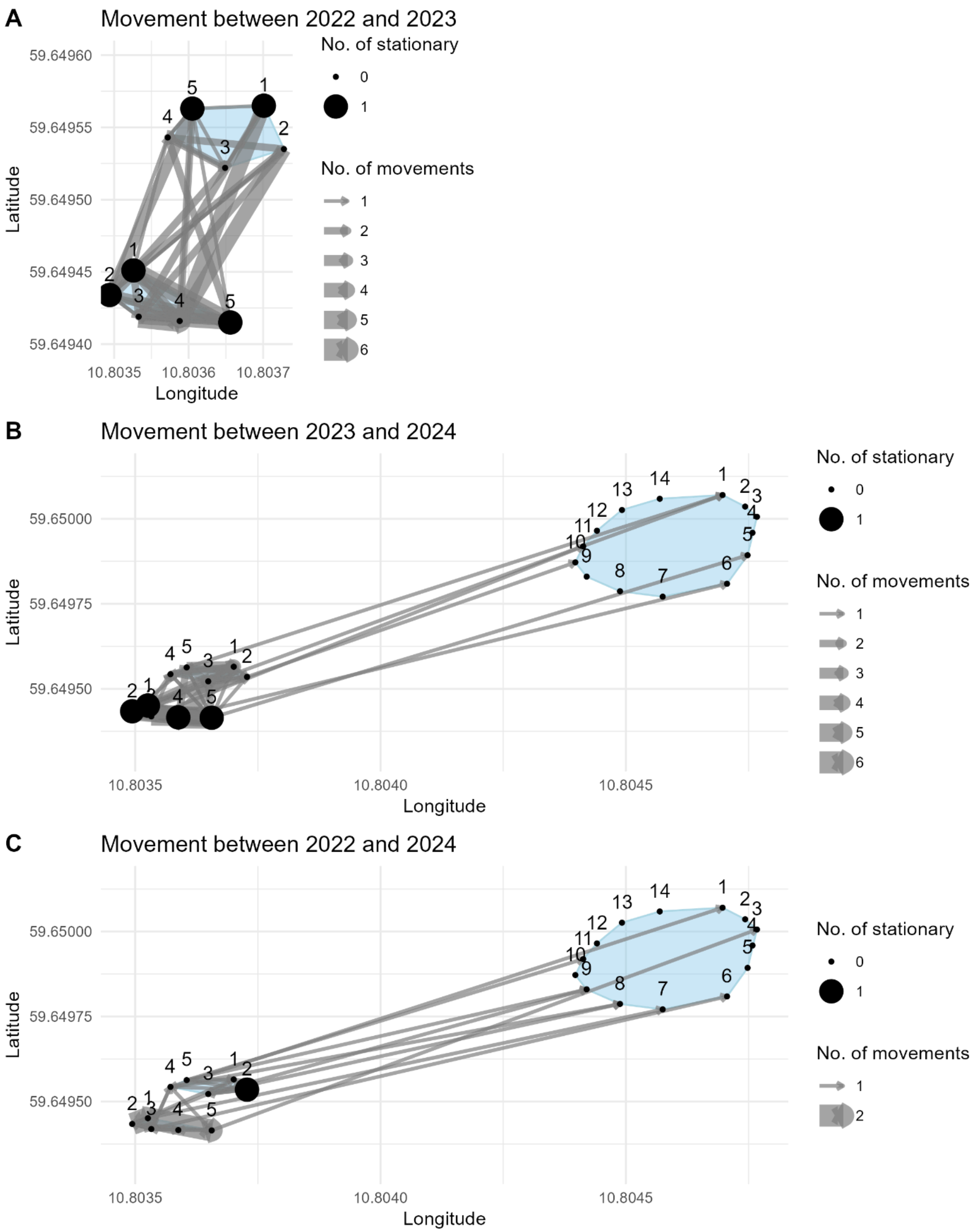

Figure 12: Visualization of between-season occurrences/non-occurrence of pond switches, that is, a switch in location between the last capture of an individual within a season, and the first location where the same individual is captured in the subsequent season. (A) shows switches between 2022 and 2023, (B) shows switches between 2023 and 2024, and (C) shows the switch in location for individuals present in 2022, absent in 2023, but returning in 2024.

3.1.1 Recruitment (Movement) to Triturus Pond

During the 2024 season 48 adult individuals were caught in the newly established Triturus pond. No newts were caught on the first day of data collection when the turbidity levels of the pond were high. The water had cleared up on 24. April 2024 and two days later the first great crested newt was trapped.

Overall, thirty-two newts (66.7 %) were caught for the first time, that is, they had not been captured in the Nylenna Ny or Nylenna Gammel ponds before. Nineteen of them were males, two were juveniles and eleven were females. However, sixteen newts (33.3 %) were recaptured individuals from Nylenna Ny or Nylenna Gammel. Five of these sixteen individuals had previously been captured in both of the Nylenna ponds. All observed pond switches to Triturus, except one, occurred before data collection began in 2024.

The average body weights of the individuals that had switched ponds, and that had been previously caught in Nylenna Gammel (9.5 g ± 0.9), Nylenna Ny (8.2 g ± 1.3 SD) or both (10.8 g ± 2.4 SD) were higher than for individuals that had never been observed to switch pond (7.0 g ± 1.9 SD). These differences were statistically significant between stationary Triturus individuals and individuals that had previously been in Nylenna Gammel or all ponds (Tukey HSD, $p = 0.035$ and $p < 0.001$, respectively), but not for the ones that had been in Nylenna Ny ($p = 0.439$).

Across all the individuals in Triturus, the newts had significantly lower weight than the ones in Nylenna Gammel and Nylenna Ny (Tukey HSD, $p = 0.006$ and $p < 0.001$, respectively). There was no significant difference between the Nylenna Gammel and Nylenna Ny individuals however ($p = 0.575$). The newts in Triturus had a mean weight of 7.8 g ± 2.2 SD, whereas the individuals in Nylenna Ny were 9.2 g ± 2.5 SD and 8.9 g ± 2.5 SD in Nylenna Gammel for the same year.

Additionally, egg strips placed in Triturus confirmed that the newts that had moved to this newly established compensation pond were using the pond for breeding as eggs were laid on them. Furthermore, several hatchlings were observed, and two juveniles were caught in the middle of May.

3.1.2 Body Weight, Sex and the Number of Pond Switches

The highest number of pond switches by an individual was three within a season, and the highest number within and between breeding seasons combined was five. The individuals moving between ponds one or two times within a season, in one case three, had higher mean weights than those that stayed put in one pond the whole season (figure 13, table 4). The results of the ordinal logistic regression showed that by every gram increase in weight, the odds of being in a higher pond switch category increased by about 16.3 % for females. There was a marginally significant interaction between weight and sex, suggesting that the influence of weight was stronger for males as they got bigger: light males switched less than light females, but heavy males switched more than heavy females. According to the model, the odds of being in a higher pond switch category increased by about 40.3 % for male newts for every added gram.

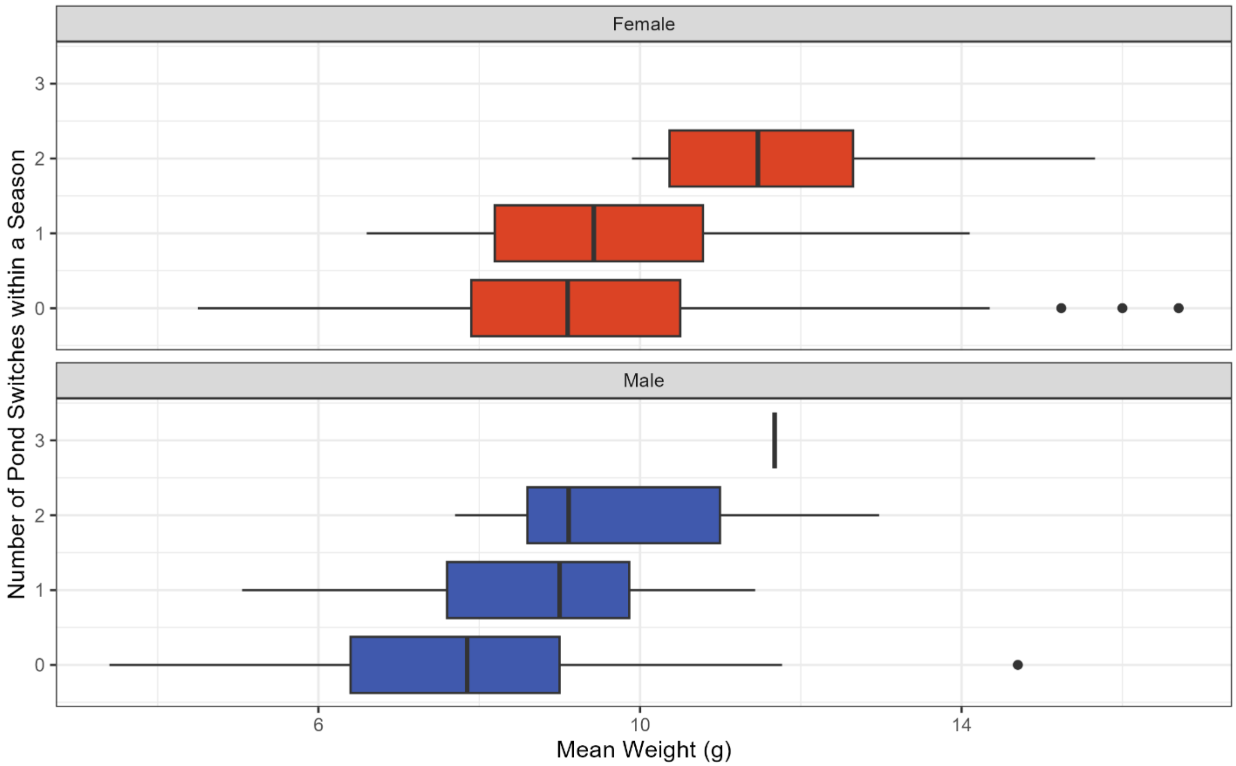

Figure 13: The number of pond switches made by each newt within a season, analyzed by sex and mean weight. This graph includes data from all years.

Table 4: The results of an ordinal logistic regression of the influence of mean weight, sex and year on number of pond switches. The response variable (number of pond switches) was divided into three categories: 0, 1 and ≥2.

Explanatory variable	*Value*	*Std. Error*	*T*	*P*
Mean Weight	0.151	0.068	2.24	0.025
Sex (Male)	-1.709	1.047	-1.632	0.103
Year (2023)	0.168	0.290	0.577	0.564
Year (2024)	0.250	0.267	0.936	0.349
Mean Weight × Sex (Male)	0.191	0.114	1.672	0.095

3.2 Movements by Individuals *within* Ponds

Across three years (2022-2024), the newts were on average caught in 2.47 (± 1.57 SD) different funnel traps. The highest number of different traps for one individual was nine across three years and five within a season. Looking at the trap catches for 2024 – when all individuals were released at the same place in the pond as where they were caught – most newts were only caught in one or two traps (figure 14).

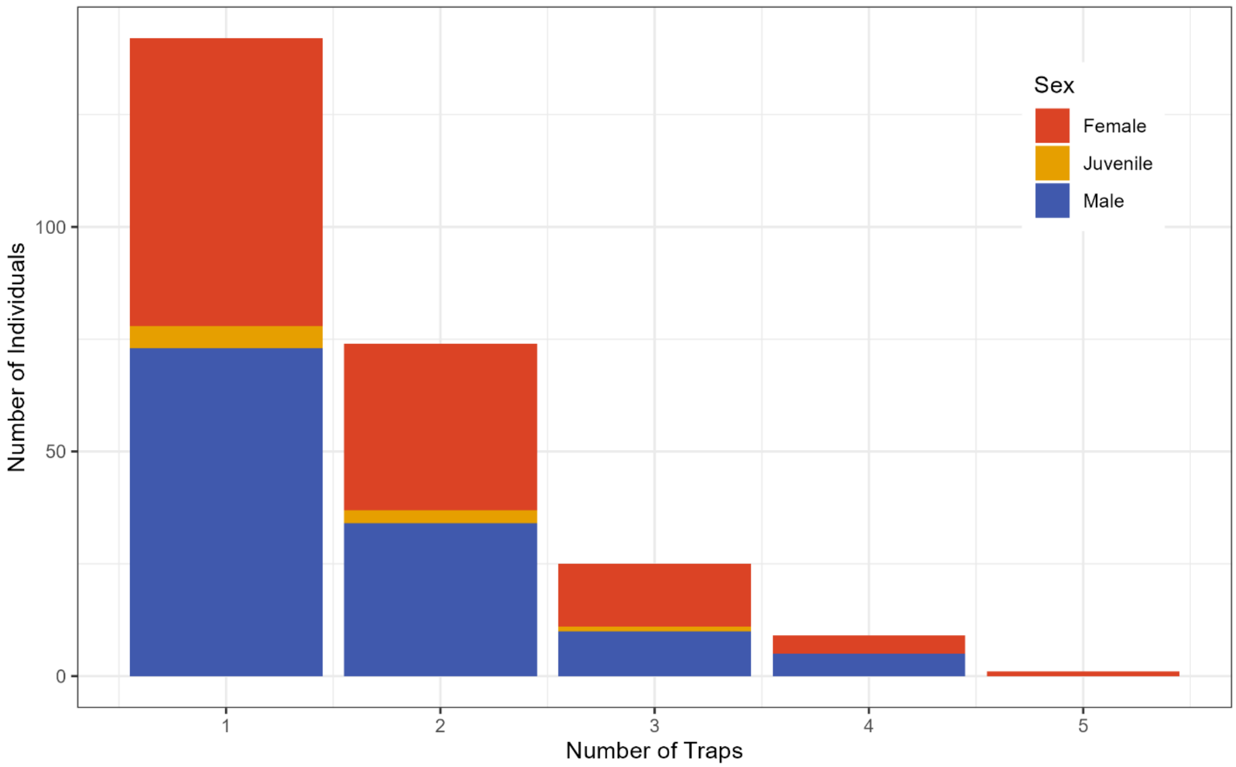

Figure 14: The number of traps the newts are caught in during the 2024-season.

I found no significant difference between males and females (table 5) or between adults and juveniles (table 6) in the number of traps they were caught in.

Table 5: The results for the glm with poisson distribution of the influence of sex on the number of traps the individual newts were caught in during the 2024 season. Female was the reference level.

Explanatory variable	*Estimate*	*Std. Error*	*Z*	*P*
Intercept	0.516	0.071	7.313	<0.001
Sex (Male)	-0.068	0.101	-0.669	0.504

Table 6: The results for the glm with poisson distribution of the influence of maturity level on the number of traps the individual newts were caught in during the 2024 season. Adult was the reference level.

Explanatory variable	*Estimate*	*Std. Error*	*Z*	*P*
Intercept	0.482	0.051	9.550	<0.001
Maturity Level (Juvenile)	-0.040	0.272	-0.149	0.882

3.2.1 Body Weight and the Number of Trap Switches

There was a significant positive relationship between a newt's weight and the number of trap switches it made (figure 15, table 7). Note that the response variable 'number of times an individual was caught in a different trap from the last' only accounted for whether a newt was recaptured in a different trap from the last capture but does not say whether a newt was moving between the same two traps or multiple traps. The results showed that for every added gram, a newt was expected to make 15.8 % more trap switches. The relationship between number of trap switches and body weight did not depend on sex (sex × weight interaction: $p = 0.705$) or year (year × weight interaction: $p = 0.787$ for 2023 and $p = 0.430$ for 2024). The model also indicated that the newts moved more between traps in 2022 than the following years.

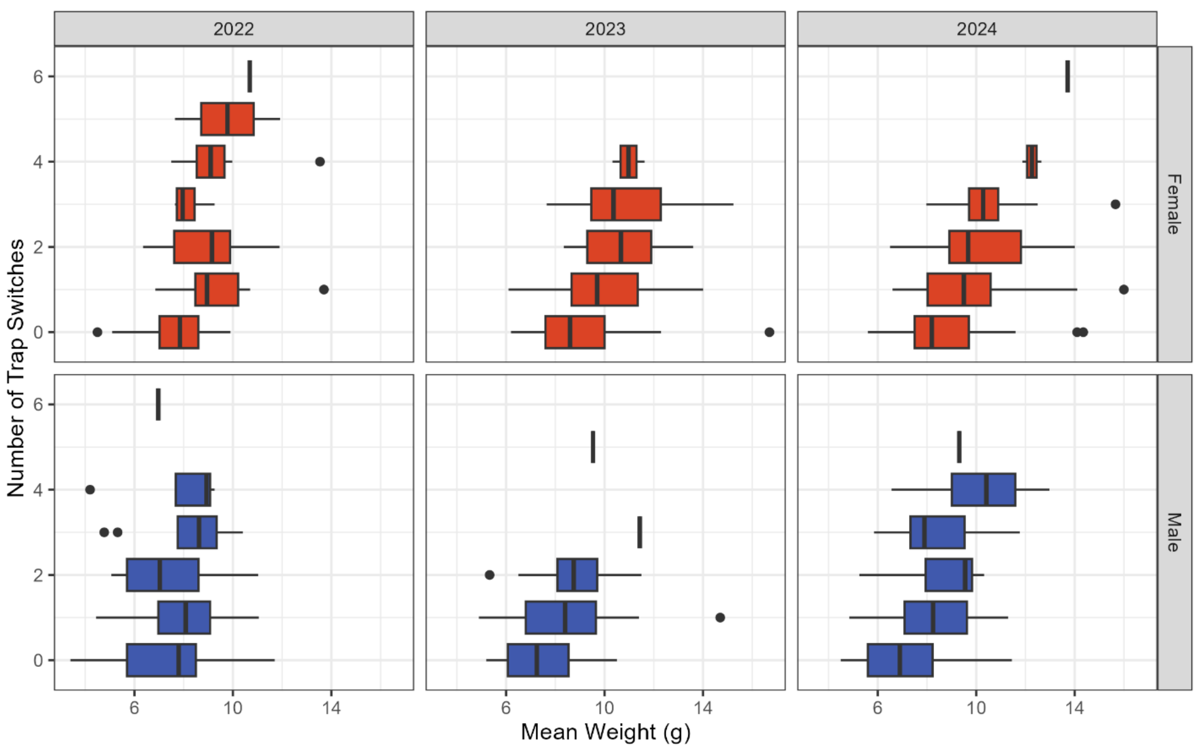

Figure 15: Visualization of the number of times an individual was caught in a different trap from the last, analyzed by the individual's mean weight and sex.

Table 7: The results of a general linear model with poisson distribution on the influence of weight, year and sex on number of trap switches a newt made within a season. The year 2022 and female were the reference levels.

Explanatory variable	*Estimate*	*Std. Error*	*Z*	*P*
Intercept	-0.969	0.197	-4.917	< 0.001
Mean Weight	0.147	0.019	7.655	< 0.001
Sex (Male)	0.068	0.084	0.812	0.417
Year (2023)	-0.504	0.108	-4.656	< 0.001
Year (2024)	-0.229	0.092	-2.490	0.013

3.3 Fall Migration – Movements from Ponds to Terrestrial Habitats

During the juvenile migration period from the ponds to terrestrial habitats, in the late summer-fall season of 2024, a total of 16 great crested newt individuals were caught in pitfall traps (figure 16). These included one adult female, three adult males and twelve juveniles.

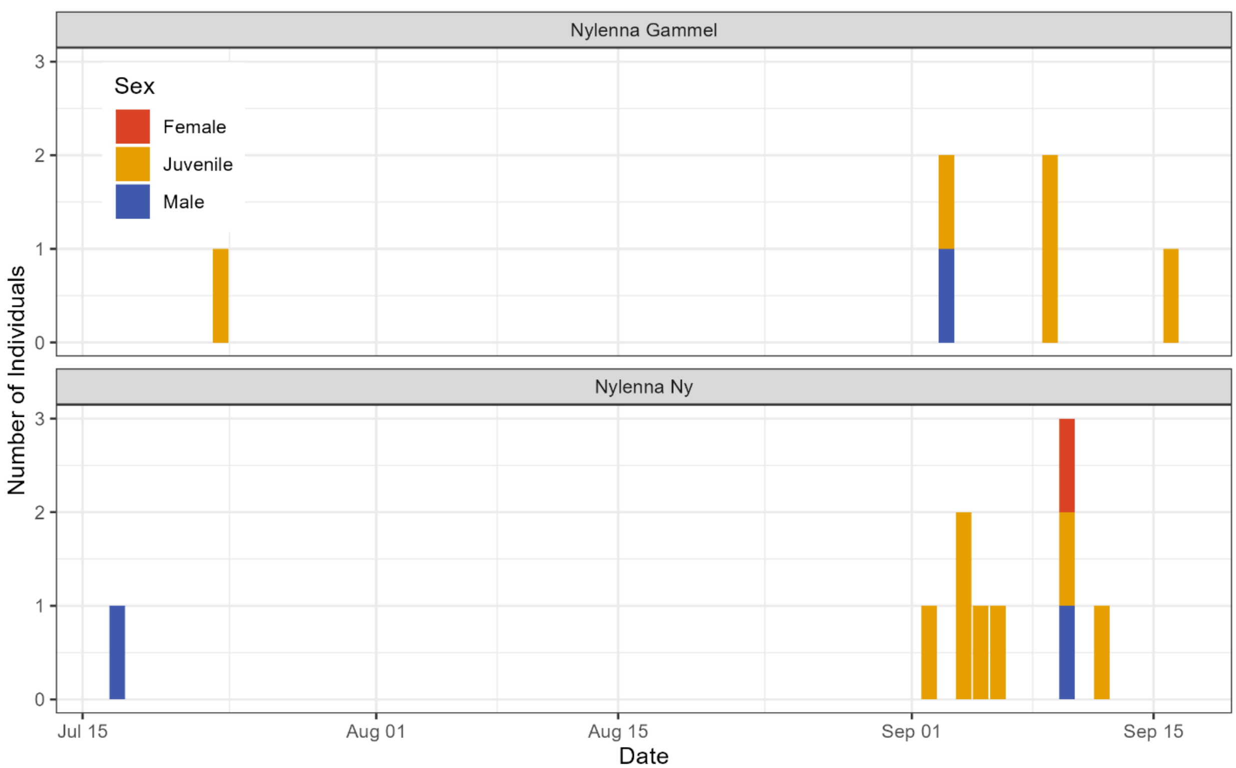

Figure 16: The pitfall trap catches during the 2024 season by date and pond.

Twelve juveniles were caught between 23. July 2024 and 16. September 2024. Their mean weight was 1.7 g, with the smallest individual being 1 g and the biggest being 4.3 g. One juvenile and four adults caught in the pitfall traps had previously been caught in funnel traps during aquatic data collection. The first adult individual caught in the pitfall traps of Nylenna Ny was captured on 17. July 2024. After that there was a long period with zero great crested newt catches. On 03. September 2024, an adult male was caught in a Nylenna Gammel pitfall trap. He had switched ponds since previous capture in a funnel trap in Nylenna Ny in early May. Additionally, the adult female caught in Nylenna Ny had also switched ponds since the aquatic data collection had ended. She was previously caught in Triturus in the end of May, yet she was also present in Nylenna Ny in the early 2023-season. The last adult male had not switched ponds since previous capture.

Most of the newts in Nylenna Ny and Nylenna Gammel were caught in pitfall trap number 3 of both ponds, which are the ones closest to the forested areas and Triturus (figure 17). In that direction, there was also a suitable overwintering habitat in an old potato cellar with a foundation of stone (see figure 5).

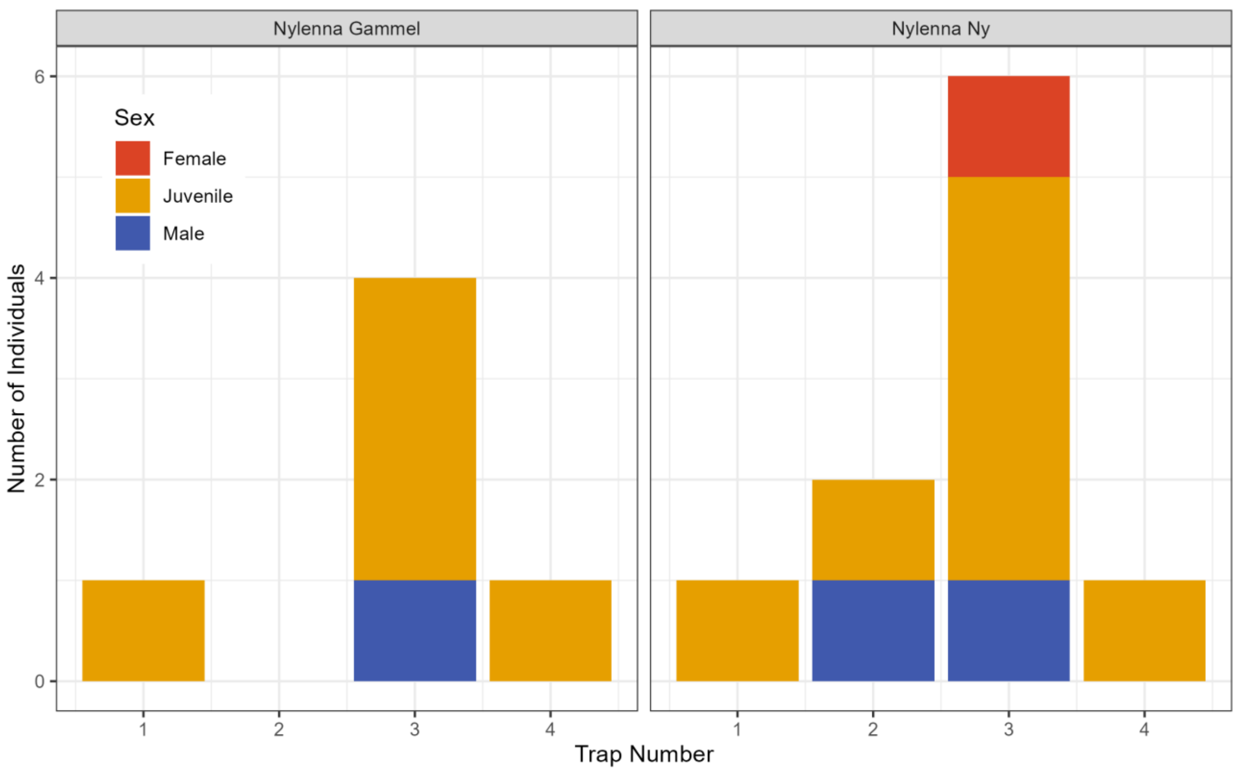

Figure 17: Pitfall trap catches in the period July 17th to October 7th for the two Nylenna ponds in 2024.

3.4 Factors Influencing Trappability

3.4.1 Trapping Frequency

In 2022 data was collected on two consecutive days weekly in the Nylenna ponds. The median count of the first data collection days (average across all traps in two ponds) was significantly higher than the second day data collection days (Wilcoxon signed rank exact test, V = 36, N = 8, p = 0.004, Figure 16). The seven individuals caught in Nylenna Gammel and the 21 individuals in Nylenna Ny on 23. April 2022 were not photographed, neither were the five caught in Nylenna Gammel and the twelve individuals in Nylenna Ny the day after. The data collected on these dates were therefore excluded from the count of total unique individuals.

Looking at the unique newts caught in the fourteen data collection events across the next seven weeks, a total of 158 unique individuals were trapped. Of these, 134 were trapped on one of the first data collection events of a week, meaning twice the catch effort resulted in only an additional 24 individuals. As seen in figure 18, the total catch by date was lower on the second data collection day for 7/8 weeks for each pond. In total, the second collection day of each week caught 101 of the individuals.

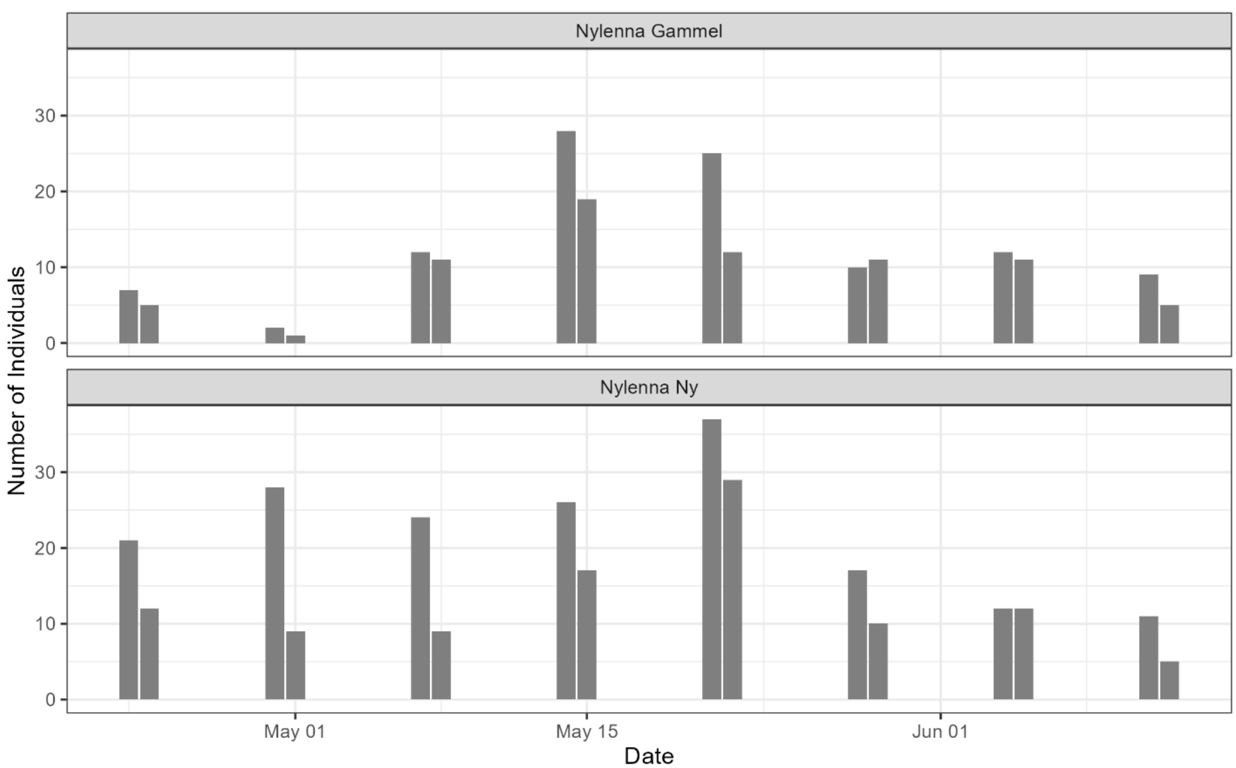

Figure 18: Number of individuals caught by date in 2022.

3.4.2 Timing of Surveys

In several instances, between 30 and 40 % of the total yearly catch was captured on just one survey day (figure 19). There was some variation across the years in terms of when the highest catch occurred, but it was generally around early to mid-May for all ponds and years (figure 19).

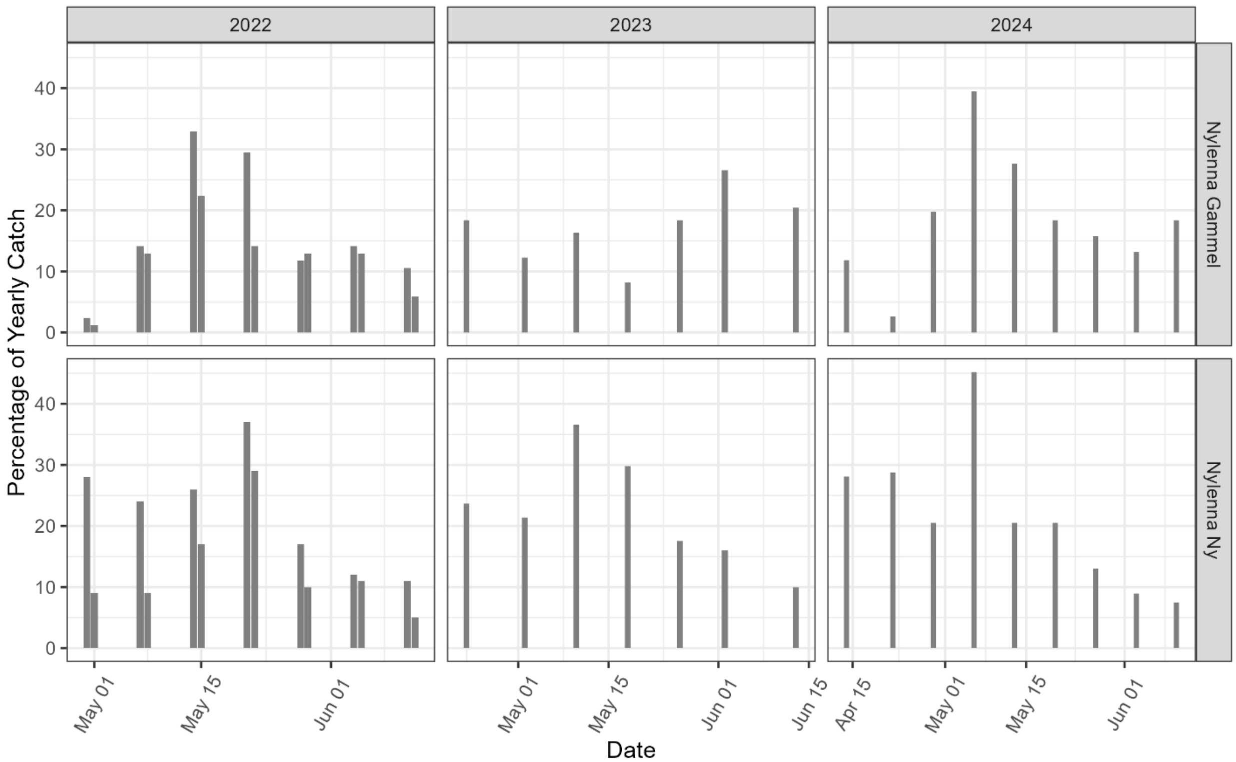

Figure 19: Percentage of uniquely identified individuals caught on each sampling date per year. The graph does not distinguish between recaptures and new individuals.

Figure 20 below shows the cumulative count of new individuals caught in the Nylenna ponds each season. It also shows a cumulative count of when they were not caught again that season.

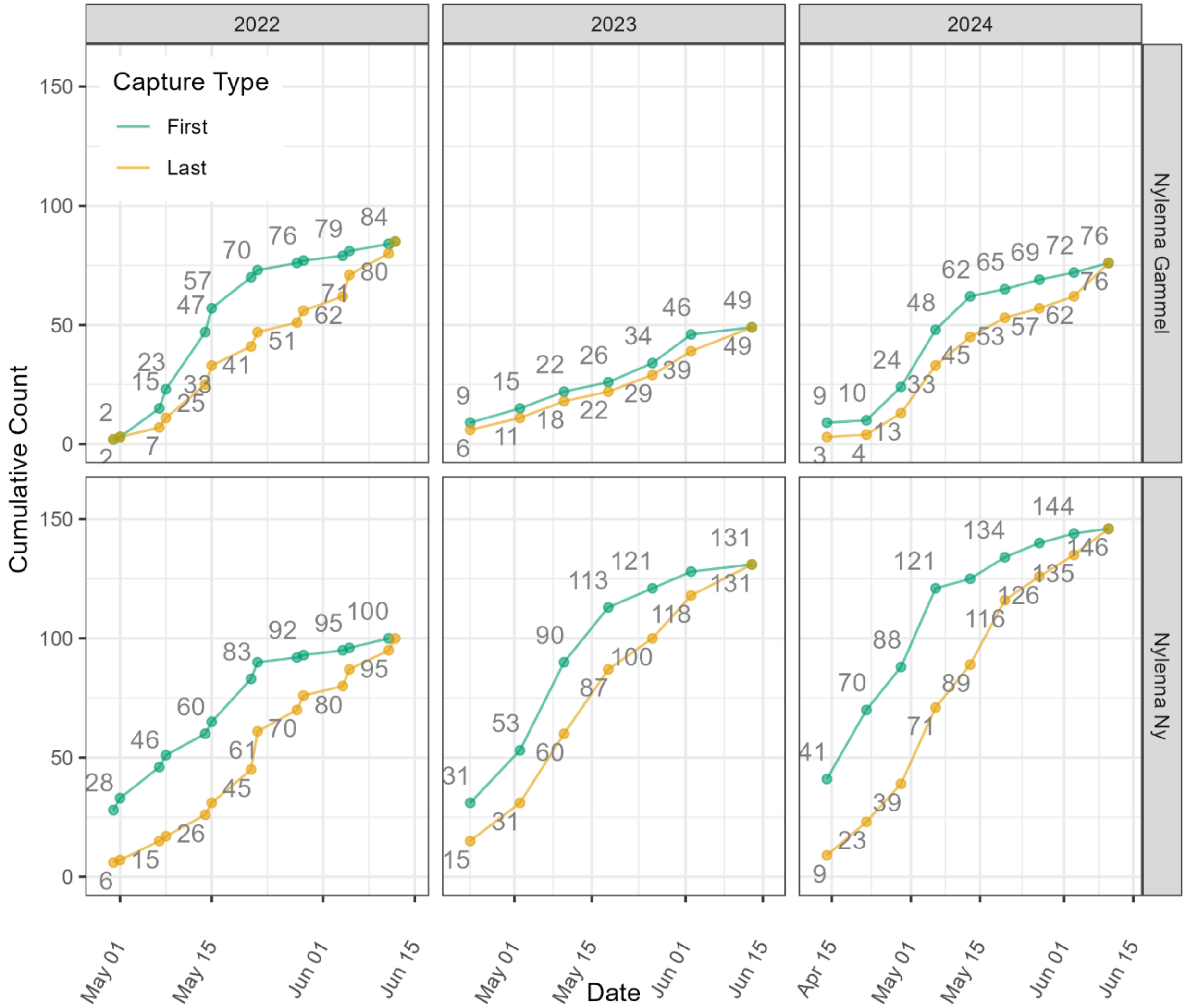

Figure 20: Cumulative count of when individuals were caught for the first and last time for the season in each pond. For 2022, the number shows the first data collection day of the week.

There were steep increases in the number of new individuals at the beginning of the seasons, but the increase leveled out towards the end of May as newts were rather recaptured than captured for the first time as the season progressed. Yet, some individuals were still caught for the first time towards the end of May and early June. In addition, there were several individuals that were only trapped in April. Using Nylenna Ny as an example, six of the 28 individuals on 30. April 2022 were not recaptured at a later date that season. On 23. April 2023, 15 individuals were caught and not recaptured. If excluding 14. April 2024 and 22. April 2024, 23 individuals were lost from the total individual count.

3.4.3 Release Location

In 2022 and 2023, the newts were released together in the same spot within the pond. Whereas, in 2024 they were released in the same spot as they were caught. Figure 21 shows how many traps the newts were caught in across four sampling events between the end of April and mid/late May for each year in the Nylenna ponds.

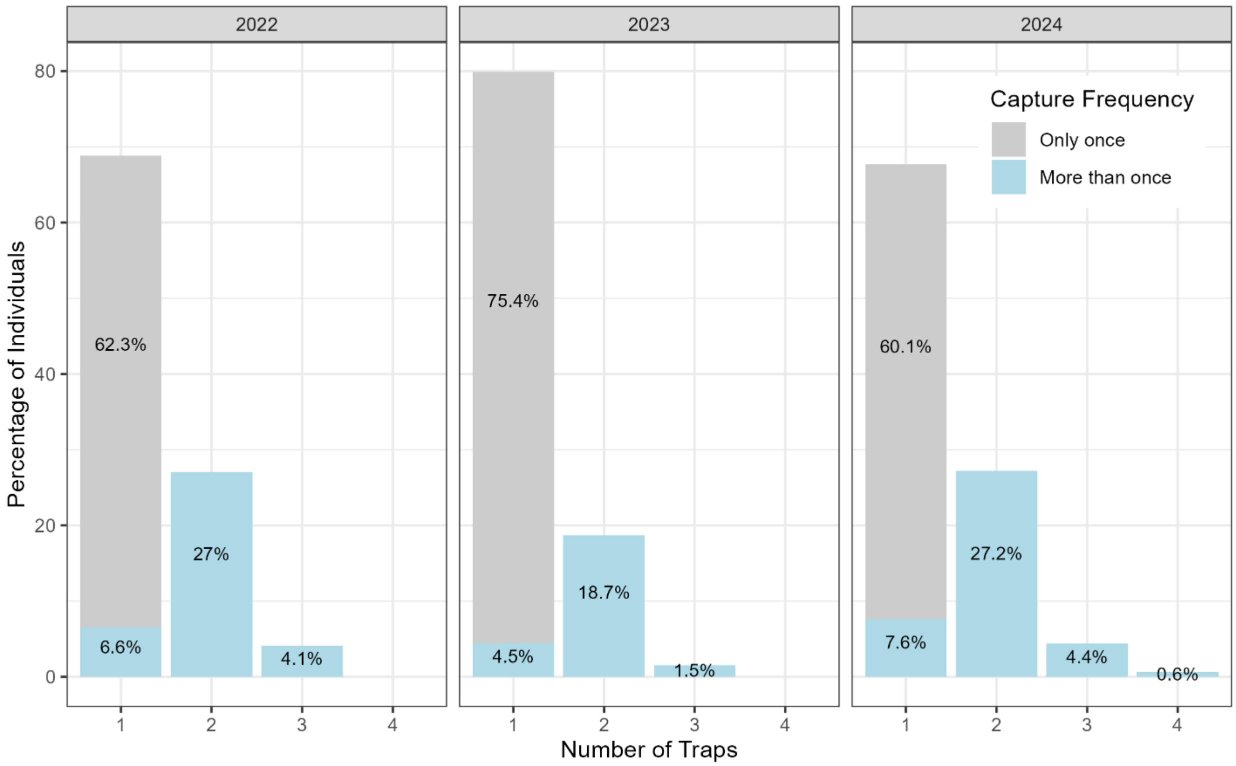

Figure 21: The data filtered to include four comparable data collection events between the end of April and mid/late May for each year. Therefore, the number of traps for 2024 is lower than in figure 14. For individuals captured during the relevant period, I calculated the percentage that were caught in varying number of traps.

3.4.4 Body Weight

Ninety-nine of the individuals were only caught once, whereas 32 individuals were trapped eight or more times over the three-season period. The mean number of catches per individual newt was 3.3 ± 2.7 SD. The highest number of catches of an individual was 16 times. The second most caught individual was also the individual switching ponds the most. Within seasons, the highest number of catches was eight (figure 22). I found a positive relationship between the number of catches and body weight, and significantly fewer catches per individual in 2023 and 2024 compared to 2022 (table 8). The relationship between number of captures per individual and body weight did not depend on sex (sex × weight interaction: $p = 0.385$) or year (year × weight interaction: $p = 0.863$ for 2023 and $p = 0.957$ for 2024).

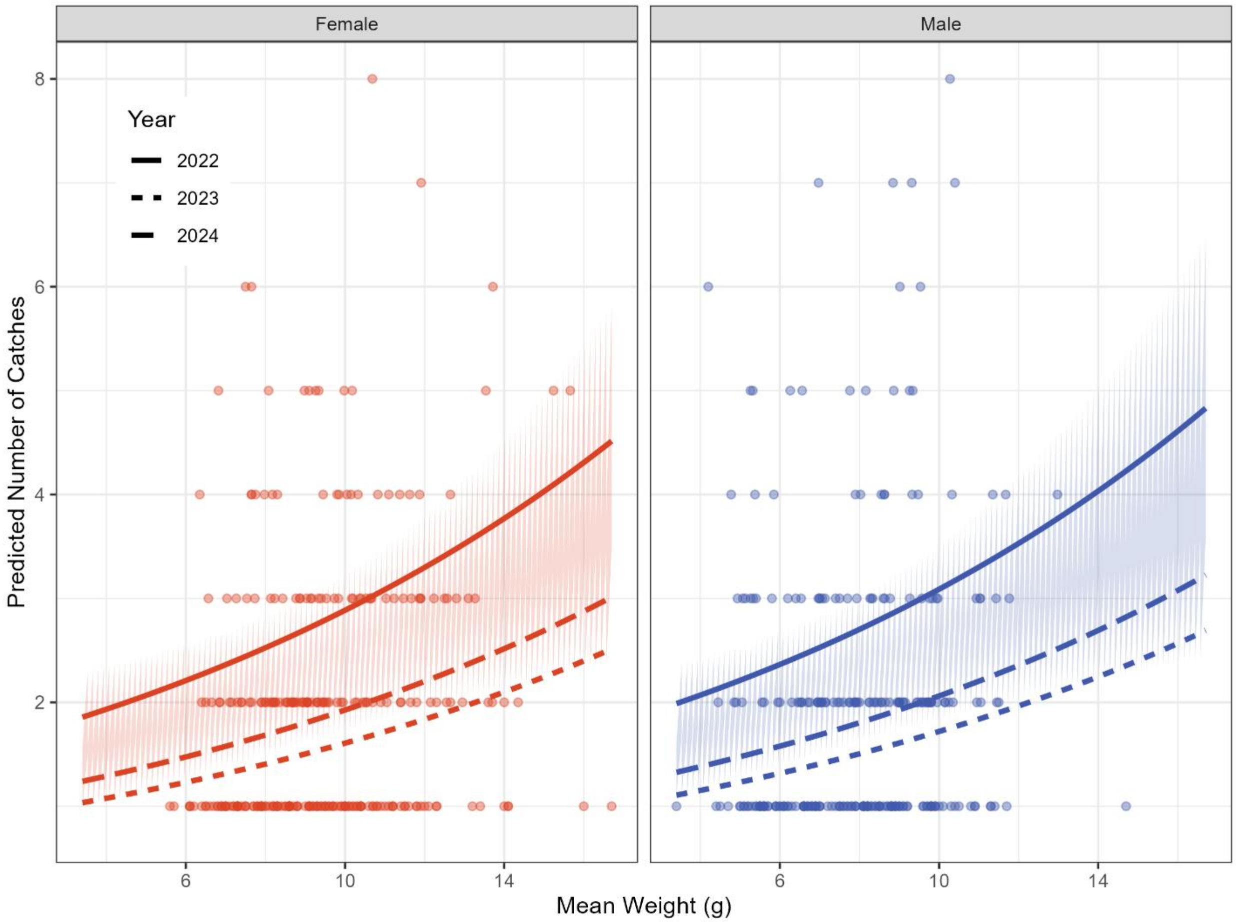

Figure 22: Estimated relationship between the number of times an individual newt was captured and body weight, for different years. The lines are estimated means from a negative binomial model of number of catches by mean weight and year (Table 8). The points are observed values. The same individual may be presented thrice by points with different catch and weight values depending on the year.

Table 8: The results of a negative binomial model of the relationship between number of catches and the newt individual's mean weight, sex and year of capture. Female and 2022 were the reference levels.

Explanatory variable	*Estimate*	*Std. Error*	*Z*	*P*
Intercept	0.392	0.153	2.557	0.01
Mean Weight	0.067	0.015	4.312	<0.001
Sex (Male)	0.068	0.064	1.055	0.291
Year (2023)	-0.586	0.081	-7.230	<0.001
Year (2024)	-0.404	0.069	-5.842	<0.001

4. Discussion

In this thesis, I examined how pond fidelity, movement and trappability varied between great crested newt individuals. I found that most individuals returned to the same pond between breeding seasons, however, many also established themselves in a different pond from the last season. Furthermore, some moved between ponds within a season. The individuals that moved between ponds one, two or three times during breeding seasons were characterized by a higher weight than those that stayed put. Though marginally significant, the influence of weight was stronger in males. Larger individuals were also observed to move between unique traps more frequently than smaller individuals. There were however no significant differences between adults and juveniles in the number of unique traps they were caught in, or between males and females. Larger individuals were more likely to be caught frequently in Ortmann's funnel traps, and there was a decrease in trappability across years. I found that trapping frequency also affected trappability as total catch went down on the second day if sampling on two consecutive days, but the numbers rose again by the next week.

Pond Fidelity

Contrary to the common assumption that adult great crested newts return to the same pond to breed and remain there throughout the breeding season, my findings indicate greater variability in their pond use strategies. As seen in figure 8, most individuals (73.8 %) were only caught in one pond. However, more than a quarter of the population moved between ponds at some point. The number of individuals moving between ponds in this system was likely an underestimation as many individuals were only caught once and one cannot know if they moved ponds or not. The number of individuals caught in two or three ponds may also have been higher, had data been collected in Triturus in 2022 and 2023 as well. The number of individuals present in multiple ponds is quite high compared to a study from Germany where the authors found that 99 % of recaptured adult individuals returned to the same pond (Kupfer & Kneitz, 2000).

I found that return rates were higher when all ponds were considered collectively rather than when each pond was analyzed individually. Some individuals would return from the previous year but establish themselves in a different pond from the last season. In previous studies of the great crested newt, it is commonly assumed that one pond equals one population. However, the substantial overlap of individuals between the Nylenna ponds suggests otherwise; it is not a closed system. Whether or not one ought to consider Triturus as part of the same population or just the same metapopulation can be debated. Although more separated from the Nylenna ponds, the ponds are all within the distances of a newts' functional area, which suggests that they are in the same population. Either way, the overlap in individuals does at the very least place it in the same metapopulation as the Nylenna ponds. Still, at what point one makes the distinction is tricky to determine, and this pond system demonstrates how nature does not operate in hard lines, and that the separation between populations is gradual.

Site fidelity may be more related to the general area than to a specific pond, and the degree of movement between ponds is likely the result of several factors. The pond availability and distance between ponds may partly explain why there was more movement between ponds in this system than in the study by Kupfer and Kneitz (2000). In their study the distances between their seven ponds varied from 430 to 1940 meters. However, the Nylenna ponds are only eight meters apart and Triturus roughly 50 meters away. In the Belgian study by Denoël et al. (2018) they also observed adult individuals dispersing to new ponds. Their study area consisted of 73 ponds within an area of 423 x 293 meters. The mean ± SD distance and the nearest distance separating each pond inhabited by the newts was 149 ± 75.2 meters and 21.1 ± 13.3 meters, respectively (Denoël et al., 2018). Such distances are more comparable to my study system, although the Belgian study area consisted of far more ponds. A high number of ponds present within a close distance may lower the risk associated with movement on land. The newts are believed to be able to smell ponds, an important feature for recruitment to new ponds (Langton et al., 2001). The newts in the study by Kupfer and Kneitz (2000) were likely faced with a higher risk of desiccation due to the longer distances between ponds than the newts in the research by Denoël et al. (2018). With more ponds and moist areas between populations, the newts may also have better dispersal capacity. In wildlife ecology, stepping stones between suitable habitats have been demonstrated to be important for the resilience of the overall metapopulation (Hanski et al., 1994).

The quality of the land areas surrounding ponds has been found to impact gene flow between great crested newt populations. A Norwegian study comparing two forested great crested newts sites, one in a recently clear-cut forest and one with little anthropogenic disturbance, found that geographic distance, gravel roads and south/south-west facing slopes reduced landscape permeability and increased genetic differentiation whereas streams had the opposite effect, likely favoring dispersal (Haugen et al., 2020). They also found that population within and near old growth forests had a higher allelic richness than the populations in the managed forest (Haugen et al., 2020). Kupfer and Kneitz's (2000) study site was located within an agricultural area, and they pointed out that one of the ponds was potentially isolated by a road. In contrast, the study site of Denoël et al. (2018) was a flat non-urbanized area well protected within a military base. I believe my site to be less impacted by anthropogenic change than the German site, but less protected than the Belgian one. The passage between the Nylenna ponds is short and relatively flat, whereas the passage to Triturus would require the newts to climb up a south-west facing slope, deemed unfavorable by Haugen et al. (2020). Still, the distance is relatively short and the outflow in the southern section of Triturus provides moist terrain for the newts to walk on.

My findings of a relatively high proportion of the population (26.2 %) present in multiple ponds may also be influenced by the pond size and resource availability. Great crested newt ponds tend to be between 100 and 6000 m^2 in Eastern Norway, with an average of 1000 m^2 (Dervo & van der Kooij, 2020). The Nylenna ponds are particularly small compared to average great crested newt pond size in Norway, only 42 m^2 and 32 m^2. The newts may be moving around more to compensate for the lower resource availability in smaller pond habitat. Triturus is closer to the norm with its 677 m^2. This pond is however newly constructed, presumably with lower resource availability as the vegetation and insect communities are still developing. The higher return rates of Nylenna Ny than Nylenna Gammel may suggest that resource availability influences pond switches. There were more newts switching from Nylenna Gammel to Nylenna Ny for a new season (26) than the other way around (11). Although Nylenna Ny is 10 m^2 smaller than Nylenna Gammel, it is also in a sunnier and more prolific area. Denoël et al. (2018) found that the newts from ponds with bigger pond surface were more likely to belong to the low pond fidelity type. Looking at the study site of Kupfer and Kneitz (2000) where they found strict pond fidelity, however, their seven ponds ranged from 64 to 1200 m^2. Still, the environmental conditions in Belgium (Denoël et al., 2018) and Germany (Kupfer and Kneitz, 2000) are not directly comparable to Norwegian conditions, where pond size may affect resource availability differently.

Finally, I found that movement between ponds was influenced by body weight. In my study system, several individuals moved between ponds once or twice, in one case thrice, during the course of a breeding season. This is contrary to much of the current literature that states that the newts generally establish themselves in a pond for the breeding season then stay there until it is time for the fall migration (Langton et al., 2001). If the newts moved between ponds due to competitive pressure, one would expect small individuals with less reproductive success or ability to fend for themselves to be the ones moving. Yet, figure 13 shows the contrary: big individuals are more likely to switch ponds, even though these are also likely the newts that have the best reproductive success (Díaz-Paniagua, 1989; Palau Daval et al., 2018). Denoël et al. (2018) also found a positive correlation between the likelihood of displaying the low site fidelity phenotype and body weight. For larger individuals, movement on land may be worth the risk and energy spent moving if they find more resources in a different pond or are able to further increase their reproductive success.

Timing of Pond Switches

Although some individuals were observed in all three ponds across seasons, no individuals were seen in more than two unique ponds within a single season. Between the Nylenna ponds, I observed an equal number of pond switches within the breeding season (58) as between breeding seasons (58). However, there was far less movement observed between Triturus and the Nylenna ponds during the breeding season.

A third of the individuals in Triturus (16/48) had previously been caught in one or both of the Nylenna ponds. With the exception of one individual moving from Nylenna Gammel to Triturus in mid-May, none of these newts were observed in either Nylenna pond during the 2024-breeding season. Although some may have been in a Nylenna without being trapped, the data suggests that most of these pond switches happened prior to the start of data collection in Triturus on 17/04/2024. Fall and spring migrations may therefore be important times for adult recruitment to a newly established pond. The high catches in pitfall traps 3 of Nylenna Ny and Nylenna Gammel support this. Most of the pitfall catch happened in September, which indicates that many newts were heading in the direction of the forest between Nylenna and Triturus to overwinter. Previous movement to Triturus may have happened in chunks; half on their way from Nylenna to their overwintering spot and the second half in the spring. It is not uncommon for newts to walk that far in one night though: Newts can walk at a speed of 0.5-1.0 meters per minute and up to 200 meters in one night (Dervo & van der Kooij, 2020). Within seasons though, the Nylenna individuals likely have no reason to walk all the way to Triturus if there are available resources in close proximity, particularly as they are vulnerable to both predation and desiccation during such a move. The newts always need some degree of moisture, particularly during the breeding season when they adapt their skin to display sexual characteristics and to increase oxygen uptake in the pond (Dervo & van der Kooij, 2020; Langton et al., 2001). Hence, precipitation has been found to be important for migration patterns of great crested newts (Dervo et al., 2016). For further details on movements between ponds in relation to date and environmental conditions, see figures S3 and S4 in Supplementary Material.

Finally, the pitfall trap catch provides evidence that adults may move to land but return to ponds occasionally even after the breeding season is over. One individual was found in a pitfall trap by Nylenna Ny after having been caught in Triturus during the summer. Furthermore, another pond switch was observed between the Nylenna ponds. The pitfall trap catches therefore demonstrate that there were more pond switches happening in the late summer season. Although the breeding season is over, they may choose to seek out the ponds to feed if they are not finding enough food on land.

Recruitment to Triturus

I found that thirty-two (66.7 %) of the forty-eight individuals caught in Triturus were trapped for the first time. The new individuals had significantly lower mean weight than those previously caught in Nylenna and the Nylenna individuals overall, providing evidence that the Triturus individuals were generally younger. No juveniles were seen observed to move between ponds, but juveniles in their land-dwelling stage are the main dispersers and colonizers of new ponds (Dervo & van der Kooij, 2020; Langton et al., 2001). The individuals caught in Triturus, and for the first time, may have spent the last two or three years primarily on land, finally seeking out the ponds to breed as sexually mature adults. These newts may originate from ponds outside the study area as juveniles can walk long distances during this life stage. For instance, Kupfer and Kneitz (2000) recaptured thirty-five metamorphized juveniles and found them to have walked distances as far as 860 meters from their natal pond the same year. However, most do not walk far. Many of the new adults likely originate from Nylenna, and as juveniles spend several years on land, this would mean that they left before data collection started in the Nylenna ponds in 2022.

Regardless of origin, a newly established pond with less competition is a good choice of pond for small adults. Most of the new individuals were also males: Nineteen were males, two were juveniles and eleven were females. Females chose which males to mate with; hence young males would face less competition from large males and have greater chance of reproductive success in a less populated pond (Hedlund & Robertson, 1989; Palau Daval et al., 2018). The sex ratio looked different for the individuals previously caught in the Nylenna ponds: Thirteen of sixteen were females. Seen in the context of the model of the influence of weight and sex on the number of pond switches, this may be explained by females generally being larger than males (Dervo & van der Kooij, 2020). As for juveniles and newly sexually mature adults, it is not unlikely that once they find a suitable pond, they choose to stay put there, resulting in their low pond switch category.

Movement within Ponds

I did not find any significant differences between males and females, or between adults and juveniles, in terms of the number of unique traps they were caught in. My findings also do not indicate that the newts exhibit within-pond site fidelity. For instance, figure 12 does not show more than a few individuals being caught in the same trap at the end of the previous breeding season as the beginning of the next. Figure 21 does not indicate site preference within the ponds either. In 2022 and 2023 the newts were gathered in a big container and released together once the sampling of their pond was done, but in 2024 they were released where their specific trap had been. Of the individuals captured more than once, a higher proportion was caught in only one trap in 2024 than in 2022 and 2023, yet the differences were small. However, whether the newts exhibit site preference is difficult to assess, as the spatial extent of within-pond fidelity has not been clearly defined. The Nylenna ponds are exceptionally small; therefore, sampling an area of equivalent size within a more typical great crested newt pond could yield different results. It will be interesting to see the differences in within-pond fidelity in the small Nylenna ponds and the larger Triturus pond in the future.

There was a strong correlation between the total number of times an individual was caught and the number of traps it was caught in (see figure S5, Supplementary Material). The trend line did not follow a 1:1 ratio though, suggesting that some individuals stayed in certain areas within the pond. For instance, an individual captured seven times was only caught in three different traps: one time in Nylenna Ny trap 3, three times in trap 4 and three times in trap 5. Although my findings do not provide evidence of site fidelity within the ponds, they indicate that there were some clustering tendencies. Some traps within the pond had higher catches than others (figure S6, Supplementary Material). In Triturus, the trap closest to the Nylenna ponds had the highest catch, and some traps had no catch at all and only one newt. In Nylenna Gammel there were between twenty and forty newts in traps one to four, but trap five had a much lower catch. The low catch of trap five in Nylenna Gammel – which was in the shallowest part of the pond – could be partially explained by lower water levels as the summer temperatures got higher. I observed considerable variation in which traps yielded the highest catches over time. As seen in figure S7 (Supplementary Material), both the total trap catches and sex composition changed over time. There were some clustering tendencies amongst male newts for some dates, for instance on 14. April 2024 and 06. May 2024, which may be explained by lekking behavior in males (Hedlund & Robertson, 1989). Looking at the data as a whole, one can deduce that the distribution of newts within the ponds is influenced by environmental and social factors, rather than within-pond site fidelity. The newts may choose where to be in the pond based on a combination of water level, food availability and the presence of other newts and their activity. As far as I have been able to determine, no previous studies have examined movements between traps within the same pond.

Regardless of the specific trap locations, some individuals were more likely to move between traps multiple times. I found a significant relationship between body weight and the number of times they moved between traps within a year, both in males and in females. Again, higher body weight indicates better body condition, hence they can afford to be more active. The year also had an impact on the number of trap switches. I have no clear hypothesis to explain this finding, but interannual variation in resource availability, known to influence movement in wildlife populations, may be a contributing factor (Fryxell & Sinclair, 1988; Mueller & Fagan, 2008). It may also be partially explained by differing pond temperatures, affecting their activity levels (Langton et al., 2001).

Trappability

The research presented in this thesis contains data collected across three breeding seasons at quite high trapping frequency. This level of effort and detail in great crested newt research is uncommon, and one can gain important insights that inform monitoring strategies by following individuals across longer periods of time. Yet, it can be challenging to know whether frequent capturing has negative effects on animals, especially with animals such as newts that display emotions very differently from humans. For newts, the hormone corticosterone is used as a physiological indicator of stress (de Assis et al., 2015). However, sampling blood in individual newts can be invasive, and requires permits. The use of eDNA is a good alternative, but it is used to detect stress on the population level (Narayan et al., 2019). In the absence of corticosterone data, one can instead evaluate the methods used and limit potential impacts by ensuring the research is conducted as efficiently as possible. A critical evaluation of individual behavior can provide some insight into whether animals are affected by trapping. Ecological studies that are able identify individuals, such as this one, can pinpoint more of the variation at play within a population.

I found that the timing, duration and frequency of trapping events impacts how many individuals one captures. Figure 20 demonstrates some of the challenge of capturing all individuals: Some individuals are captured in the beginning not to be recaptured again whereas others are captured for the first time towards the end of the field season. Whether first and last captures are good indicators of when the newts arrive and leave the breeding ponds is hard to know. These individuals may still be or have been present for a longer period of time without being trapped. Many newts were only captured once, and there are most likely some individuals that are never captured at all.

One may be tempted to increase the seasonal duration or frequency of trapping to capture all the individuals. Yet, it is impossible to know when one has gotten them all. One should also consider the impact of frequent trapping on the individuals being trapped. Too frequent trapping likely causes many individuals to avoid traps, demonstrated by lower catch on second day when collecting two days a week in 2022. As the catches for 2022 go back up after seven or six days of no trapping, one can hypothesize that many forget what happened the previous week. Yet, some individuals are trapped almost every data collection day. The extent of which the newts can learn to seek out or avoid traps is hard to know by certain, but several of the results indicate they do to some extent. With this in mind, it is not unlikely that some individuals are avoiding the traps even though they are moving around the pond. An alternative reason may be that the newts are tired after being trapped and reduce their activity level afterwards. However, there are also significant differences in trappability between 2022 and the following year. The expected captures of 2023 were about 44 % lower than 2022, and in 2024 they were 33 % lower than 2022. Though this may be due to differing trapping efforts, it may also be an indication that the newts are avoiding the traps more.

Yearly differences in trappability can also be explained by environmental factors and natural fluctuations in the population. The total number of individuals caught in the Nylenna ponds stayed relatively stable over the three-year period ranging from 49 to 85 individuals in Nylenna Gammel and from 100 to 146 in Nylenna Ny. Similar findings have been found in other regions of Europe. Fluctuations in population size are not unnormal, however. A French study documented a doubling in population size (Miaud et al., 1993), whereas a study in south-western Sweden had a halving in population between two consecutive years (Hagström, 1979). In central England, a rapid three-fold increase in population size was seen after the crash of predatory three-spined sticklebacks that likely had held the newt recruitment in check (Baker, 1999). Though not a drastic change, I found that the total number of unique individuals was higher in 2023 and 2024 than in 2022, which can explain some of the differences in trappability between years. With more individuals, it is also harder to capture them all.

My findings also suggest that there was a difference between bigger and smaller individuals in trappability. I found that a newt is about 7 % more likely to be caught per added gram. There may be several reasons for this. Bigger individuals may seek out the traps more frequently or alternatively, smaller individuals will learn to avoid them. Bigger individuals may find that the traps are areas with high food availability, as they eat insects and occasionally smooth newts (Langton et al., 2001). The smaller individuals may however find the experience of being trapped more stressful than larger individuals. As indicated by figure 15, they may also be less active, hence less frequently caught. Alternatively, they may also move around more but not be caught in the traps as frequently. Furthermore, though not statistically significant, males had about 7 % higher chance of being captured than females. This is contrary to earlier findings on funnel traps, which found that though the traps were deemed as suitable and effective traps for catching great crested newts, they were more efficient to catch females than males (Dervo et al., 2014). The influence of sex on trapping may instead vary with the time of season and activity, such as egg-laying in females or lekking behavior amongst males. These contrary results stress how there is yet more to be learned about the trappability of great crested newt and that their life histories may affect research in surprising ways.

5. Management Implications

The great crested newt's dual dependence on both terrestrial and aquatic habitats can make them challenging to conserve. There are, however, some signs of hope for the newts. In recent years, restoration efforts have gained more traction and the Nature Restoration Law of the European Union was implemented (The European Parliament, 2024). This enhanced focus on restoration provides a special opportunity to turn the tide for the newts. However, to maximize the success and cost-efficiency of habitat restoration efforts, a better understanding of how newts utilize their habitat is essential. The results of this study provide some important insights, which can inform habitat restoration efforts to suit the species, as well as adding to existing knowledge of dispersal to and establishment in new and restored ponds.

Firstly, I found that adult newts may move between ponds during the breeding season. This stresses the importance of having multiple ponds within newt walking distance, particularly a distance they can easily cover overnight. As the traffic between the Nylenna ponds, just eight meters apart, is higher than between them and Triturus, 40 - 50 meters further away, one can deduce that newts benefit from having neighboring ponds in close proximity.

Secondly, I believe the time between breeding seasons to be significant in the recruitment of adult individuals from a pre-existing pond to a new one. Only one of sixteen pond switches from Nylenna to Triturus were observed to happen during the breeding season. This highlights the importance of conserving not only the ponds but also their terrestrial habitats and corridors including suitable overwintering habitats between ponds. I hypothesize that adult great crested newts can contribute significantly to the recruitment of new and restored ponds if they are close enough to existing breeding ponds with good land habitat in between.

Thirdly, the results also provide some important lessons for surveying. The data show that 34/158 newts present in 2022 were not captured in 2023 but recaptured in 2024. If there had been data collected in Triturus in 2023, one might have found some of these individuals. Still, these findings are important as they demonstrate why the absence of a newt in a given year should not be immediately interpreted as mortality. Instead, these newts may be avoiding the traps, be on land or in a different pond. Furthermore, the observed differences in trappability are of interest. Population estimates and models can be helpful to identify extinction threats and evaluate the viability of a population. Seeing as one individual was caught sixteen times over the three-year period whereas many were only caught once, or once in 2022 and a second time in 2024, there is quite a lot of variation between individuals. Population models may therefore be influenced by the individual behaviors of the newts as some may be more trap shy and trap happy.

Fourthly, the timing of the data collection is also important. Although one can catch a high percentage of the newts during certain periods, as seen in figure 19, figure 20 demonstrates how there is great variation in when newts are caught for the first time and last time within a season, emphasizing the importance of doing multiple surveys across several weeks. One should not survey on two consecutive days, however, as the catch is significantly lower on the second day (figure 18).

Finally, the results of this study did not indicate that the newts had site fidelity within the ponds. However, it remains good practice to limit one's potential impact on the animals and to consider their differing pond usages by releasing the individuals back into the same area as they were caught.

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7. Supplementary Material

Population Size Estimates

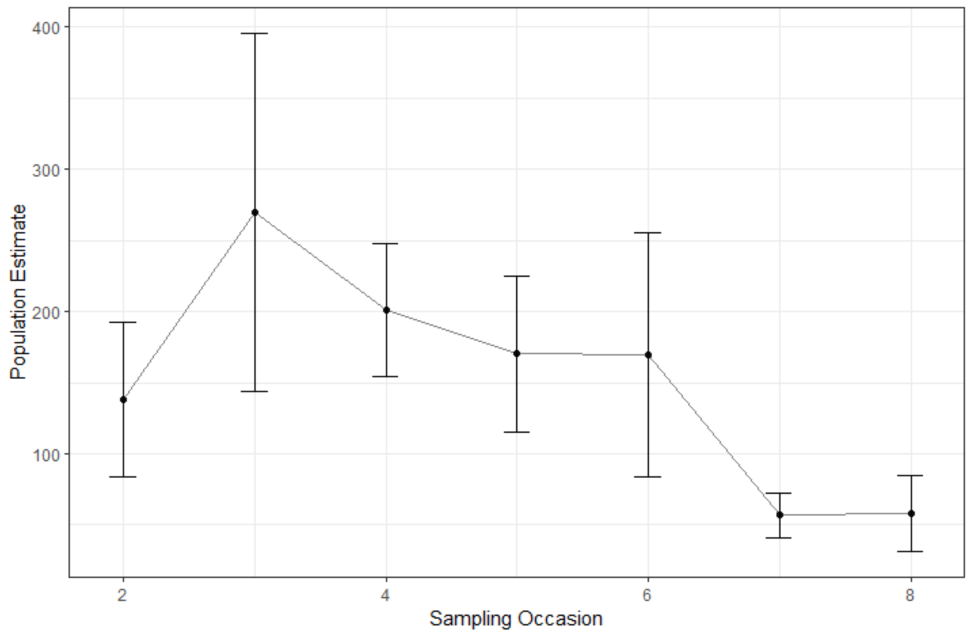

Figure S1: Jolly Seber population size estimates with error bars for the Nylenna ponds in 2024.

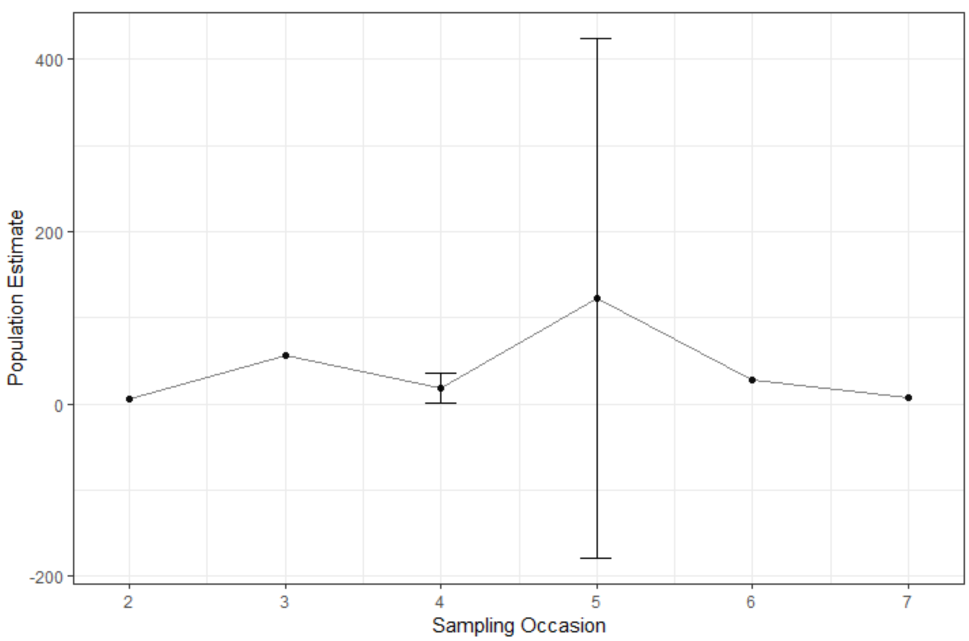

Figure S2: Jolly Seber population size estimates with error bars for Triturus in 2024.

Abiotic Factors and the Timing of Pond Switches

As seen in figure S3 there appeared to be some events where more individuals moved one Nylenna pond to the other. The highest pond switch peak in 2022 can be partly explained by the wrongful release of some Nylenna Ny individuals into Nylenna Gammel. The first columns for 2023 and 2024 show newts that had switched ponds since the previous season. The mean pond temperatures in Nylenna Ny during data collection were 12.9 (2022), 13.2 (2023) and 13.0 degrees Celsius (2024), and for Nylenna Gammel they were 13.2 (2022), 13.0 (2023) and 11.3 degrees Celsius (2024).

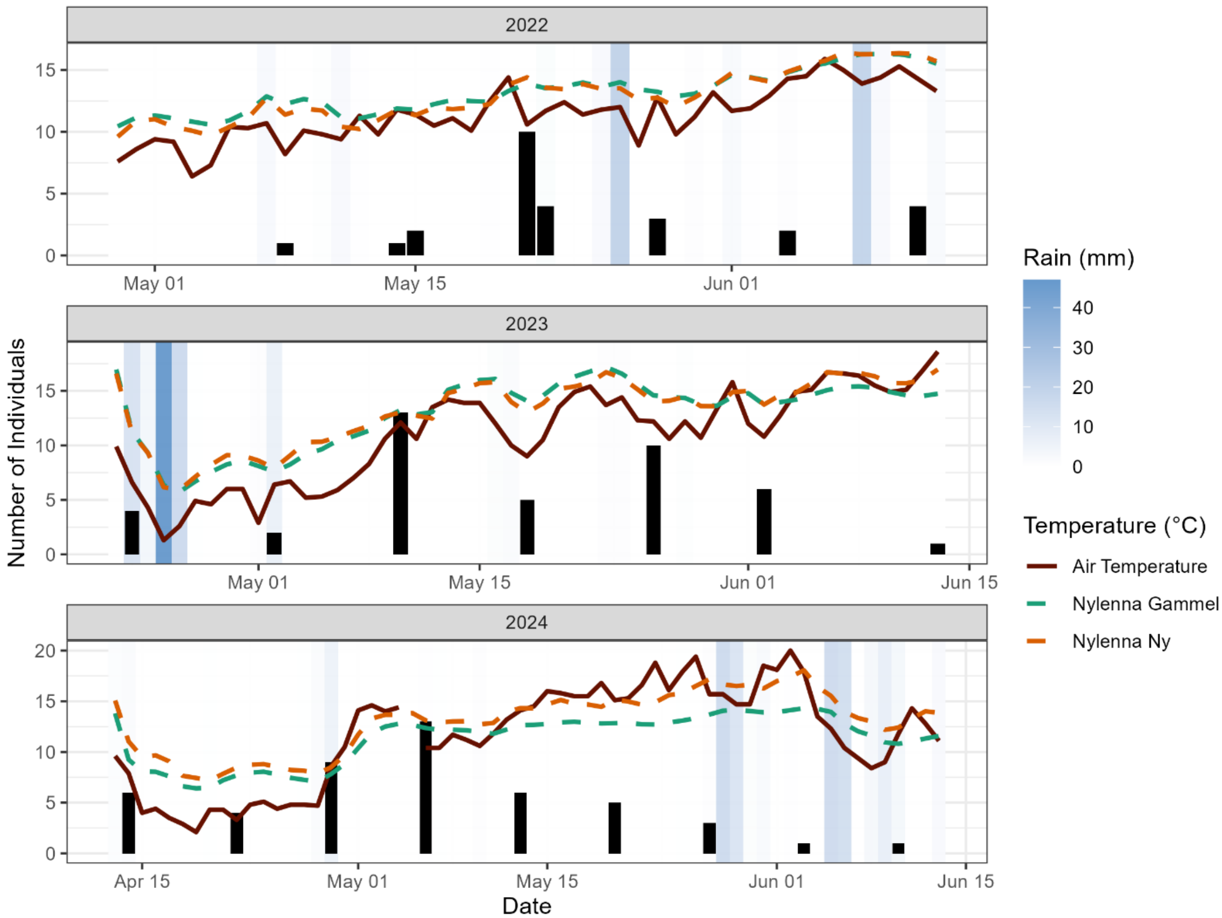

Figure S3: The graph shows the timing and number of pond switches between the Nylenna ponds as well as the daily mean air temperature, the daily mean pond temperatures and daily rain fall. Weather data were retrieved from the weather station Ås – Rustadskogen on Norsk Klimaservicesenter (Norsk Klimaservicesenter, 2024). If there were missing values, they were added from the Ås weather station. The water temperatures of the ponds were from the temperature loggers.

Generalized linear regression with negative binomial distribution revealed significant influence of year ($p = 0.002$ for 2023 and $p = 0.001$ for 2024), but air temperature, pond temperature and rain did not significantly affect the number of pond switches ($p = 0.137$, $p = 0.290$ and $p = 0.298$, respectively).

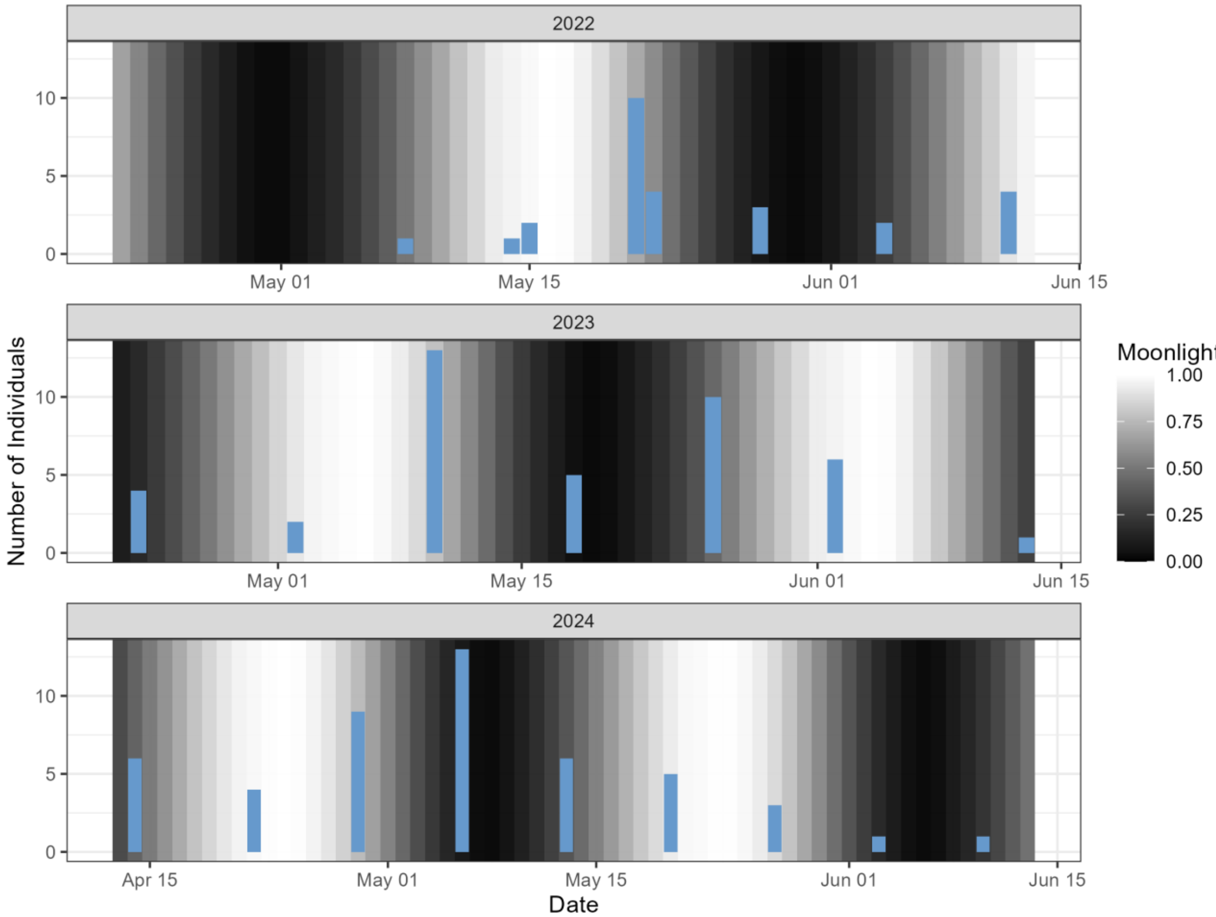

Figure S4: The graph shows the number of pond switches between the Nylenna ponds by year and moonlight. Moonlight is displayed in the background with the color scale of black (new moon) to white (full moon). The moonlight data was specific for Ås and retrieved from timeanddate.no (timeanddate.no, 2022, 2023, 2024). The average of the light measurements from the day before and after was used if there was missing moonlight data.

I also ran a negative binomial distribution model to examine the influence of moonlight and year on movement counts (Figure S4). I found no statistically significant relationship between movement counts and moonlight ($p = 0.242$). There were significant differences between years ($p = 0.003$ for both 2023 and 2024). These results can be partly explained by 2022 being the first year of data collection, meaning pond switches were only detected as individuals were recaptured again over time.

However, more research is needed on the topic. There is some uncertainty around the results as data was only collected once a week (twice a week in 2022) and the newts may have moved earlier than the night before data collection. In fact, they may also have moved prior to the previous data collection event as not every individual was caught every week.

Number of Traps and Total Catch

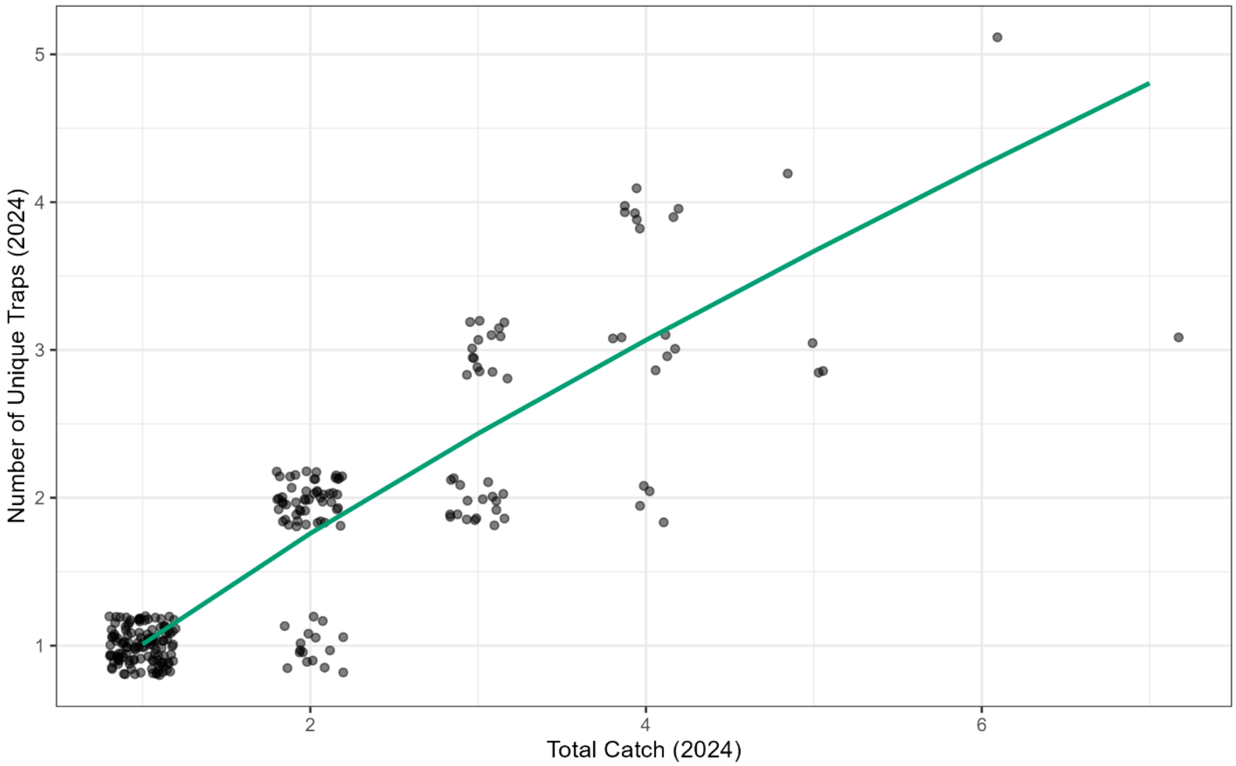

Figure S5: The estimated relationship between the number of traps a newt was caught and the number of times it was caught in total in 2024. The original observed data is displayed as points in the background.

Table S1: The results for the glm with poisson distribution of the relationship between the number of traps a newt is caught and the number of times the newt is caught in total for 2024. The explanatory variable is log-transformed as it improved the model fit to the data.

Explanatory variable	*Estimate*	*Std. Error*	*Z*	*P*
Intercept	0.009	0.0804	0.109	0.913
Log(Number of Catches)	0.802	0.089	8.992	<0.001

Trap Catch

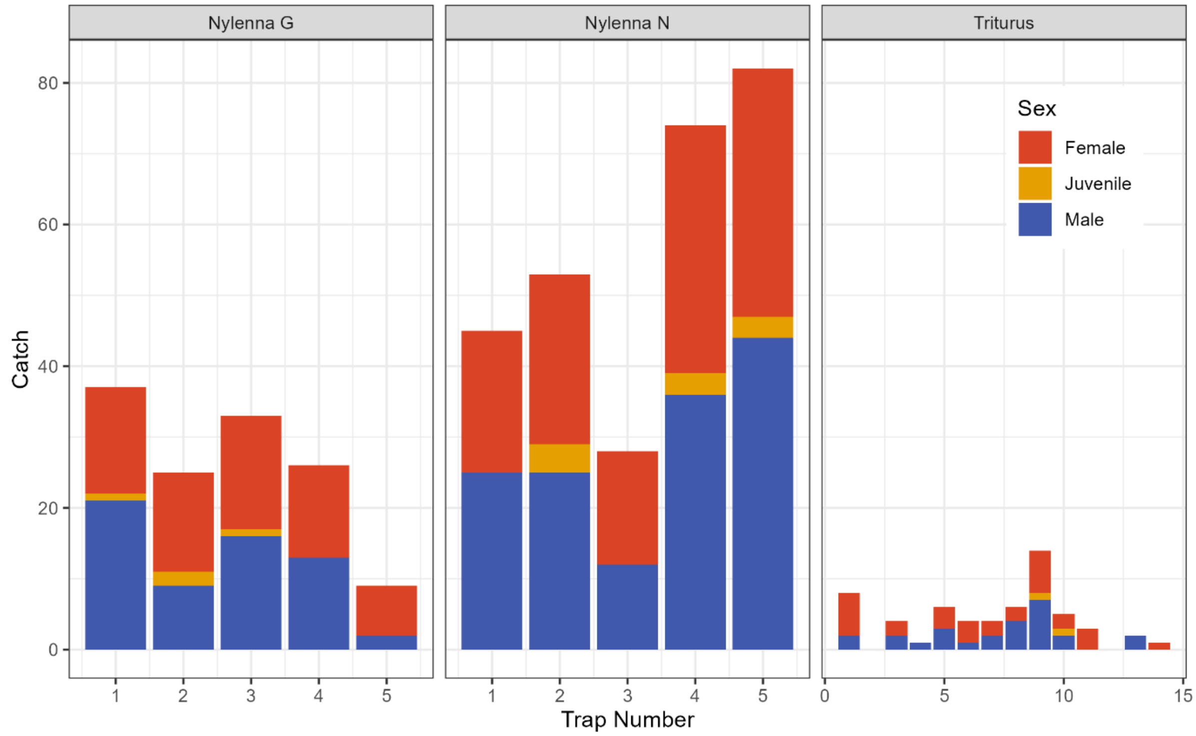

Figure S6: Total trap catches for each pond in 2024.

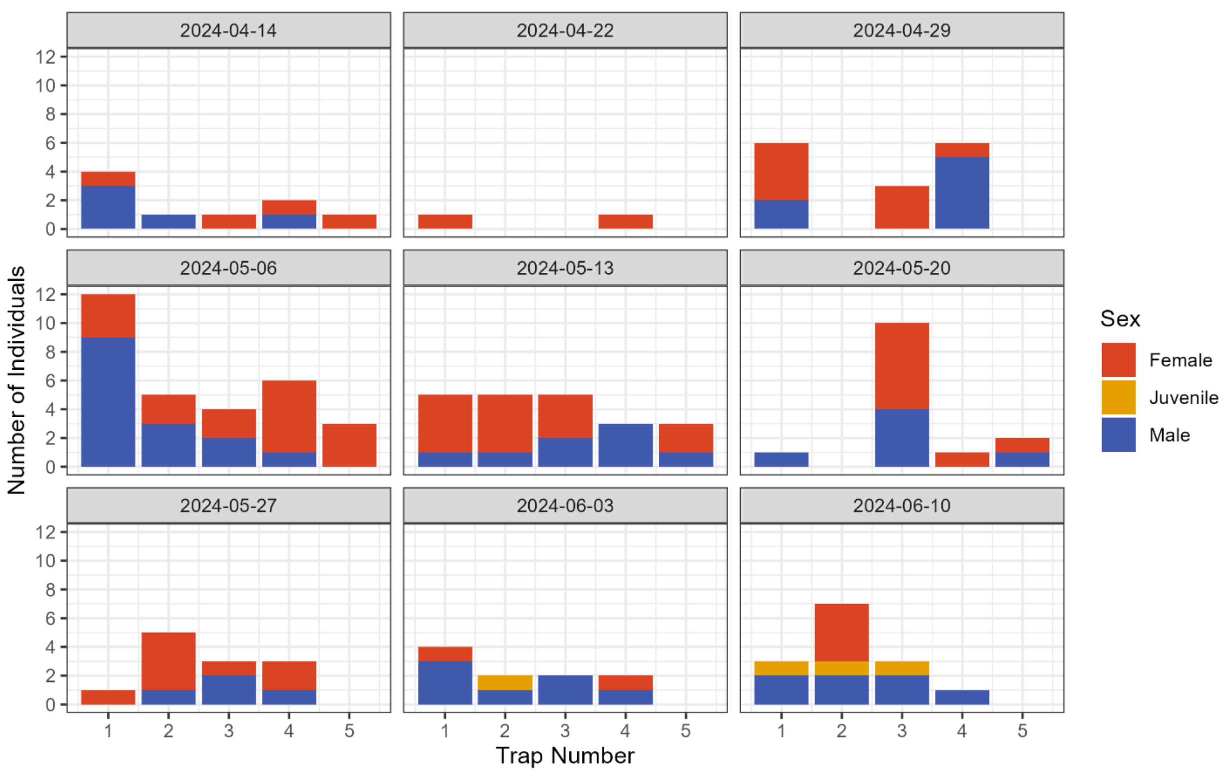

Figure S7: Trap catch by date for Nylenna Gammel in the 2024-season.

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