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Connectivity, land use, and fish presence influence smooth newt (*Lissotriton vulgaris*) occurrence and abundance in an urban landscape

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Introduction: Urban areas are challenging environments for wetland species with complex habitat requirements and life cycles. However, even semiaquatic species, representing such complex wetland groups, can be provided with adequate conditions through thorough understanding of their habitat requirements coupled with comprehensive wetland management.

Methods: We studied the occurrence and abundance of the smooth newt (*Lissotriton vulgaris*), a widely distributed amphibian, in an urban landscape in metropolitan Helsinki, Finland. We classified 50 randomly selected urban wetlands based on their connectivity by applying isolation scores counted using principal component analysis (PCA) and measured the occurrence and abundance of smooth newts in these locations.

Results: Our analyses showed well-connected wetland sites to differ significantly in smooth newt occurrence from both isolated and partially connected sites. Additionally, smooth newt abundance in well-connected wetlands differed from isolated sites. A PCA model with residential buildings (negative effect) and aquatic vegetation (positive effect) best explained smooth newt occurrence and total and male abundance, and female newt occurrence was best explained by a model also incorporating forest and natural open areas. Predation pressure by fish negatively influenced both smooth newt occurrence and abundance.

Discussion: Tighter networks of constructed wetlands and stricter management guidelines for urban wetland planning and fish community management could increase the suitable habitat for smooth newts in urban landscapes. Managing such areas for the common smooth newt offers potential broad benefits to the conservation of other semiaquatic amphibians and reptiles in urban wetlands and to urban wetland biodiversity in general. Our results show that smooth newt presence may indicate sustained wetland connectivity in an urban landscape and could even be used to signal successful urban planning.

KEYWORDS
amphibians, connectivity, infrastructure, newts, urban landscape, urban planning, urban wetlands, wetland conservation

1 Introduction

Freshwater wetlands are biodiverse and economically paramount ecosystems worldwide (Emerton and Bos, 2004; Dudgeon et al., 2006; Russi et al., 2013) but have concurrently become some of the most endangered and deteriorated habitats (Darwall et al., 2009; Davidson, 2014). Kingsford et al. (2016) estimated over 70% of the world's wetlands to have been destroyed or impaired, and two-thirds of European wetlands have experienced serious degradation or destruction (Amezaga et al., 2002). Urbanization is a significant driver of wetland degradation, inducing losses to connectivity and changes in water chemistry and temperature (e.g., Brabec et al., 2002). Anthropogenic disturbance is recognized as a major cause of habitat fragmentation, especially in freshwater ecosystems (Brauer and Beheregaray, 2020), leading to great reductions in wetland biodiversity and increasing species endangerment (Clark et al., 2014; Kingsford et al., 2016). The importance of connectivity is emphasized in urban environments, where dispersal barriers and anthropogenic habitat alteration are more profound.

Semiaquatic amphibians and reptiles require both terrestrial and aquatic habitats (Semlitsch and Bodie, 2003; Cosentino and Schooley, 2018). Amphibians are globally affected by habitat loss and fragmentation, often resulting from urbanization (Stuart et al., 2004; Cushman, 2006; Hamer and McDonnell, 2008). The need for aquatic habitat, along with low mobility and a seasonal migration between breeding ponds and hibernation sites cause amphibians to be particularly vulnerable to habitat fragmentation (deMaynadier and Hunter, 2000; Bowne and Bowers, 2004; Cushman, 2006), which leads to a loss in habitat functional connectivity (Joly et al., 2001; Baguette and Mennechez, 2004). Anthropogenic factors, such as roads and traffic, act as barriers to dispersal (Marsh et al., 2005) and gene flow (Garcia-Gonzalez et al., 2012; Pittman et al., 2014) and may impact amphibians through direct mortality (Beebee, 2013; Hamer et al., 2021; reviewed by Fahrig and Rytwinski, 2009). Buildings and altered light regimes caused by artificial lighting may also affect the breeding behavior of amphibians (Dias et al., 2019) and impede or even prevent their migration and distribution (Perry et al., 2008). Despite numerous threats, healthy amphibian and reptile populations can survive in urban environments (e.g., Perry et al., 2008; Brand and Snodgrass, 2010; Garcia-Gonzalez and Garcia-Vazquez, 2012; Guzy et al., 2013; Scheffers and Paszkowski, 2013; Konowalik et al., 2020).

The smooth newt (*Lissotriton vulgaris*) is a rather common and widely distributed European semiaquatic salamander, yet its populations are declining (IUCN Red List of Threatened Species 2018). Habitat fragmentation and isolation possibly play exceedingly large roles in altering its population dynamics (Denoël and Ficetola, 2007). Smooth newts inhabit both artificial and natural wetlands (Mulkeen et al., 2017; Mulkeen, 2018; Buono et al., 2019; Rannap et al., 2020), which allows breeding even in urban environments. They utilize a wide variety of waterbodies (Mulkeen et al., 2017) for reproduction, although they prefer still and shallow ponds (e.g., Kinne, 2004) and exhibit less strict aquatic habitat requirements when compared to other pond-reproducing newts (e.g., Skei et al., 2006; Gledhill et al., 2008; Vuorio, 2016). As smooth newts show extensive terrestrial stages in their life cycle and juveniles remain on land for several years until reaching reproductive readiness (e.g., Bell, 1977; Heiss et al., 2015), they require suitable terrestrial areas for hibernation, migration, and dispersal (Mulkeen et al., 2017).

Smooth newts and other European *Lissotriton/Triturus* newts show site fidelity by returning to the same breeding ponds (Joly and Miaud, 1993) and terrestrial refugia (Jehle, 2000; Müllner, 2001; Malmgren, 2002; Denoël et al., 2018) and by utilizing the same migration routes (Vuorio et al., 2015). However, habitat degradation and edge effect create challenges for their dispersal and migration to spawning areas even at these short distances (Semlitsch, 2000; Houlahan and Findlay, 2003). Smooth newts have a rather low annual survival rate, with ~50% yearly mortality according to Bell (1977). In addition to anthropogenic-related mortality, fish and invasive alien crayfish are known to affect smooth newt populations through predation (Stenson and Aronsson, 1995; Falaschi et al., 2022).

Because of its characteristics, the smooth newt is a potential species to aid in recognizing amphibian- and reptile-friendly urban environments. The species' requirement for connected landscapes may make it particularly vulnerable to urban land use changes and therefore an indicator of well-connected urban wetlands (for non-urban areas see Malmgren, 2002). To understand the key mechanisms driving smooth newt occurrence in urban areas, we examined the presence and abundance of smooth newts in 50 wetlands in metropolitan Helsinki, Finland. Our aim was to investigate whether buildings, other constructed elements, environmental variables, and fish presence affect urban smooth newts. We first hypothesize that smooth newt occurrence and abundance will be greatest in well-connected sites and second that smooth newt occurrence and abundance will be greater in urban waterbodies with forest or meadow environments nearby. Third, we assume that smooth newt presence and abundance are greater in fishless waterbodies compared with aquatic habitats with predatory fish. Fourth, we hypothesize that road networks will negatively affect smooth newts in urban settings. To our best knowledge, this study is the first to investigate how urban infrastructure affects smooth newt occurrence and abundance.

2 Materials and methods

2.1 Study sites

Our study was conducted in metropolitan Helsinki (60°13'N, 24°51'E), located in southern Finland. The study area comprised three cities: Espoo, Helsinki, and Vantaa (Fig.1), with a total land area of 669 km^2 and approximately 1.16 million residents. Metropolitan Helsinki is the most populous urban area in Finland. The area belongs to the southern boreal vegetation zone (Ahti et al., 1968), with a forest cover of >30%. Forests are predominantly coniferous, with interspersing deciduous patches. Metropolitan Helsinki is located by the Baltic Sea, with more than 100 km of coastline. Soils are low in nutrients, with glacial and sandy tills being the dominant soil types. Annual average precipitation reaches approximately 700 mm, and the thermal growing season is 175–185 days (Finnish Meteorological Institute, n.d.), although the growing season of 2018 was exceptionally long (214 days; Finnish Meteorological Institute, 2018). Four native amphibian species occur in the area: smooth newt, common frog (*Rana temporaria*), moor frog (*Rana arvalis*), and common toad (*Bufo bufo*).

First, we located all the wetlands in our study area using maps and satellite images. We found 152 urban wetlands and randomly chose 50 of these for our study (Figure 1; detailed information in Vehkaoja et al., 2020). Randomization was performed in the R program with the 'randomizeR' package. Our wetlands included both temporary (N = 10) and permanent (N = 40) waterbodies. Ten of the 40 permanent wetlands were classified as stormwater wetlands while the remaining 30 were natural.

2.2 Sampling

The smooth newt breeding season in the boreal zone begins in April at the earliest, and in Finland occurs after ice-melt, i.e., at the turn of April and May (Vuorio et al., 2015). Juveniles begin their post-metamorphic dispersal in search of suitable terrestrial habitats for overwintering around August and September in the boreal zone (Malmgren, 2002), including Finland (Koskela, 1984). Adult smooth newts leave the aquatic habitat after egg-laying (in May) and spend the rest of the year on land (Vuorio et al., 2015).

We collected the smooth newt data between April 30 and May 19, 2018. We standardized the weather conditions of the sampling days as much as possible by avoiding heavy wind (over 5 m/s), rain, and cold (below +5°C) conditions. We tested our capture success against the following weather variables (we calculated the daily means of all weather variables): air temperature, cloud cover, air pressure, rainfall, air humidity, and wind velocity. The weather variables did not significantly differ between the sampling days, nor did they have an effect on the number of captured individuals.

We selected spring (post-snowmelt) as the sampling season because smooth newts reproduce and are active in water at this time and are therefore more likely to be captured. We set 10 activity traps at even spacing in the waterbody of each site. We used 1-L glass jars and transparent plastic funnels with 120-mm openings at the wide end and 20-mm openings at the narrow end (see, e.g., Elmberg et al., 1992; Elmberg et al., 1993). The activity traps were submerged at an approximate depth of 1 m. Each wetland site was sampled for a total of 48 h, with traps emptied every 12 h to avoid premature death of the animals. With this method, the capture effort was the same for each site and the number of captured individuals does not indicate the actual size of the population. We then calculated and sexed all captured individuals in the field. The trapped individuals were afterwards released back into the wetland, which might have resulted in some individuals being recaptured.

2.3 Environmental and land cover variables

We measured riparian canopy cover and submerged and emergent vegetation coverage as environmental variables for all study sites (see more details for canopy cover and emergent vegetation measurements in Vehkaoja et al., 2020). Submerged vegetation coverage was calculated using four randomly chosen 1-m^2 vegetation squares from each study site.

We calculated the land cover and road variables (length) from a 500-m radius circle around the study sites. This scale was selected to match the smooth newt's average maximum dispersal distance from the breeding waterbody, as defined by Kovar et al. (2009). We processed the landscape and road data using ArcMap 10.3.1 (ESRI, 2015).

Land cover data were extracted from the Finnish national version of the CORINE Land Cover 2012 database, where land use in Finland is presented with a pixel size of 20 m × 20 m (Finnish Environment Institute, 2014). To reduce the number of land cover variables in our models, we reclassified CORINE data by combining

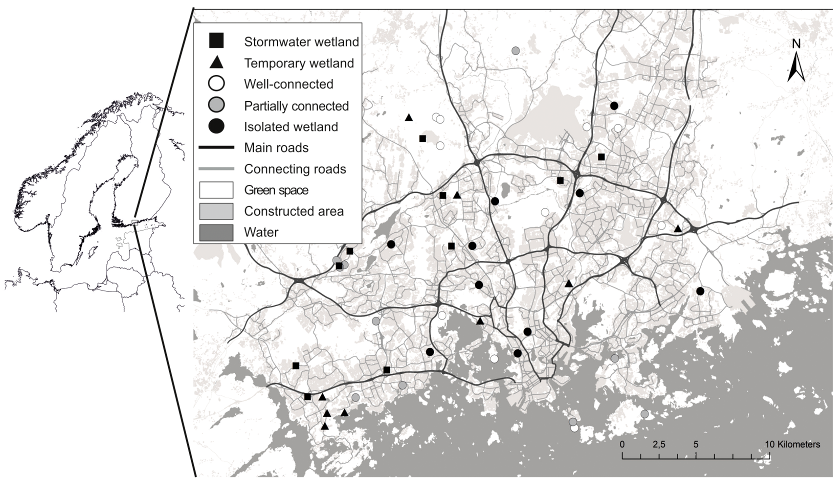

FIGURE 1
Map of the study area, metropolitan Helsinki.

ecologically comparable habitat subclasses such as various coniferous forest or wetland types. Reclassification was performed using ArcMap version 10.3.1 (ESRI, 2015). Our final land cover variables were the coverage of 1) residential buildings, 2) industrial and service buildings, 3) other buildings, 4) recreation area, 5) farming area, 6) deciduous forests, 7) coniferous forests, 8) mixed forests, 9) other open natural areas, 10) wetlands, and 11) water systems (mainly sea area).

The road data were extracted from Digiroad, the national database of the Finnish road and street network (Finnish Traffic Agency, 2018). We used the following road classes 1) main roads, 2) connecting roads, 3) streets, 4) walkways, and 5) all road and street types together.

2.4 Fish occurrence

We assessed fish occurrence using fish traps (wire mesh traps), activity traps, and visual sightings. One fish trap was submerged into each waterbody at an approximate depth of 1 m. The fish traps remained in the waterbody for the duration of the newt trapping, and each fish trap was emptied every 12 h concurrently with the newt traps. All fish were released back into the waterbody afterwards.

2.5 Principal component analysis

Initially, we analyzed the 18 environmental and land cover variables using principal component analysis (PCA; see, e.g., Pimental, 1979; Gauch, 1982) to investigate the main environmental factors defining the study sites. We chose PCA because it enables statistically categorizing the study sites into appropriate isolation gradients.

The first and second PCA components explained 29.1% and 17.6% of the total variation in the habitat data, so combined these two components explained 46.7% of the variation. The score values of the first component organized the wetlands on an isolation gradient: habitats with forest and recreation areas nearby, rich emergent vegetation, and location next to other wetlands were situated at the positive end of the gradient, while habitats with roads and various building types were at the negative end. All 50 wetlands were categorized according to their isolation scores received from the PCA. Sites with an isolation score between −3 and −0.5 were categorized as isolated. Wetlands that scored between −0.5 and 0.5 were categorized as partially connected, and wetlands with a score >0.5 were categorized as well connected.

2.6 Statistical analyses and model selection

The occurrence and abundance of smooth newts, and the number of females and males were calculated for each site (N = 50). We analyzed smooth newt occurrence by comparing the presence–absence data with the environmental and land cover variables, in addition to fish presence and the wetland type from the PCA. Smooth newt abundance was a count datum with a Poisson distribution (log). The abundance data were overdispersed due to the many zeros (no smooth newts on a site). Thus, we used negative binomial modeling with the glm.nb function, which is suitable for overdispersed data. We used the packages 'mgcv' (Wood, 2006) and 'MASS' (Venables and Ripley, 2002) from the software package R (R Development Core Team, 2013). Wetland type (received from the PCA: well connected, partially connected, and isolated) and fish presence were used as categorical parameters, and the other explanatory parameters were continuous parameters.

Smooth newt occurrence and abundance were tested against wetland type. These were tested separately with the glm.nb function. Next, we used model selection to determine the effect of fish and the 18 environmental and land cover variables against smooth newt occurrence, abundance, and the number of females and males. Model selections for presence–absence (i.e., occurrence) and for female, male, and total smooth newt abundance data were made by dropping out explanatory variables one at a time until all remaining variables had at least a 95% significance level (Zuur et al., 2009). With these model selections, we wanted to explore which variables are important for smooth newts.

3 Results

We captured a total of 447 smooth newts, which were recorded from 18 of our 50 study wetlands. Smooth newts were detected from both temporary (4/10) and permanent (14/40) waterbodies, including one permanent stormwater wetland. Of all newts caught in the whole study area, 72% were males and 28% were females. However, the sex ratio in the most populous site was approximately 50:50, with 41 males and 40 females. The sex ratio did not differ between wetland types (Partially connected t value: −1.320, SE: 0.128, p value: 0.207; Isolated t value: −0.088, p value: 0.931) or with fish presence (t value: −0.035, SE: 0.173, pvalue: 0.843).

Over 70% of the well-connected wetlands had smooth newts, whereas the species only occupied 22% and 29% of the partially connected and isolated wetlands, respectively (Table 1). The wetland isolation level significantly influenced smooth newt occurrence (Figure 2). Well-connected sites also had a significantly higher abundance of smooth newts when compared with isolated wetlands and a non-significantly higher abundance when compared with partially connected wetlands (Table 2).

The model with fish, open natural areas, residential buildings, and aquatic vegetation was the best model at explaining smooth newt total abundance (males and females together) and male smooth newt abundance, when considering every environmental and infrastructural variable (Table 3). Residential buildings and fish had a significant negative effect on total abundance, i.e., the higher the share of residential buildings located near a smooth newt breeding site or the larger the number of fish, the fewer smooth newts were observed. On the other hand, aquatic vegetation cover and open natural areas had a significant positive effect on total abundance. Female smooth newt abundance, however, was best

TABLE 1 Characteristics of study wetlands.

Wetland id	Area (m^2)	Isolation score	Isolation_type	Number of newts	Aquatic vegetation cover	Number of fish
1	234	0.05	Partially connected	0	0.54	0
2	767.4	−0.27	Partially connected	58	0.81	0
3	1880	−0.21	Partially connected	0	0.59	0
4	1040.8	−0.12	Partially connected	20	0.56	0
5	848	0.64	Well connected	3	0.82	0
6	623	0.37	Partially connected	0	0.81	518
7	490	0.32	Partially connected	0	0.18	0
8	2108	0.15	Partially connected	7	0.82	0
9	376	−0.87	Isolated	0	0.89	39
10	2667.8	0.06	Partially connected	0	0.2	11
11	619	2.18	Well connected	44	0.51	0
12	1042	−0.75	Isolated	0	0.32	2
13	3034	0.50	Well connected	0	0.38	18
14	340	0,28	Partially connected	0	0.54	4
15	4400	0,15	Partially connected	0	0.63	0
16	158	−0.16	Partially connected	1	0.73	0
17	1570.6	1.61	Well connected	23	0.87	0
18	7889.6	1.63	Well connected	6	0.63	0
19	296	1.94	Well connected	65	0.93	0
20	56100	−1.35	Isolated	21	0.75	10
21	3118.9	−0.59	Isolated	0	0.68	0
22	113.7	0.16	Partially connected	0	0.15	0
23	174.7	0.13	Partially connected	0	0.17	0
24	723.3	1.78	Well connected	0	0.68	1
25	3078	−0.74	Isolated	0	0.71	0
26	1251.8	−2.12	Isolated	0	0.55	7
27	929.5	−0.21	Partially connected	0	0.28	0
28	1316	0.30	Partially connected	0	0.52	131
29	372	−0.28	Isolated	0	0.42	4
30	2040.4	0.16	Partially connected	0	0.64	0
31	218	0.34	Partially connected	0	0.63	1
32	623.9	2.53	Well connected	0	0.18	1
33	843	0.86	Well connected	81	0.64	0
34	608.3	−1.08	Isolated	14	0.82	0
35	1380.8	1.55	Well connected	69	0.88	0
36	105	−1.04	Isolated	0	0.03	0
37	1441.6	−0.61	Isolated	0	0.78	1
38	1251.5	0.87	Well connected	0	0.86	0

(Continued)

TABLE 1 Continued

Wetland id	Area (m^2)	Isolation score	Isolation_type	Number of newts	Aquatic vegetation cover	Number of fish
39	5271.5	0.07	Partially connected	0	0.13	3
40	1240.4	−2.20	Isolated	2	0.73	0
41	572.9	−1.21	Isolated	0	0.34	0
42	1793	−0.50	Isolated	0	0.04	0
43	2500	−0.59	Isolated	6	0.19	7
44	148034	−0.67	Isolated	2	0.76	0
45	422	0.06	Partially connected	0	0.64	0
46	400	−0.77	Isolated	0	0.45	17
47	810	0.58	Well connected	6	0.27	0
48	16870.6	0.28	Partially connected	0	0.21	1
49	414	−0.34	Partially connected	9	0.38	0
50	11500	−1.71	Isolated	0	0.08	0

explained by the model that incorporated forests and natural open areas in addition to fish presence, residential buildings, and aquatic vegetation. Each of these five variables had a significant effect on female smooth newt abundance, with residential buildings and fish showing a significant negative effect and the remaining variables showing a significant positive effect (Table 3). The model with fish, residential buildings, and aquatic vegetation was the best model at explaining smooth newt occurrence. Fish and residential buildings had a negative effect on occurrence, whereas the effect of aquatic vegetation cover was positive.

We recoded several fish species in our study wetlands, e.g., perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), pike (*Esox lucious*), and Crucian carp (*Carassius carassius*). All these species are predators of newts or newt eggs. We found more smooth newts from fishless wetlands, as 89% of the newt-inhabited wetlands (16/18) were fishless, and fish presence (18/50 wetlands) significantly influenced both smooth newt abundance and occurrence in our study (Table 3).

4 Discussion

Our results show that smooth newts can utilize all three of our wetland types (temporary and permanent, including permanent stormwater wetlands). As predicted, wetland isolation levels strongly affected smooth newt occurrences in our study. We observed a significant difference in smooth newt occurrence between well-connected (smooth newts recorded on 70% of sites) and partially connected and isolated sites (<33%). This is not surprising, as many studies have shown habitat fragmentation to

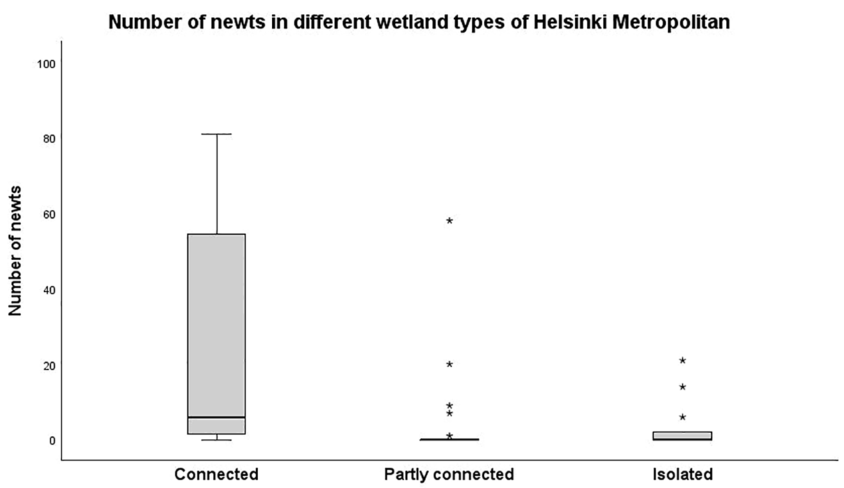

FIGURE 2
Smooth newt abundance in wetland types of metropolitan Helsinki. * denotes outliers.

TABLE 2 Differences between well-connected, partially connected, and isolated wetlands in terms of smooth newt abundance and occurrence, in addition to the effect of fish presence on newts.

	Estimate	Std. error	z-value	P
Newt abundance				
Well-connected wetlands (intercept)	3.296	0.838	3.932	8.43e-05
Partially connected wetlands	−1.833	1.031	−1.778	0.075
Isolated wetlands	**−2.322**	1.085	−2.140	**0.032**
Newt abundance				
No fish (intercept)	2.550	0.504	5.064	4.1e-07
Fish present	−2.145	0.859	−2.498	**0.013**
Newt occurence				
Well-connected wetlands (intercept)	0.981	0.677	1.449	0.147
Partially connected wetlands	−2.205	0.847	−2.603	**0.009**
Isolated wetlands	−1.856	0.861	−2.155	**0.031**

Significant p-values in bold. Value represents the wetland type coefficient, Std. Error denotes standard error, z-value the test value, and p-value the statistical significance. The value of the intercept is compared to values from the other sites. If this value is negative, it is subtracted from the intercept value and, if positive, it is added to the intercept value.

TABLE 3 Environmental factors affecting smooth newt abundance. The best models explaining newt abundance in urban wetlands.

	Estimate	Std. error	z-value	P
Newt abundance				
Intercept	1.539	1.098	1.402	0.161
Aquatic vegetation cover	3.366	1.424	2.363	**0.018**
Residential buildings	−2.707	0.818	−3.307	**<0.001**
Male newt abundance				
Intercept	1.226	1.081	1.134	0.257
Aquatic vegetation cover	3.257	1.402	2.324	**0.020**
Residential buildings	−2.720	0.808	−3.367	**<0.001**
Female newt abundance				
Intercept	−4.053	1.638	−2.475	0.013
Aquatic vegetation cover	4.247	1.387	3.061	**0.002**
Residential buildings	−1.723	0.804	−2.144	**0.032**
Forests	1.660	0.663	2.505	**0.012**
Natural open areas	6.397	3.082	2.076	**0.038**
Newt occurrence				
Intercept	−1.321	1.136	−1.163	0.245
Aquatic vegetation	3.922	1.576	2.489	**0.013**
Residential buildings	−2.002	0.833	−2.404	**0.016**

Significant p-values in bold. Value represents the wetland type coefficient, Std. Error denotes standard error, z-value the test value, and p-value the statistical significance. The value of the intercept is compared with values from the other sites. If this value is negative, it is subtracted from the intercept value and, if positive, it is added to the intercept value.

strongly influence amphibian populations due to impaired movement caused by poor vagility ability, high traffic mortality (Cushman, 2006), patch isolation (Vuorio et al., 2015), and broken migration routes (Joly, 2019). Additionally, Gledhill et al. (2008) observed strong positive correlation between aquatic plant and invertebrate species richness and pond density. Well-connected sites therefore potentially increase the smooth newt's chances of finding food resources, breeding sites with abundant aquatic vegetation for egg-laying and for juveniles, and suitable overwintering refugia. Despite less stringent habitat requirements, habitat diversity has been shown to drive the movement patterns of the species (Pittman et al., 2014; Vuorio et al., 2015).

In our study, well-connected sites also harbored larger newt abundances, which shows the importance of well-connected habitats in upholding smooth newt populations. Our results on urban smooth newts are widely applicable in urban wetland biodiversity conservation, as they are in line with other studies that have explored the role of connectivity for semiaquatic amphibians and reptiles. Terrestrial connectivity and proximity to and size of green spaces benefit amphibians (Semlitsch and Bodie, 2003; Simon et al., 2009; Guderyahn et al., 2016) and turtles (Hamer and Parris, 2011; Guzy et al., 2013; Hamer et al., 2018; Santoro et al., 2020). Concurrently, aquatic connectivity increases amphibian and reptile occurrences and abundances in urban settings (e.g., Roe et al., 2003; Attum et al., 2006; Hamer et al., 2012; Fyson and Blouin-Demers, 2021). Hamer et al. (2018) showed that without adequate proximal terrestrial habitats, urban wetland conservation and management do not increase the populations of freshwater turtles in Australia, while Trovillion et al. (2023) found that adding ponds to connected greenspaces can help mitigate the adverse effects of urbanization on semiaquatic species richness in the United States. Associations across taxa have also been found, for example positive bird–amphibian co-occurrence patterns in Sweden, indicating that conservation efforts of one taxon may facilitate another (Kačergytė et al., 2023). The importance of connectivity is emphasized in built-up areas, where dispersal barriers, such as roads, other infrastructure, and habitat alteration are more profound (Bierwagen, 2007). The role of connectivity may become pronounced at the species' range margin, such as in Finland, as suggested by Rannap et al. (2012). Both range margins and urban environments emphasize the challenges faced by smooth newts and possibly other amphibian species as well. Our study combines both aspects, and our conservation suggestions can be used as guidelines in urban management planning and potentially even in rural range margin areas.

The model with residential buildings and aquatic vegetation was best at explaining smooth newt presence (46.7% of variation explained) and male and total abundances. Residential buildings negatively associated with smooth newt populations in our urban environment to a significant degree. Vehkaoja et al. (2020) previously found that residential buildings and roads also had a negative effect on aquatic invertebrate family richness and abundances in the same study area, and these lower invertebrate levels may be reflected in the results of this study. Other building types (e.g., industrial buildings) did not show a significant effect on smooth newts in our study sites. Both residential and industrial buildings require heavy infrastructure (roads, asphalt etc.) and maintenance. This leaves little favorable terrestrial habitat for newt dispersal or overwintering and hinders dispersal by decreasing connectivity. However, the lots on which industrial buildings are located may incorporate less built-up environment compared with residential areas, and may be managed less, to where such lots may contain more fallow, higher terrestrial vegetation, and other refugia (stones, dead wood) required by newts (Schabetberger et al., 2004; Denoël et al., 2013; Vuorio et al., 2015; Denoël et al., 2018) and may even be less affected by pesticides used to manage residential building lots.

Smooth newts are crepuscular (Griffiths, 1985; Paterson, 2018), suggesting individuals prefer intermediate to low light conditions (Hill et al., 2018). Evidence also indicates their activity levels may be influenced by the lunar cycle and cloud cover (Deeming, 2008; Warren and Büttner, 2008; Phillips, 2020; but see also Paterson, 2018). Residential buildings or areas may more strongly influence local light conditions than industrial buildings, which are well lit during the day compared with residential buildings, where lighting is brightest in the mornings and evenings. Light pollution, resulting from this high-intensity lighting of residential buildings and street lighting in the mornings and evenings, may interfere with how smooth newts perceive natural illumination regimes (including the lunar cycle), thus hindering smooth newt activity in adjacent waterbodies and terrestrial patches (Feuka, 2016).

Likewise to the Rannap et al. (2012) review, our study shows a significant positive association between aquatic vegetation and smooth newts. Newt eggs are laid on the leaves of aquatic vegetation. The larval stage prefers dense vegetation for foraging, and both adult and larval smooth newts utilize aquatic vegetation as refuges against predatory fish. Invertebrate assemblages are most diverse in ponds with richest aquatic plant diversity (Gledhill et al., 2008), potentially leading to more food sources for newts. This effect was heightened at broader landscape scales, i.e., assemblage diversities were larger when looking at pond networks compared with individual ponds.

The best model to explain female newt abundance also included forests and natural open areas, both of which associated positively with female numbers. Why these two variables were important only for females remains an open question. Previous studies (e.g., Malmgren, 2002; Vuorio et al., 2015) show canopy cover and various forested and open natural areas to play roles, but there is no distinguishing difference between newt sexes. Male lekking behavior may lead to female-biased dispersal in newts (Matos et al., 2017; Cayuela et al., 2020). In our study, this phenomenon may be exacerbated by both predator avoidance and avoidance of density-dependent male harassment. These factors may push female smooth newts towards more frequent and longer-distanced dispersal. In turn, this may lead to the exaggerated importance of terrestrial habitat factors (forest and natural open areas) for females as opposed to male smooth newts. The females' larger size may also either be an attribute of female-biased dispersal, where larger size aids in migratory survival dispersal (Matos et al., 2017; Cayuela et al., 2020) or it may cause females to need more sheltered terrestrial habitat to guard against predators.

Somewhat surprisingly, we found no significant effect of road networks on smooth newt occurrence or abundance, despite this factor having previously been identified as playing a negative role (e.g., Fahrig et al., 1995; Glista et al., 2007). It is possible that the scale chosen for our study fails to show this effect; 75% of dispersing newts have been found to stay within ~300 meters of a pond (Kovar et al., 2009). On the other hand, our study is also located in an area with Finland's densest road network crisscrossing the entire study area, which may cause subtle impacts to go unnoticed.

Fish presence negatively influenced smooth newt occurrence in our study. Our observation was in line with previous studies, which have found that smooth newts can coexist with fish (Dolmen, 1988; Skei et al., 2006; Rannap et al., 2012; Kačergytė et al., 2021), but their populations may be limited in waterbodies with fish (Denoël et al., 2013).

Negative responses by numerous organism groups, including invertebrates, amphibians, and birds, have previously been reported for fish-related predator–prey interactions, competition, and trophic cascading (e.g., Carpenter et al., 1985; Stenson and Aronsson, 1995; Reshetnikov, 2003; Eaton et al., 2005; Väänänen et al., 2012; Milardi et al., 2016). In amphibians, predator avoidance may determine breeding site selection more than competition avoidance (Indermaur et al., 2010). Nomadic behavior is typical for smooth newts, not only when migrating between overwintering and reproductive areas, but also when choosing sites according to other habitat characteristics such as predator prevalence (Malmgren, 2002; Denoël et al., 2013; Denoël et al., 2018). High waterbody connectivity leads to increased movement opportunities between individual ponds during the breeding season. Newts may aggregate into few suitable predator-free waterbodies, thereby exhibiting predator avoidance over competition avoidance.

For example, Winandy et al., 2017 showed alpine newts (*Ichthyosaura alpestris*) to exhibit clear predator avoidance by leaving/aggregating in ponds with fish presence/absence. While predator avoidance may be an effective short-term strategy, such circumstances may lead to density-dependence problems, e.g., harassment in dense populations, food resource shortages, or reproductive disruptions (Winandy et al., 2017). An example of this was shown in Winandy et al. (2017), where predator avoidance indirectly led to increased female aggregation in terrestrial habitats, with female newts using the terrestrial habitats seven times more frequently than males during the breeding season. Urbanization may further exacerbate the fish effect because urban green and blue spaces incorporate numerous disturbances and hazards affecting newts. However, a Norwegian study (Skei et al., 2006) did not detect any significant vulnerability of smooth newts to fish, and a review by Rannap et al. (2012) observed that the fish effect was not geographically unified, as smooth newts appeared to tolerate fish presence to a larger degree in more northerly regions of Europe.

Most of our sites showed male preponderance, corresponding with previous studies (e.g., Arntzen, 2002; Grayson et al., 2012). Our result may be due to intense mate competition by males. A female within a trap can lure several reproductive males into the trap, resulting in trapping favoring male newts. Newt males often exhibit coercive behavior during the mating season. The arrival time of male and female smooth newts into the breeding ponds may be another explanation for our skewed sex ratios. Previous studies (e.g., Griffiths, 1984; Arntzen, 2002) have investigated whether males enter breeding ponds earlier after ice-melt than females, with varying results. However, in our study area, ice-melt occurred in the second half of April in 2018 (Finnish Environment Institute TARKKA portal). It is therefore likely that both females and males were present in the breeding ponds during our study period (30 April–19 May 2018). Also, only males (no females) were trapped from two of our study wetlands and only females (no males) were caught from one site. A third possibility is that females in our sample may be showing stronger predator avoidance to fish presence, leading females to enter the breeding ponds less frequently.

Given increasing global urbanization along with the continued decrease in smooth newt numbers, understanding how to conserve and construct suitable aquatic and terrestrial habitats for newts is important for their future. Smooth newts can utilize artificial wetlands, which is a positive aspect for their conservation. However, several factors should be ensured. Urban wetland management and conservation should ensure adequate pond densities and adjacent terrestrial habitats, maintain sufficient landscape connectivity between breeding sites, uphold sufficient distances between urban waterbodies and residential buildings, and keep fish removal and aquatic vegetation assemblages in mind. Introducing artificial overwintering hibernacula or newt hotels and migration tunnels and fences (Matos et al., 2017; Helldin and Petrovan, 2019; Matos et al., 2019) should also be considered. However, tunnels and fences should be studied more to ensure newts truly utilize the structures rather than them being obstructive to dispersal (Matos et al., 2017; Helldin and Petrovan, 2019; Jarvis et al., 2019; Matos et al., 2019). They must also lead to suitable breeding and/or overwintering habitats to be worthwhile.

Our study contains certain limitations. We excluded artificial lighting as a study variable and were thus unable to examine its role in newt habitat selection. Future studies should investigate the topic in addition to how artificial wetland types affect smooth newts at various developmental stages. We also did not examine the effect of any physicochemical elements, such as pollutants or calcium levels, which may directly affect smooth newt occurrence/abundance (e.g., Skei et al., 2006) and which concurrently may be greatly altered in urban wetlands. Understanding how such mechanisms affect newts in an urban setting is an important step for their conservation. The 20 × 20-m CORINE data may also be slightly coarse, leading to very fine-scale results being lost in the analyses. However, the data are equal in all habitat types, causing no systematic bias in the results, and data of this scale are widely used in habitat studies.

5 Conclusions

Urban wetlands are potentially suitable habitats for several semiaquatic amphibian and reptile species. Amphibians indicate terrestrial and aquatic conditions. Smooth newts exhibit less stringent habitat requirements than many other newt species, meaning they may be able to tolerate human presence and modification to a greater degree. Nonetheless, our study shows that wetland connectivity, aquatic vegetation, terrestrial habitat, and residential buildings play important roles in determining smooth newt population occurrence and abundance in urban areas. Smooth newts in urban areas may experience a bottleneck caused by their terrestrial habitat preferences. Their less strict aquatic requirements allow them to inhabit and breed in urban or artificial waterbodies, whereas occurrence in adjacent terrestrial habitats may prove detrimental or impossible if these habitats are unsuitable or if habitat isolation prevents the migration and dispersal of various age groups and between aquatic and terrestrial life stages. Fish presence also influenced newt occurrence and abundance. Fish impede numerous organism groups through predator–prey interactions, competition, and trophic cascading, in both natural waterbodies and man-made ponds. None of the fish species we detected are endangered in Finland but rather are common and abundant throughout the country. On the contrary, smooth newts and several other amphibian species have declined widely in Europe. Controlling fish populations is therefore an important step in upholding biodiversity in systems with naturally fishless waterbodies, such as our study area. As smooth newts in urban areas favor high connectivity, the species can be used by urban planning and management to identify well-connected wetland areas. Also, managing such areas for smooth newts offers potential broad benefits to wetland biodiversity conservation in general. Protecting any semiaquatic species requires treating aquatic and terrestrial areas jointly. Failing to uphold the connectivity and condition of both habitats leads to weakened biodiversity of urban wetlands. Identifying not only potential smooth newt breeding ponds but essential terrestrial corridors could help urban planners prioritize and conserve important amphibian and reptile environments, construct artificial wetlands if needed, and thus maintain urban wetland biodiversity.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://doi.org/10.5281/zenodo.7598682.

Ethics statement

The animal study was approved by the Centre for Economic Development, Transport, and the Environment (issued on 14 March 2018). The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

MV, MN, ST, and V-MV contributed to the conception and design of the study. MV performed the data collection, fieldwork, and statistical analyses. MN performed the GIS analyses. ST wrote the first draft of the manuscript, and all authors contributed to editing and revising it. All authors have read and approved the submitted version.

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Conflict of interest

Author MN was employed by the company Latvasilmu osk.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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