Conservation and development of great crested newt (*Triturus cristatus* Laurenti, 1768) populations in the west and south-west of Luxembourg

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Abstract. For this paper, we analysed a large dataset of amphibian records collected over several decades with regard to the distribution of the great crested newt (*Triturus cristatus*) in the western and south-western parts of Luxembourg. We linked these data to another dataset containing ponds created or restored by the syndicate for nature conservation SICONA to assess the success of said conservation measures with regard to great crested newt conservation. In more detail, we analysed the dataset on the level of individual ponds to gain insight into the process and timing of pond colonization, the validity of null observations as a means to determine great crested newt absence, the calculation of average trap catches as a rough indicator for population strength and the co-occurrence of the great crested newt with other amphibian species. Our results indicate that the observed expansion of the great crested newt in the study area can be linked to the creation and restoration of ponds. In most new ponds with great crested newt occurrence, arrival of the species was detected within the first ten years after creation. In this context, the proximity to ponds with high average trap catches appears to play an important role in the colonization process. We discuss our results in terms of their usability for applied great crested newt conservation and make suggestions for further research.

Keywords. Amphibian conservation, distribution, population development, colonization, pond creation, habitat management.

1. Introduction

The great crested newt (Fig. 1), although officially no longer considered a threatened species according to the Red List of Amphibians of Luxembourg (Proess 2016), remains at risk due to the direct loss of spawning waters through drainage and overbuilding, deterioration of habitat characteristics in the vicinity of spawning grounds through agriculture and forestry, as well as to an increasing isolation of sub-populations mainly caused by settlement expansions and the construction of new traffic routes (Proess 2016, Lüttmann et al. 2013, Glandt 2011). The great crested newt is legally protected under national (Mémorial 2009) and European law (JOCE 1992) and is, as a species of community interest, a preferred target of special protection measures.

SICONA, as a municipal syndicate for nature conservation in the western and south-western parts of the country, is responsible for a majority of great crested newt populations in Luxembourg, thus making it a key player for the species' protection on a national scale. Since its foundation over 30



Fig. 1. Great crested newt (male). Photo: Liza Glesener, 30/04/2022.

years ago, SICONA has created or restored (i.e. desilted or enlarged) over 500 ponds on behalf of its member municipalities, with surface areas ranging from eight to 6,200 square meters and spread over 325 sites. 467 of these ponds, as well as an additional 20 ponds not created or restored by SICONA, are currently under SICONA management. Furthermore, SICONA has established a monitoring scheme to follow the great crested newt populations within its operating area and ascertain the success of its conservation efforts. Between 2000 and 2021 a total of 711 trap nights in 420 ponds were conducted by or on behalf of SICONA.

This paper aims to provide answers to questions relevant to great crested newt conservation and thus contribute to improving practical measures for the species within the study area and beyond. Specifically, we examined which parts of the study area are currently colonized by the great crested newt and how the species' distribution has evolved over time. In addition, we analysed the available data with regard to the most likely source populations for great crested newt dispersal, the colonization of newly created ponds and the association of the great crested newt with other amphibian species.

2. Species ecology

Great crested newts colonize a wide range of habitats in semi-open and open landscapes of the lowlands and hills with a mosaic of farmland, grassland and woody biotopes (Glandt 2008). The presence of suitable terrestrial habitats in the immediate vicinity of suitable spawning habitats is crucial for permanent site colonization. An adequate density of suitable migration routes between sites is an important prerequisite for the colonization of an entire region. While terrestrial habitats are usually located in the immediate vicinity – and no further than several hundred metres – of the spawning waters (Glandt 2008, Acemav coll. 2003), migrations of up to one kilometre from the spawning waters are possible (Brunken 2004, Stoefer & Schneeweiß 2001). The availability of four to eight suitable sites per square kilometre is considered optimal by Acemav coll. (2003).

Suitable terrestrial habitats include structures rich in cover such as grassland fallows, wet meadows, bushland or wooded areas, which are used as hunting habitats and refuge in unfavourable weather (Langton et al. 2001). Hibernation usually takes place in frost-proof terrestrial quarters such as rock crevices, burrows and root cavities, under moss or leaf litter, in cairns, sand piles or under rotten tree trunks (Glandt 2011, Acemav coll. 2003). In addition, autumnal return and hibernation in spawning waters is possible (Glandt 2011, Laufer et al. 2007), particularly for juveniles and adult males (Acemav coll. 2003, Thiesmeier & Kupfer 2000).

While the great crested newt prefers deep and shady breeding pools in some parts of France, the opposite was observed in Lux-

embourg, where the species mainly spawns in open, sunny meadow ponds, lakes and oxbows, preferably devoid of fish (Proess 2016, Acemav coll. 2003). Mating and spawning take place from March onwards. An average of 200–400 eggs per female (Laufer et al. 2007, Acemav coll. 2003, Thiesmeier & Kupfer 2000) are each wrapped in a leaf of submerged pond vegetation. The larvae emerge three to five weeks after egg laying (Acemav coll. 2003, Langton et al. 2001), with the exact duration being largely dependent on water temperature (Thiesmeier & Kupfer 2000). After spawning, adult individuals may stay in the breeding pond for five to six months (Glandt 2011) but may also leave it after as little as a few days (Hagström 1979). Juveniles most commonly leave the breeding ponds between August and November (Thiesmeier & Kupfer 2000).

3. Materials and Methods

3.1. Study area

The study area corresponds to the SICONA territory which includes 42 municipalities in the west and south-west of Luxembourg and covers 834 km² (status: November 2021). The area is part of the three ecological regions Ösling, Gutland and Minette in the south-west of the country (Fig. 2). The Ösling foothills mark the southern edge of the Ardennes massif and lead over from the Ösling moun-

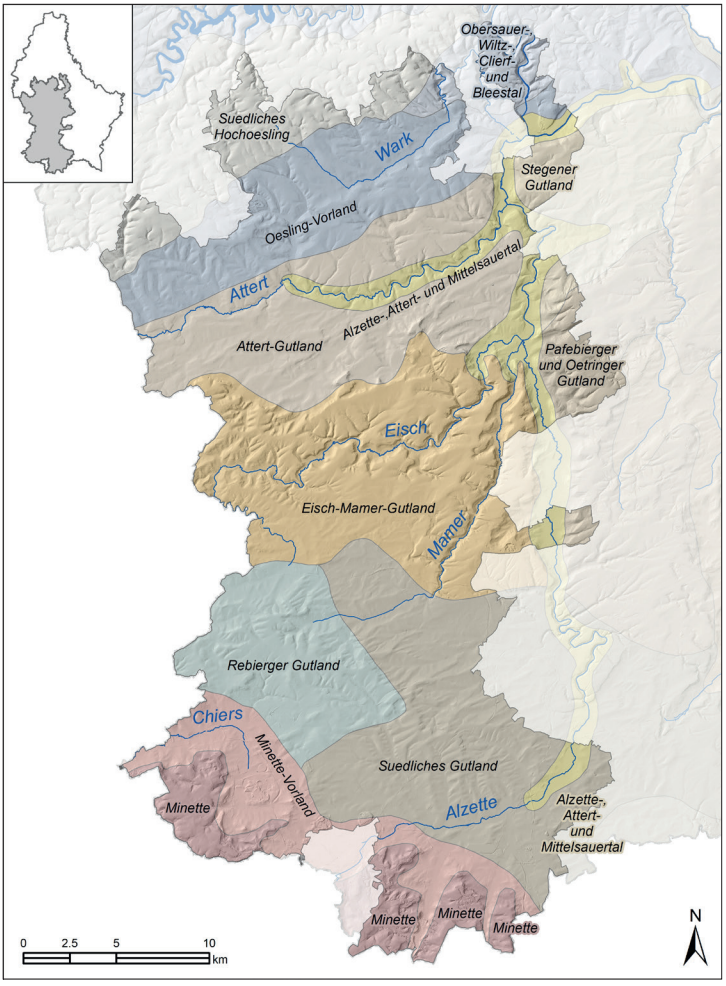


Fig. 2. Study area in the west and south-west of Luxembourg with the SICONA territory highlighted and underlaid with the ecological sectors. Data source: © Administration de la nature et des forêts (ecological sectors), © Administration du cadastre et de la topographie Luxembourg (digital elevation model, hydrological data).

tains to the rolling hills of the Gutland. The geological subsoil of this area consists of Triassic formations with Buntsandstein, Muschelkalk, and Keuper. Predominant soils in this region are loamy and clayey brown earths and luvisols. In its eastern part, the predominant soils consist of sand and clay above a bedrock of bunter sandstone or shell sandstone. The central Gutland consists of various natural subregions (ecological sectors) and is characterised by a hilly landscape with stepped slopes (cuesta landscape). The underlying bedrock in this area is diverse and consists of Keuper and liassic sandstones ("Luxembourg sandstone") in its northern and central part as well as of liassic marls and limestones in the southern part. The resulting subsoils in the marl and Keuper areas are mostly impermeable. Only in the central study area, around the Mamer and Eisch valleys, a bedrock of Luxembourg sandstone leads to sandy, well-drained and often podzolic soils. In the southern part of the study area, the Minette region is characterised by a softly undulating landscape in its foreland with isolated witness buttes leading over to the adjoining Dogger ridge. In this area, the predominant soil types are heavy, clayey brown soils, luvisols, and terra fuscae with mostly impermeable subsoils (Service géologique 2018, Schneider 2011, Administration des Eaux et Forêts 1995, Service de pédologie 1999).

3.2. Data collection

The complete amphibian dataset collected by SICONA (2000–), complemented by additional amphibian data held by the National Museum of Natural History (MNHNL 2000–), forms the backbone of our analysis. At time of retrieval (12/11/2021), both datasets combined held 12,201 samples gathered in the study area. Each sample marks either an actual survey event (e.g. trapping, lamping or netting session) or a subset of species records gathered at a specific survey event (e.g. the contents of a single trap of several). Moreover, samples can also represent random encounters with single individuals of amphibian species. More than half of the samples can be attributed to survey methods with a high likelihood of detecting great crested newt (trapping or lamping) – among these 3,013 samples gathered within the scope of SICONA's great crested newt monitoring scheme and related projects.

Within the study area, location and shape of most ponds situated in open grasslands as well as the location of many forest ponds were collected and digitised via ESRI ArcMap. The resulting pond dataset includes ponds as (re)created by SICONA and additional ponds recorded within the framework of the national biotope inventory in open landscapes (Administration de la nature et des forêts 2021). Furthermore, records of particular interest (i.e. ponds containing great crested newt populations) that were initially missing from these datasets, were located via geographically precise species records and added to the pond dataset. The (re)creation dates of ponds created or restored by SICONA were retrieved from the syndicate's dedicated site management database. (Re)creation dates of other ponds past the year 2000 were noted where known. In some cases, these dates were approximated via a time series of aerial photographs (Administration du cadastre et de la topographie du Grand-Duché de Luxembourg 2001–2020).

3.3. Data preparation and analysis

Great crested newt records contained in the dataset were aggregated on the basis of a 1 x 1-kilometre grid (LUGRID) in order to visualise spatial and temporal development of the species' distribution within the study area. The first two time periods (1960–1979 and 1980–1999) cover twenty years each, the third period (2000–2009) ten years and the last period (2010–2021) twelve years. Longer periods were chosen for the first two periods because records are sparse, as systematic surveying of amphibians in Luxembourg only started in the late 1990s (Proess 2016). Thus, these data were grouped over longer periods to show a more comprehensive picture. The last period is two years longer than the second to last purely for practical reasons. However, since we do not make direct statistical comparisons between the different periods, we do not see any methodological problem in comparing periods of different lengths.

In order to standardize the dataset, each record was assigned a level of geographical precision derived from the stored coordinate information and a unified sampling method was inferred from the data. These steps were necessary to allow for filtering of samples with specific sampling methods and to generate great crested newt absence records (null observations). We generated these null observations based on the following conditions: the original sample had to be obtained either from traps left in the pond overnight (sampling type: trap, Fig. 3) or via a lamping survey (sampling type: active lighting) and the original sample had to contain at least one of the following species with similar habitat requirements to those of the great crested newt: common toad (*Bufo bufo* Linnaeus, 1758), common tree frog (*Hyla arborea* Linnaeus, 1758), alpine newt (*Ichthyosaura alpestris* Laurenti, 1768), palmate newt (*Lissotriton helveticus* Razoumovsky, 1789), smooth newt (*Lissotriton vulgaris* Linnaeus, 1758), water frog (*Pelophylax* spec. Fitzinger, 1843), grass frog (*Rana temporaria* Linnaeus, 1758). The underlying assumption was, that if great crested newt had been present, the likelihood of it being recorded would have been high in these cases.

When analysing the dataset in ArcMap, it quickly became apparent that, even for geographically precise records, the geographical location assigned to the species records does not always overlap with the pond the data was gathered in. Within ArcMap, we therefore employed an incremental buffer operation around the digitised ponds (buffer steps: 0, 1, 5, 10, 20, 30, 40, 50, and 100 m) in order to automatically assign great crested newt presence and absence records to the closest pond in our pond dataset. Thus, only records with a minimal precision of 100 metres were included and any records with a distance of more than 100 metres from any pond were discarded. The automatically generated allocation of species records to nearby ponds was then checked and, if necessary, manually corrected.

A time sequence over the period spanning 2000 to 2021 was used to analyse the temporal development of presence and absence records for each of the ponds cre-



Fig. 3. Two types of funnel trap used for great crested newt monitoring. To the left a bucket trap ("Ortmann-Eimerreuse") adapted after Siedenschnur & Schikore (2014), in the centre and to the right two PE-frame-mesh traps ("Gaze-Kasten-Reuse"). Photo: Liza Glesener, 02/08/2021.

ated by SICONA in the same period and for which survey data was available (n = 255). This allowed us to determine time spans after which colonization was first recorded, while controlling for earlier surveys recording absence. In a further analysis, we used abundance data referring explicitly to either adults or juveniles to calculate the average number of metamorphosed individuals trapped per night and pond, in order to use this as a rough indicator for population strength (in this context, null observations were not taken into account). This analysis is based on 217 trap nights in 94 ponds. The year 2000 was deemed a good cut-off point, as it marks the start of the time period where more precise geographical localisation of data is available and surveying has become more effective.

Finally, we searched for correlations between great crested newt occurrence and the presence of other amphibian species. The available dataset was analysed for co-occurrence of these species, defined in this context as common presence in the same pond and at the same time (year-level). Amphibian nomenclature follows Speybroeck et al. (2010). Data preparation and analysis was conducted via Microsoft Excel and ESRI ArcMap.

4. Results

4.1. Distribution of great crested newt (1 x 1-kilometre grid)

Within the study area, great crested newt distribution derived from our data shows local hotspots in the southern Gutland and in the Minette region, as well as further north in the vicinity of the Attert valley and the Ösling foothills. By contrast, in the central part of the study area (i.e. in the surroundings of the Mamer valley and Eisch valley), only very few records of the species were found. This area seems to be largely uninhabited by the great crested newt (Fig. 4).

A comparison of the different time periods shows notable temporal and spatial differences in the distribution of the species across the study area (Table 1): from 1960 to 1979, the species was recorded in only 15 of 987 1 x 1-kilometre grid cells within the study area (frequency = 1.5 %). All records in the period were gathered in the southern half of the study area with apparent clustering in municipalities bordering the capital. In the time period between 1980 and 1999, great crested newt presence was recorded almost all across the southern part of the study area, as well as in the northern region around the Attert valley and further north in fringes of the Ösling foothills. The resulting distribution for this period already clearly resembles the current distribution of the species across the study area. With 40 out of 987 grid cells, the species shows a much higher frequency across the study area (4.1 %) than in the preceding time period. From 2000 to 2009, great crested newt distribution shows a similar pattern, albeit with a slightly lower frequency across the grid cells of the study area (3.3 %). In the most current time period from 2010 to 2021, 75 out of 987 grid cells (7.6 %) contain records of the great crested newt. Compared to the period between 2000 and 2009, the frequency has more than doubled. However, there are currently still 31 grid cells without recent records, but where the species was known to occur in the past. 56 of 75 grid cells (74.7 %) with recently recorded presence of great crested newts also contain ponds created or restored by SICONA whereas only one fourth of the species' recently detected occurrences lie in grid cells without such ponds (Fig. 4).

4.2. Colonization of newly created and restored ponds

In terms of individual water bodies in the study area, 516 out of 947 ponds contained in the pond dataset could be linked to great crested newt records. These records include 120 ponds where great crested newts were found and 396 ponds with null observations only, which were generated as outlined in chapter 3.3. In reverse, 99 % of all great crested newt samples collected in the study area over the years 2000 to 2021 could be assigned to a pond. Among the ponds linked to great crested newt records, 255 were created and 27 were restored by SICONA in the time period between 2000

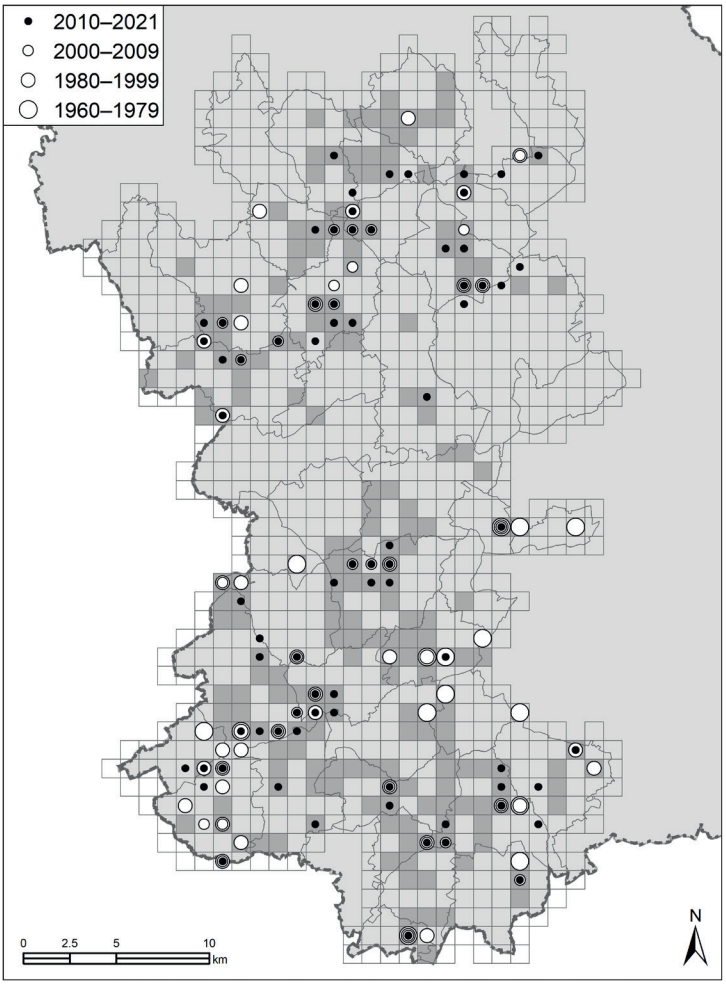


Fig. 4. Great crested newt distribution in the study area shown on the basis of a 1 x 1-kilometre grid and for different time periods. Grid cells highlighted in grey contain water bodies created or restored by SICONA.

and 2021. Another 85 ponds precede this period. An overview of all newly created or restored ponds, grouped by period, is shown in Table 2.

To date, great crested newts have been found in 36 of the 373 ponds created by SICONA between 2000 and 2021 (Fig. 5). These findings represent 14.1 % of all the ponds in that category that have been surveyed (n = 255). When viewing only the ponds created between 2000 and 2009, the percentage rises to 22.9 % (n = 83). It is noteworthy that 85.6 % of all ponds created in the first time period have been surveyed at least once, while the same is true for only 62.3 % of the ponds created in the second time period. For the 33 ponds that were restored between

Table 1. 1 x 1-kilometre grid cells with presence of the great crested newt.

Time period	Grid cells (total = 987)	Frequency
1960–1979	15	1.5 %
1980–1999	40	4.1 %
2000–2009	33	3.3 %
2010–2021	75	7.6 %

Table 2. Numbers of newly created or restored ponds, grouped by time period.

Period of creation or restoration	Before 2000	2000–2009	2010–2021	Total
Number of ponds	101	106	300	508

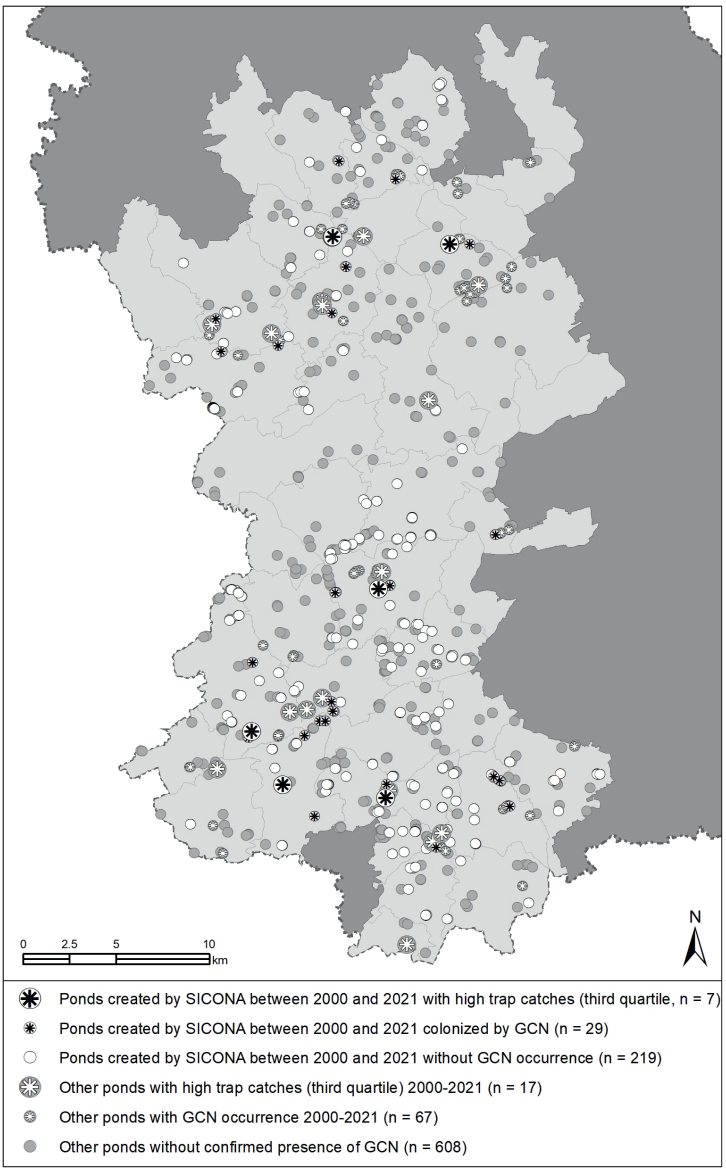


Fig. 5. Great crested newt (GCN) pond colonization in the study area for the time period from 2000 to 2021 with indication of ponds with high average trap catch.

2000 and 2021, the data is inconclusive and was omitted from further analysis. Three possible colonizations by great crested newt following the restoration of ponds were detected, but there is no sufficient proof of previous absence. A breakdown of our findings can be seen in Table 3, while Figure 5 visualises the distribution of colonized and uncolonized ponds with indication of high average trap catch (cf. chapter 4.3.).

Figure 6 shows that first records of colonization were common in the two classes covering the first/second year (16.7 %) and the third/fourth year (13.9 %). Another 25 % of colonization events were recorded five to six years after pond creation. Although many ponds were colonized after only a few years, 9.6 % were still not colonized by the great crested newt after more than 15 years. In this context, we need to mention that only random sampling occurred, and none of

Table 3. Colonization events in newly created ponds, grouped by time period and combined for both periods.

Period of creation	2000–2009		2010–2021		Both periods	
	n	%	n	%	n	%
Ponds (colonized)	19	22.9	17	9.9	36	14.1
Ponds (not colonized)	64	77.1	155	90.1	219	85.9
Ponds (surveyed)	83	85.6	172	62.3	255	68.4
Ponds (not surveyed)	14	-	104	-	118	-
Ponds (total)	97	-	276	-	373	-

the ponds was systematically searched for the first appearance of great crested newts. Incidentally, the time sequences showed that in 25 % of all colonized ponds, two great crested newt presence records were separated by at least one trap night indicating the absence of the species.

4.3. Average trap catches

When calculating the average number of adult and juvenile newts trapped per night and pond over the last 21 years, clear differences become apparent: while the median lies at 5 individuals per night and pond, the third quartile is 14.7, and the highest number of adult and juvenile newts recorded in a single pond, averaged over the number of catches, is 70.8 (Fig. 7). The visualisation in ArcMap shows a relatively even distribution of the ponds in the highest interquartile range (n = 24) throughout the area currently populated by the great crested newt (Fig. 5).

4.4. Association with other amphibian species

The great crested newt was found to be most frequently associated with the three other native newt species (Fig. 8): In 215 cases, the great crested newt occurred together with the alpine newt (*Ichthyosaura alpestris*). This corresponds to 75.2 % of great crested newt occurrences. Association of the great crested newt with the palmate newt (*Lissotriton helveticus*) was found in 184 cases (64.3 % of great crested newt occurrences) and with the smooth newt (*Lissotriton vulgaris*) in 162 cases (56.6 % of great crested newt occurrences).

Co-occurrence with pond frogs (*Pelophylax* spec.) was found in 154 cases (53.8 % of great crested newt occurrences), whereas co-occurrence with the grass frog (*Rana temporaria*) was much less common with a total of 71 co-occurrences (24.8 % of great crested newt occurrences). In addition, great crested newt co-occurrence was found with the tree frog (*Hyla arborea*, 15 cases = 5.2 % of great crested newt occurrences), the common toad (*Bufo bufo*, 14 cases = 4.9 % of great crested newt occurrences) and the midwife toad (*Alytes obstetricans* Laurenti, 1768, 2 cases = 0.7 % of great crested newt occurrences).

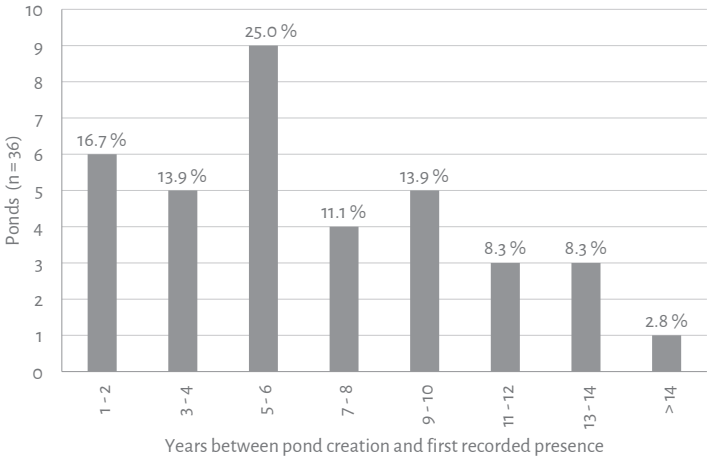


Fig. 6. Time intervals between pond creation and first recorded presence of the great crested newt.

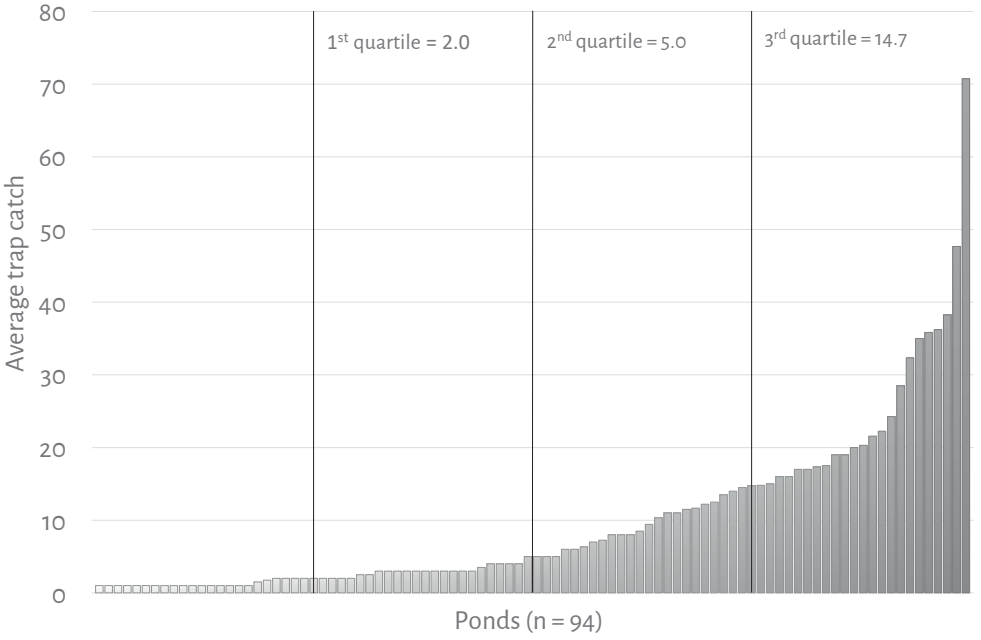


Fig. 7. Average number of metamorphosed individuals (juveniles and adults) trapped per night and pond over the years 2000 to 2021, with indication of quartiles for average trap catch.

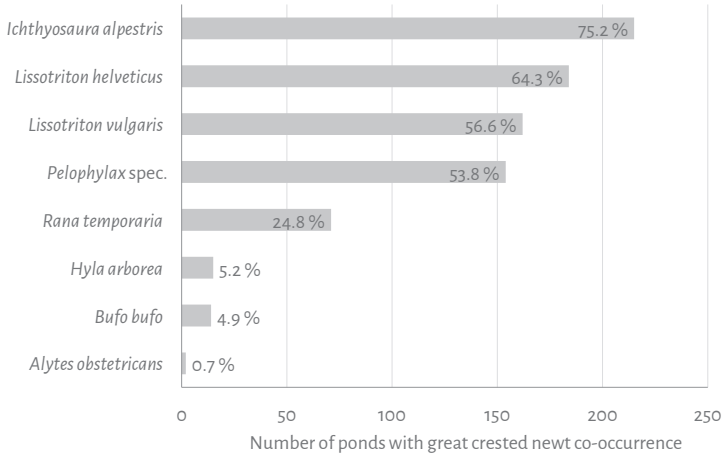


Fig. 8. Co-occurrence of the great crested newt with other amphibian species.

Although the following amphibian species are also present in the study area as well as in our dataset, co-occurrences of the great crested newt with the yellow-bellied toad (*Bombina variegata* Linnaeus, 1758), the natterjack toad (*Epidalea calamita* Laurenti, 1968), and the fire salamander (*Salamandra salamandra* Linnaeus, 1758) were not found at all.

5. Discussion

5.1. Population development and spread (1 x 1-kilometre grid)

The historical distribution of the great crested newt derived from our dataset for the period from 1960 to 1979 shows hotspots to the west and south of the capital, as well as sporadic records from the Minette region. Although

there is no evidence of great crested newt occurrence in the northern part of the study area from this period, we presume that the species was already present. Data available from this period are assumed to be patchy and not suitable to show an accurate picture of the great crested newt distribution. Instead, these data presumably indicate areas where the species was found at the time rather than its actual distribution. This situation appears to change with regard to the period from 1980 to 1999: data from this period already resemble the current distribution pattern of the species, with hotspots in the southern Gutland and the Minette region, as well as in the Attert valley and the Ösling foothills. Data from the period from 2000 to 2009 further refine this picture, but do not close further gaps, so that at this point it can be assumed that the distribution of the great crested newt in the study area is almost completely known. Thus, we assume that recent data from 2010 to 2021 can be used to show actual changes in the distribution of the species within the study area. The increase by 40 colonized grid cells (i.e. plus 60.6 %) observed in this period thus shows an actual expansion of the species between 2010 and 2021. Moreover, a comparison with grid cells containing ponds created or restored by SICONA shows that the majority of the recently colonized grid cells (74.7 %) also contains such ponds. Together with our results from chapter 4.2., we therefore conclude that the systematic creation of new ponds over the past two decades promoted the observed expansion of the great crested newt and that our results show evidence for the effectiveness of species protection measures taken for the great crested newt in the study area.

The distribution gap in the Eisch-Mamer-Gutland reflected in our data is likely due to the prevalence of Luxembourg sandstone in the area. The subsoil formed from this bedrock is permeable, and naturally prevents the formation of water bodies suitable for the great crested newt. The connection between great crested newt presence and the occurrence of damming subsoils favouring the development of natural small water bodies has already been mentioned by Proess (2016) as an explanation for the natural distribution of the species in Luxembourg.

5.2. Dispersal to newly created ponds

The colonization of only 14.1 % of the ponds created and surveyed in the period 2000–2021 seems somewhat unsatisfactory at first glance. It can be relativized by several factors however, with location being a major one. Assuming a maximum dispersal distance of one kilometre (Brunken 2004, Stoefer & Schneeweiß 2001), it is clear that natural colonization of ponds by great crested newts can only originate from source populations in the close proximity. This is reflected well in Figure 5 which shows a strong spatial relationship between existing great crested newt occurrences and newly colonized areas. In a few cases however, ponds at a greater distance from any known populations were also colonized, suggesting established great crested newt populations in the direct vicinity that have not been detected yet. Although SICONA puts an emphasis on securing sites close to existing great crested newt populations for the creation of new ponds, the syndicate's conservation efforts are dictated by availability. New ponds are created where circumstances allow it (i.e. where land is available) and their spatial location may not allow for colonization by the great crested newt in the short-term. Nevertheless, these ponds fill an important role in terms of habitat connectivity and can be reached by the great crested newt in the long-term.

A second key factor is the time frame available for colonization. Intuitively, ponds created within the time period from 2010 to 2021 and particularly those created in the latter half of this period have a lower chance to be already colonized by now than those created in the time period from 2000 to 2009. The percentage of colonized ponds calculated for ponds created between 2000 and 2009 (22.9 %) should indicate a closer approximation to the real colonization rate than that of the period from 2010 to 2021 or that of both periods combined. Other factors hindering dispersal of amphibian species, like the motorway network and dense urbanised areas are assumed to have further influence in this context (Proess 2016, Lüttmann et al. 2013, Glandt 2011) but were not investigated in the current study.

The location of many of the colonized ponds in close proximity to ponds with a high average trap catch (Fig. 5) underlines the assumption that these are the ponds with high population sizes suited to act as source populations for further spread. However, we also identified seven ponds with high average trap catch among ponds created and colonized within the last 21 years. We can only assume that conditions in these ponds are particularly suited for great crested newts and suggest further analysis.

Although we were able to identify recently colonized ponds, our data does not allow us to determine the exact timing and line of dispersal. Our analysis merely provides the time interval between pond creation and first detection of great crested newt, which, for almost half of the ponds, coincided with the first survey after creation. Nonetheless, our results provide a good indication that, under suitable conditions, colonization of newly created ponds often occurs as early as the first six years after pond creation. Longer time spans between pond creation and colonization can either be explained by late monitoring or by the distance to source populations – a late colonization event could simply be one in a chain of subsequent colonizations of a number of spatially related ponds functioning as stepping stones in habitat connectivity. Finally, it is possible that prior colonizations were not detected even though trapping did occur. Great crested newts are considered highly faithful to their chosen breeding ponds (Laufer et al. 2007, Thiesmeier & Kupfer 2000). Assuming an annual presence of the great crested newts in a pond once colonized, our results suggest that non-detection of great crested newts, particularly as the result of one single trap night, is not a definite indicator for absence. We can therefore add our own experience to the statements of many other authors as to the relative difficulty of detecting the species (Thiesmeier & Kupfer 2000). Likewise, it can be implicated that a sudden absence of great crested newts from a pond need not be an immediate reason for concern, but requires further survey effort to be confirmed or refuted.

5.3. Average trap catches as a rough indicator for population size

The detection rate of great crested newts, i.e. the fraction of the entire population that is detected in a single trap night, can differ enormously: values reported on the basis of several long-term studies vary from 0.34 to 45 % (Jarvis 2010, Cooke 1995, Karlsson 2004, Langton et al. 2001). Data from single trap nights are thus not suited to infer great crested newt population size estimates. In terms of the number of individuals caught per trap night, our own analysis shows substantial differences between catches resulting from different trap nights at the same pond in the same year, confirming the abovementioned statement. The observed differences in catch numbers can be the result of any or a combination of the following factors: timing of the survey, number of traps, arrangement of traps in a pond, pond structure and vegetation, weather conditions, and even the lunar cycle or characteristics of the preceding winter (Jarvis 2010, Ortmann 2009, Deeming 2008, Thiesmeier & Kupfer 2000).

Nonetheless, our analysis suggests that average adult and juvenile catches do outline differences between ponds and that these differences can be regarded as a rough indicator for low, medium and high population sizes. The reliability of average catch numbers with regard to population size increases with the number of trap nights. In this respect, our analysis was limited by the total number of trap nights conducted, their spread over a long time period, and partly also by imprecise documentation of sampling types and catch numbers. Particularly the combination of low catch numbers and a small number of trap nights can lead to high degrees of uncertainty in our analysis. The resulting low average catch number can reflect low population size just as much as unfortunate trapping conditions. High average trap catches, on the other hand, indicate the baseline for a minimum population, even if they cannot be used to estimate true population sizes. While the use of average trap catches to categorize populations compensates for trapping uncertainties and natural yearly fluctuations in population size – which can be considerable (Langton et al.

2001, Cooke 1995, Blab 1986) – it cannot be used to show real fluctuations in time. These can only be established through thorough and regular surveying of specific ponds.

5.4. Species associations

In our study, great crested newt populations occurred most frequently together with one or more of the three other native newt species. This is in line with the findings of Proess (2016), who also described a frequent association of great crested newt populations with other newt species in Luxembourg.

However, while other studies particularly emphasize the pairing with smooth newt (Proess 2016, Maletzky et al. 2007), our results show that in the study area, the alpine newt is most commonly associated with great crested newt. One reason for these differences could be that we did not investigate co-occurrence of species via individual catch events where individuals of both species were caught together, but rather compared the records available for a water body over a whole year. Moreover, alpine newt records were by far the most frequent newt records in our dataset: with 1,198 records, the number of alpine newt records was higher than that of palmate newt records (1,046) and almost twice the number of smooth newt records (608). Glandt (2015) describes the alpine newt as extraordinarily variable in terms of the nature of both terrestrial habitats and spawning waters, which may explain the wide distribution of the species. With regard to Luxembourg, Proess (2016) states that the alpine newt is as widespread as the palmate newt, with the alpine newt tending to form larger populations, making it the most common newt species in Luxembourg. The more frequent sympatry of alpine newt and great crested newt in our study could thus also be influenced by the generally high abundance of the alpine newt in our study area. On the other hand, when comparing the share of smooth newt detections in the total number of detections (9.4 %) with the share of smooth newt detections in ponds harbouring great crested newt (56.6 %), it becomes apparent that the smooth newt was found six times more frequently in ponds with great crested newt than would be expected from its general frequency in our dataset alone. This finding can be interpreted as in line with the abovementioned statements from Proess (2016) and Maletzky et al. (2007) showing common habitat requirements of both species.

Among the frogs, water frogs (*Pelophylax* spec.) and to a lower extent, grass frogs (*Rana temporaria*) were most frequently associated with the great crested newt. In terms of the water frogs, this reflects the similar habitat requirements of the species: both the great crested newt and water frogs of the genus *Pelophylax* prefer sunlit, nutrient-rich ponds in open landscapes (Proess 2016, Baker et al. 2011). On the other hand, the grass frog is a common species inhabiting a wide range of different types of water bodies (Glandt 2008) so that frequent co-occurrence with the great crested newt was to be expected. Due to their toxicity and bitter taste, larvae of the common toad are not preyed upon by fish (Proess 2016, Baker et al. 2011). In his analysis of amphibian habitat determinants in south-east England, Beebee (1985) also reports a striking association between common toad and the presence of fish. Great crested newts, on the other hand, avoid ponds with fish, and are known to prey on common toad tadpoles (Langton et al. 2001), which might explain the low rate of co-occurrence observed in the present study. The common tree frog is a generally rare species occupying only 28 sites in our study area (Siebenaler et al. 2021) whereas for the midwife toad, only 16 records in our dataset could be assigned to specific ponds. Thus, our data basis about these species is not sufficient to draw any conclusions.

Habitat requirements of yellow-bellied toad and natterjack toad (both species spawn in temporary, shallow and vegetation-free waters) as well as of the fire salamander (viviparous in small, fast-flowing streams) differ largely from those of the great crested newt (Proess 2016, Laufer et al. 2007). The differences in habitat requirements of these species as compared to the great crested newt can explain why co-occurrence of these species with the great crested newt was not observed in the present study.

6. Conclusion

With the advent of funnel traps as the regional survey method of choice, thought to have occurred around 2003 (Proess 2016), monitoring for great crested newt has become infinitely more efficient. Nevertheless, uncertainties concerning trapping effort, particularly the number of traps employed, remain. A standardized method, employed on a regional scale, would be highly desirable to enhance data comparability. Such a method should not only outline the procedure in the field, but also provide detailed instructions concerning data input into the national data repository Recorder LUX (MNHNL).

Moreover, the emphasis is often placed on the collection of distribution data. While this practice has its own merits, a more focussed effort on a select set of newly created ponds would help to enhance knowledge about timing and the spatial process of dispersal: yearly surveys, starting with the year of creation, would provide more accurate knowledge with regard to the time scale required for colonization, while, when performed on a regional scale, would allow for the tracing of lines of dispersal as well. In this context, the time scale required for colonization could also be used to assess habitat suitability of the pond: structural issues at pond level may need to be redressed or dispersal routes to the pond optimized. Possible measures range from small scale habitat improvements to the construction of wildlife crossings in the vicinity of major roads (Proess & Schneider 2018, Administration de la nature et des forêts 2017, Junck et al. 2005). In some cases, the most effective method to re-establish a species may be through reintroduction (Scherzinger 2017), as initiated for great crested newt in the study area in 2021 (Glesener et al. 2021). In this context, our finding that the ponds with high average trap catches appear to function as sources for natural colonization suggests that high average trap catches can be used to define suitable source populations for reintroduction as well. In order to maintain these important populations and their function, the preservation of the sites and of a good connectivity with neighbouring sites is essential. Within this context, the recent spread of the amphibian pathogen Bsal (*Batrachochytrium salamandrovirans*) into our close border regions (Lötters et al. 2020) presents an additional challenge to great crested newt conservation and monitoring. While the pathogen was first described as a threat to the fire salamander (Martel et al. 2013), it has also been identified as a threat to great crested newt populations (Lötters et al. 2020). These developments have initiated the creation of the first official national protocol concerning disinfection and practical advice with regards to contravening the spread of amphibian pathogens, currently in preparation (Stassen et al. 2021).

Capture-mark-recapture studies at a select set of sites could provide valuable information about population size. An emphasis on less obvious source populations (i.e. those with low to very low average trap catches) could help to reassess sites that have been underestimated in the past. However, traditional capture-mark-recapture studies are expensive and time-consuming and therefore seldom executed. The successful commercialisation of a novel, automated monitoring tool currently developed by the Luxembourg Institute of Science and Technology ("Newtrap"; Mestdagh 2021) may provide a major breakthrough.

Our study confirms that the distribution of great crested newt populations in Luxembourg is expanding again after long years of decline. Furthermore, this expansion can be linked to the creation of ponds. Nevertheless, there are still gaps between the colonized parts of the study area, with the potential of holding additional great crested newt populations. A research project conducted by the faune-flore foundation and the National Museum for Natural History, with the objective to elucidate great crested newt population structure and dispersal in Luxembourg via genetic methods, may provide valuable input for future targeted conservation efforts. The project's aim is to model landscape connectivity and thus predict great crested newt movement as well as identifying natural or artificial barriers to dispersal. Added to this is the targeted

development of a site selection-algorithm to identify optimal locations for the creation of new ponds (Frantz 2021). Together with our findings, the results of this study could provide an improved basis for great crested newt conservation for SICONA and similar agencies.

The continued creation (and maintenance) of ponds, as carried out by SICONA for the last 30 years, has been considered essential for the conservation of the great crested newt by Proess & Schneider (2018). This was confirmed in the present study. In addition to the direct benefit for the great crested newt, many other species linked to small water bodies and wetland habitats are affected positively. The creation of complexes containing several ponds of varying ages, size and structure is thought to be particularly effective (Grotz et al. 2018). In order to foster spread of the great crested newt, the focus should further lie on the creation of ponds in the vicinity of woods and of other ponds, ideally with spawning populations (Proess & Schneider 2018). However, sites not fulfilling these criteria should not be discarded either, if they can contribute to the long-term expansion of great crested newt populations as part of a habitat network (Baker et al. 2011).

In general, the results of this study can be seen as a confirmation of previous efforts to protect the great crested newt in the study area, encouraging us to continue our endeavours building on the success of the last 30 years.

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