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The effects of forest management on terrestrial habitats of a rare and a common newt species

Ville Vuorio · Olli-Pekka Tikkanen · Lauri Mehtätalo · Jari Kouki

Abstract Many amphibian species spend part of their life cycle in terrestrial habitats. However, their exact requirements regarding terrestrial habitats have often remained enigmatic. We aimed to compare the terrestrial habitat use of a common (smooth newt) and a rare newt (great crested newt) species around their breeding ponds, to see whether habitat preferences are linked to the rarity of a species. We tested the effects of forest habitat characteristics on newt populations of seven ponds. The ponds were monitored with terrestrial drift fences at different distances and in different habitats surrounding seven ponds in southeastern Finland during 2 years. We fitted all models using a Poisson generalized linear mixed model. Both newt species distinctly favored forests with high understory vegetation cover. Captures were most numerous in the old forests directly adjacent to the ponds. Both the common species and the rare species showed similar habitat use, but there was an indication that the rare species avoided clear-cut areas and had more need for the shelter provided by canopy and field-layer vegetation, especially when the distance to pond increased. Based on our findings, the maintenance of sheltering vegetation around the ponds is very important, especially for the rare species. However, this requires the retention of both field-layer and canopy coverage, and specific management principles—such as avoiding clear-cuts—should be adopted to maintain favorable conditions.

Keywords Triturus cristatus · Lissotriton vulgaris · Amphibian declines · Habitat preferences · Newts

Introduction

Many amphibian species have a distinct terrestrial phase in their life cycle. In fact, the recent worldwide declines and extinctions of amphibians have been linked to fragmentation and loss of the amphibian terrestrial habitats (Stuart et al. 2004). Amphibians share biological characters that make them, especially vulnerable to changes in their terrestrial habitats. These characteristics include, in particular, poor dispersal abilities (Bowne and Bowers 2004; deMaynadier and Hunter 2000; Gibbs 1998; Kovar et al. 2009; Sinsch 1990), high mortality rate when passing inhospitable terrain of roads, clear-cut areas or fields (Carr and Fahrig 2001; Cosentino et al. 2011; Eigenbrod et al. 2008; Fahrig et al. 1995; Stevens et al. 2006), and relatively narrow tolerance to abiotic conditions (Houlahan and Findlay 2003; Semlitsch 2000).

Amphibian species that live in small water bodies in forested landscapes may be affected by the management of surrounding forests. For example, intensive harvest operations (thinning and clear-cutting) may profoundly change the abiotic conditions of forests. If management includes soil preparation measures, these may affect dispersal and overwintering of amphibians directly. Forest thinning results in changes in tree species composition and forest floor properties such as the amount of dead wood and

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composition and coverage of understory vegetation. Clearcuts have even more dramatic consequences leading, in many cases, to large-scale habitat modification and may also cause direct mortality by forestry machines (Bol 2007). At the landscape level, habitat fragmentation caused by forest management reduces the size of habitat patches and increases patch isolation and, hence, extinction risk through the reduction of genetic and demographic input from immigrants (deMaynadier and Hunter 1998; Gulve 1994; Lande 1988).

Habitat connectivity has been proposed to be the main factor to ensure survival of viable populations at the regional level (Eycott et al. 2012; Hanski and Ovaskainen 2000; Van Buskirk 2012). In fragmented landscapes, the low recruitment of dispersing individuals has been thought to play a major role in the decline and extinctions of amphibian populations (Bulger et al. 2003; Vos and Chardon 1998). This is partly caused by the high mortality of juveniles during emigration resulting from the lack of connectivity to suitable terrestrial habitats (Rothermel 2004). The importance of connectivity in recolonization of local amphibian populations is documented in many cases (Gould et al. 2012; Skelly et al. 1999; Trenham et al. 2003).

Newts have a characteristic pattern of annual movement between their terrestrial hibernation sites and the aquatic breeding sites and may be highly dependent on the quality of the terrestrial habitats providing access to these sites (Patrick et al. 2006; Van Buskirk 2005). Semlitsch (2008) defines the primary adult amphibian migration as reoccurring movements from overwintering sites to ponds to breed in addition to the return of females and males to terrestrial habitats. Migrations may also occur between overwintering sites, foraging, and summer habitats (Lamoureux et al. 2002; Semlitsch 2008). Typically, the migration of adults is non-random; they enter and exit the pond in the same place and have a preference for particular travel routes (Freidenfelds et al. 2011; Müllner 2001; Rittenhouse and Semlitsch 2006, 2007; Sztatecsny and Schabetsberger 2005).

The great crested newt, *Triturus cristatus* (Laurenti, 1768) and the smooth newt, *Lissotriton vulgaris* (Linnaeus, 1758), occur sympatrically in northern European forest ponds (Denoel et al. 2013). However, their detailed distributions and areas of occupancy are quite different. The crested newt has a very restricted distribution of 16,600 km^2 (minimum convex polygon) in southern Finland, while the smooth newt is much more widespread with 212,000 km^2 (AmphibiaWeb 2014; Arntzen et al. 2009a, 2009b; Vuorio 2009). According to their geographical range, we position great crested newt to be rare and smooth newt to be common, though movements along rare–common axis are filled with complex methodological and terminological questions (Gaston 1997; Kunin 1997). Gaston and Kunin (1997b) deal with rare–common

differences with eight different traits: breeding systems, reproductive investment, dispersal ability, trophic status, homozygosity, competitive ability, resource usage, and body size. Our species pair has shared traits in the case of first four ones (breeding system: sexual, egg laying, and wrapping; reproductive investment: no parental care; dispersal ability: approximately similar distribution distances; trophic status: similar, negative effect of fish), while the three latter traits differ or presumably differ. We hypothesize the rare one to have narrower use of habitats (intolerant) and the rare one to be affected more by forest management actions.

The crested newt is classified as threatened, and the species appears to be conservation-dependent (Terhivuo and Mannerkoski 2010). Limited dispersal or highly specialized habitat use may be associated with species rarity, in general, but whether this applies to newts is unclear. In this study, we focus on differences in habitat use between the common and rare newt species. We try to clarify the responses of two syntopic newt species to terrestrial habitat change resulting from forest management.

We specifically asked

1. Do the rare and common species differ in their occurrence patterns, in relation to the quality and structure of managed forests (age, fertility, cover of canopy, and field layer) that surround breeding ponds?
2. Does the occurrence pattern of the two species change in forests that are more distant from the pond, that is, are buffer zone requirements for the common and rare species similar?

Materials and methods

Study species

The studied species belong to the subfamily Pleurodelinae of the family Salamandridae. The great crested newt has a distribution covering most of central Europe, reaching southern Scandinavia, the Baltic countries, and, in the east, south-western Siberia (Arntzen et al. 2009b). The smooth newt has a wider distribution covering most of Europe, excluding the Iberian peninsula, and reaching further north into Scandinavia and further east into Russia (Arntzen et al. 2009a).

Both species share many features in their local distributions and habitats and both are generalist predators (Griffiths and Mylotte 1987; Skei et al. 2006). Overlap in seasonal and daily activities and habitat use are found between these two species. However, smooth newts have a

larger distribution area; their pH tolerance is wider; they can breed in smaller water bodies, which may dry out annually, and they can also breed in larger lakes with the presence of fish (Dolmen 1988).

Study area

The study was conducted in eastern Finland, close to the village of Öllölä in Joensuu. The study area (62°21″N, 30°39″E) belongs biogeographically to the south boreal vegetation zone and is located at 120–170 m elevation above sea level and covers about 3×3 km. Landforms originate from the Tuupovaara end moraine, an ice-marginal formation formed during the Baltic Ice Lake (Rainio 1983). The area is characterized by sporadic, small groundwater-fed ponds where the newt species breed. Forests in the study area are commercially utilized and dominated by pine.

Study design and newt monitoring

There are 70 known breeding ponds of the great crested newt in eastern Finland. We first mapped the terrestrial habitats, i.e., delineated the forest compartments of 46 ponds (see Vuorio et al. (2013) for details) where both newt species were known to breed. Eight of them were selected for the drift fence study following two criteria: each pond should have at least three different terrestrial habitat types in the vicinity and the ponds should be relatively close to each other. The selected ponds originated from glacial processes and varied between 390 and 3,700 m^2. We differentiated six habitat types: herb-rich forest, herb-rich heath forests with deciduous or coniferous trees dominating, mesic heath forests, clear-cuts (0–5 years since clear-cutting), and young forests (6–15 years). We delineated the surroundings of each pond into three 25-m-wide zones reaching up to 75 m, starting from the shore line of each pond (Fig. 1). The compartments at different distance zones formed our study units. Each of the six selected habitat types occurred at least three times in each of the three distance zones. The only exception was the number of clear-cuts; they were found only once in the first zone and twice in the second and third zones. Within each study unit, we randomly placed one to four traps. Each trap consisted of a drift fence that was 2–10 m long. The capture effort per area remained the same in each of the study units: 1 m of fence 60 m^{-2}. We divided larger study units in size classes of 2,400–4,799 m^2 and of 4,800–7,199 m^2, in half or in thirds, respectively, and designated only one of them as a replicate in the study.

The trap fences were made from 40-cm-wide green plastic tarpaulin strips. The lower edges of the strips were dug 5–10 cm underground, and the fence was erected using
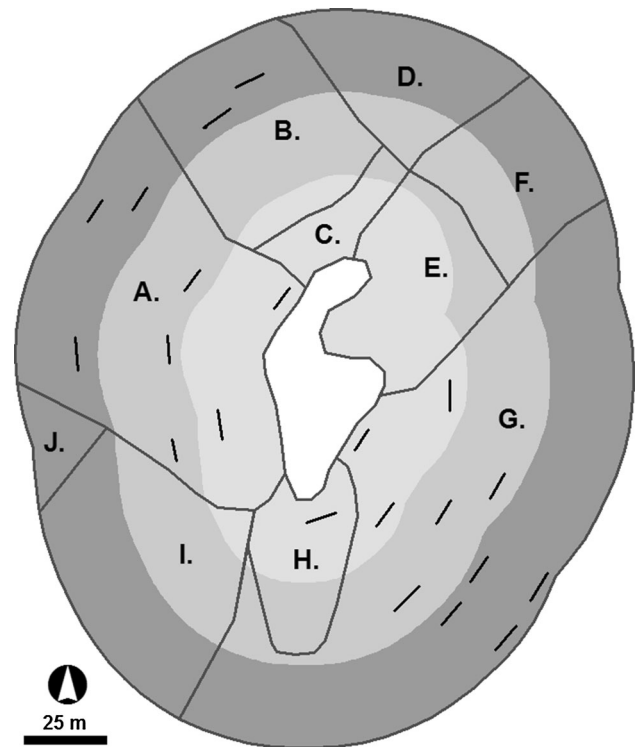

Fig. 1 Map showing the study setting in one of the ponds. *Letters A–J* indicate different habitat types. Three *shades of grey* indicate the distance from the pond in 25-m intervals. Fences are marked as *black lines*

metal stakes and cable ties. Fences were always parallel to the tangent of the closest point of the shoreline. Both ends of the fence had a 5-L bucket dug into the ground so that the rim reached the soil level. Buckets were half filled with water. Traps were checked once a day during the whole study period.

Breeding season started at the turn of April and May when ice cover melted from the ponds. Our sampling period targeted the post-breeding migration prior to post-metamorphic migration. During 2010, we operated 132 traps totalling 1,135 m of fences. Trapping was started on June 01 and ended on June 30. In 2011, trapping started on June 09 and ended on July 20, with 135 traps totalling 1,130 m of fences. The different periods of data collection were taken into account in the data analysis. In 2011, we excluded one pond due to a very low number of newt captures in 2010. To compensate for the loss of study units, we selected an equal number of corresponding habitats from corresponding zones. In 2011, we also had to replace one compartment that was logged during the winter of 2010–2011. The replacement was done following the above-mentioned rules.

Recapturing of the same individuals repeatedly from the same fence may cause some bias in our analysis. To check this, from June 05, 2010 onward, the belly patterns of the

great crested newts were photographed and recaptures were identified visually, in order to estimate the recapture rate. In total, we obtained 379 (102 males, 214 females and 63 juveniles) great crested newt captures of which 19 (6 males and 13 females) were recaptures. In 2010, we had recaptures from two of the seven ponds with total recapture rate being 4.9 %. In 2011, recaptures were recorded from three of the six ponds with 5.0 % recapture rate. Recaptures were excluded from the dataset.

Data

Field measurement of habitat characteristics

From each trapping unit, we collected compartment level data on the age and cover of the canopy together with ground layer vegetation cover and fertility (Table 1). The distance from the shoreline of the pond was divided into three 25-m-wide zones following the shape of the shoreline of the ponds. These zones were used in the analysis as categorical predictors. The age of the dominant canopy layer was measured either by auger or by counting the number of whorls of branches.

To obtain vegetation data, we placed on average 4.6 (±0.170) plots (808 in total) of 1 m^2 in each compartment to study the coverage of forest type indicator species (Hotanen et al. 2008). Species cover was estimated with the visual species percentage cover method at a 0.1–100 % scale. Based on the vegetation sampling, we counted a fertility index for each compartment. For this purpose, we summed the coverages of each herb-rich forest indicator species, and the obtained value was used to estimate the compartment level fertility. The variable was used as a fixed, continuous effect in the initial full model.

Canopy cover was visually estimated from each forest mensuration sample plot within each compartment. It was used as a continuous predictor in the analysis. The length

of each fence was used as a continuous log-transformed predictor having original range from 2 to 10 m. Year was used as a categorical predictor in the analysis.

Data classification

The age of the dominant canopy layer and the understory shelter-providing vegetation was classified into three equal percentiles to illustrate the effect of low, intermediate, and high values of each variable. Classification was based on scanned cases using the visual binning method in SPSS. Cut-levels of 40 and 50 years were used with the age of the dominant canopy layer, meaning that the youngest third had compartments of <40 years, the intermediate age class had ages of 40–50 years, while the oldest part was 50–120 years old. These age classes were used in the analysis as categorical predictors. The age distribution with numerous 40–50-year-old forests indicates extensive loggings in the 1960s in the study area.

To obtain an understory cover estimate, we summed the coverage of all shelter-providing grasses and herbs from each 1 m^2 understory sample plot. Lichens and mosses other than *Polytrichum commune* were excluded, because they form a dense mat in the ground layer. For the purpose of statistical analyses, we classified cover variables into three categories using equal percentiles based on the scanned cases function in SPSS with cut-levels of 48.5 and 63.6 %. The lowest class had values of 12.9–45.5 %, the intermediate class had values of 48.5–60.7 %, and the highest class had values 63.6–93.7 %. These classes were used in the analysis as categorical predictors.

Statistical analysis

We tested the importance of different environmental variables and their interactions for the total number of captured newts and both newt species separately. All the correlations

Table 1 Environmental variables included in modeling the habitat use of newts, rationale for predictor variables, and measurement units together with their ranges

Variable	Reasoning	Min.	Max.	Average
Distance from the pond (m), three 25-m zones	Habitats close to pond are favored; sampling effort was kept constant in all zones	3	75	41
Age (years) of the dominant canopy layer	With increasing age, there is more litter and dead wood for shelter and foraging	0	120	48
Understory cover (%)	With increasing understory cover, there are more shelter and foraging sites	13	94	55
Fertility index, counted from the cover of herb-rich forest indicator plants	Nutrient rich soil sustains more invertebrates to feed on and more moisture and cavities in the ground	0	59	9.2
Canopy cover (%)	With increasing canopy cover, there is more shelter against heat	1	80	52

between different potential predictors were low (Pearson correlation: 0.000–0.145), expect the correlation between age and canopy cover which was 0.397. Adults and juveniles of both species were pooled. Our data consisted of counts, which have the Poisson distribution under independence. We fitted all models using a Poisson generalized linear mixed model (GLMM), which is an extension of the Poisson generalized linear model to grouped datasets where observations within groups may be correlated (Bolker et al. 2009; Breslow and Clayton 1993). In the Poisson GLMM, the mean count dependent variable is related to the factors and covariates by a selected logarithmic link function, which is used to ensure a positive mean count. The data showed no signs of overdispersion. Using logarithmic fence length as a predictor in the model implies that the coefficients give the relative effect to the newts per fence meter. The model predictions can therefore be interpreted as relative estimates of newt individuals. In the initial model, zone, fertility, age, year, and logarithmic length of the fence together with all first-order interactions of categorical predictors were fitted as fixed effects, with random constant at the nested levels of individual fences, compartments, and ponds. The final model was selected by removing variables or interactions of variables with highest p value one at a time, so that at the end only statistically significant variables were remaining. The pond-level variance was 0 and therefore the final model included random constant only at the nested levels of individual fences and compartments. The pond-level variance was 0. Therefore, the final model for the number of captures in year t for fence i in stand j around pond k was: $y_{kjit} = \text{Poisson}\left(\lambda_{kijt}\right)$, where the expected value can be written as $\lambda_{kij} = \exp\left(\boldsymbol{\beta}' \boldsymbol{x}_{kijt} + b_{ki} + b_{kij}\right)$. The term $\boldsymbol{\beta}' \boldsymbol{x}_{kijt}$ includes the effects of fixed predictors and the random effects b_{ki} and b_{kij} have the normal distribution with mean of 0 and unknown variances. Means are presented throughout the paper as mean ± SE. Analyses were conducted using the statistical software package SPSS version 19.0.

Results

In 2010, we captured 58 great crested newts and 76 smooth newts, and respective captures in 2011 were 300 and 211, totaling 358 great crested and 287 smooth newts. Final GLMM model is presented in Table 2, the estimates in Figs. 2, 3, 4, 5 and in Table 3. From the initial full model, we removed nonsignificant variables (species × distance × understory cover, species × log fence length, distance × understory cover), leading to decrease in AIC-value from 2,176.4 to 1,889.8.

We found clearly fewer newts from forests that were located far from the ponds (Fig. 2a). The captures of both

Table 2 The final GLMM model of the newt habitat use based on the trapping data and significant model factors

	F	$df1$	$df2$	Sig.
Corrected model	9.786	30	128	<0.001
Species	18.911	1	467	<0.001
Distance	13.881	2	164	<0.001
Understory cover	8.591	2	33	<0.001
Age	1.105	2	34	0.343
Year	101.478	1	467	<0.001
Canopy cover	3.279	1	16	0.089
Log fence length	19.250	1	467	<0.001
Species × distance	0.067	2	467	0.935
Species × year	4.272	1	467	0.039
Species × understory cover	7.933	2	467	<0.001
Species × canopy cover	19.114	1	467	<0.001
Species × age	8.738	2	467	<0.000
Distance × age	0.183	4	165	0.947
Species × distance × age	6.026	4	467	<0.001
Species × age × understory cover	4.665	4	66	0.002

species in the 0–25 m distance zone differed significantly from those in the 25–50 and 50–75 m zones ($p < 0.01$ in all cases).

Understory vegetation cover was related to the occurrence of newts (Fig. 2b). On average, almost three times more individuals were captured from the high-cover sites compared to sites with the lowest vegetation cover (mean ± SE: 0.93 ± 0.154 and 0.32 ± 0.075, respectively, $p = 0.003$). The difference between the captures of the two species was apparent in low vegetation cover sites (Fig. 3); those sites were clearly avoided by great crested newts but not by smooth newts, which were found there over three times more often than great crested newts (interaction for species × understory cover, $p = 0.001$).

Although we did not capture any great crested newts in the clear-cut areas, their captures peaked in young sites in contrast to smooth newts, which avoided these sites (Fig. 4). Significant ($p < 0.05$) difference in captures of great crested newts was found between young and oldest sites, while smooth newt captures differed between young sites and sites of intermediate age class ($p < 0.05$). Interspecific differences were found in intermediate and old age classes ($p < 0.01$, but in youngest sites $p = 0.058$), with smooth newts dominating the captures (see interaction terms in Table 2). This pattern was valid also in all three distance classes, i.e., regardless of the distance of forest from the pond, rare species preferred young (Fig. 5a), and common species older forests (Fig. 5b). Smooth newts did not show any difference in captures in clear-cut areas

Fig. 2 Newt captures per fence (±SE) with respect to **a** distance zones and **b** cover of the shelter-providing understory vegetation
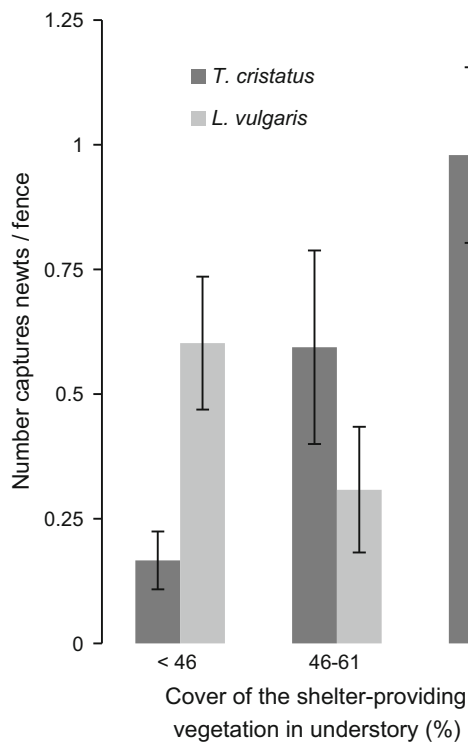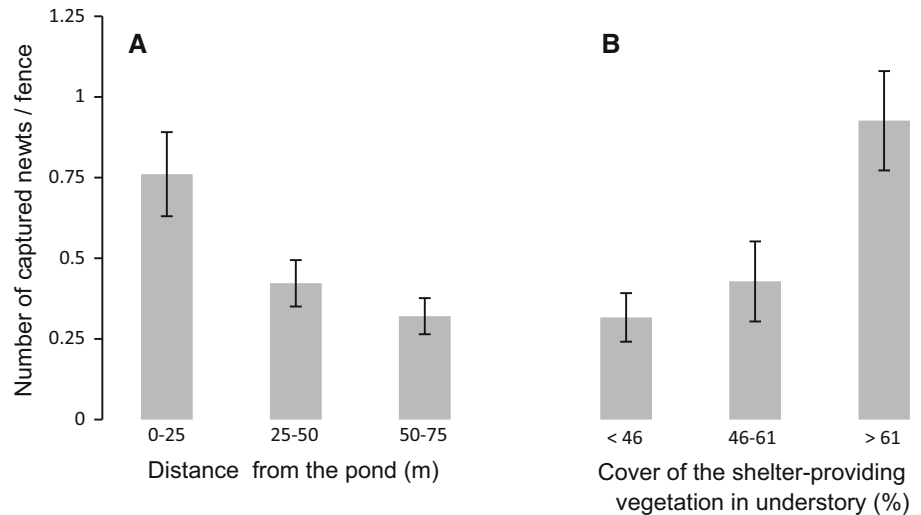

Fig. 3 Captures of both species separately (±SE) in relation to understory shelter-providing vegetation

Fig. 4 Captures of both species separately (±SE) in relation to age of the dominant canopy cover

(1.00 ± 0.356) compared with the captures of all the other fences (1.15 ± 0.136; Mann–Whitney *U* test: $p = 0.584$).

However, in the case of smooth newt, the division of the data into different distance classes (Fig. 5b) revealed more details of the general habitat use. As noted earlier (Fig. 4), smooth newt captures slightly peaked at intermediate-aged sites, but this pattern originates from zone one only (Fig. 5b).

The captures of the newt species differed markedly between the age classes having different understory cover

(Fig. 6a, b). The main difference between the species was in the middle-aged and old stands with low understory cover; those sites were strongly avoided by great crested newts but not by smooth newts. In the intermediate-aged and old forests, great crested newts occurred almost exclusively on sites where understory cover was high (Fig. 6a) ($p < 0.01$). Within the lowest cover class (<46 % cover), the youngest sites clearly had more great crested newt captures compared with intermediate and old sites ($p = 0.007$ and $p = 0.004$, respectively).

Fig. 5 a Great crested and
b smooth newt captures (±SE)
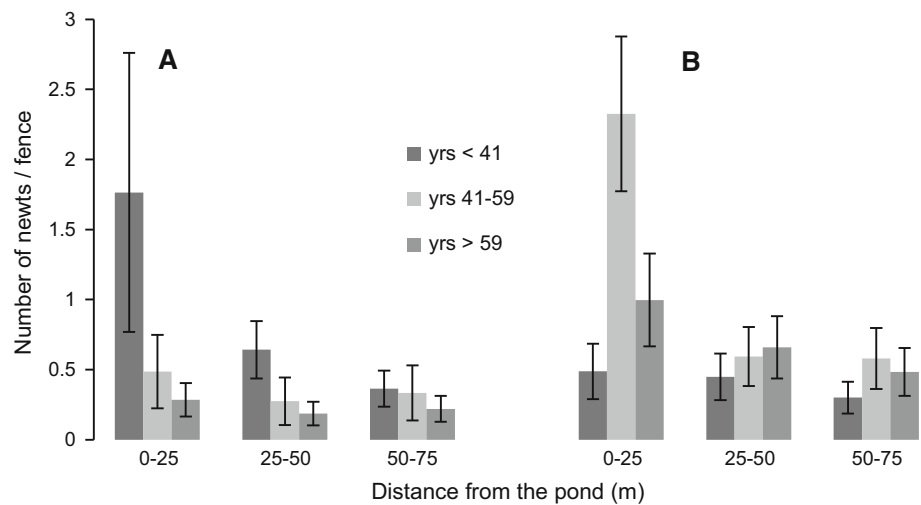in different distances and age
classes

Table 3 Coefficients of the model terms

Model term	Coefficient	SE	Exp(coefficient)
Intercept	−1.187	0.648	0.305
Tc versus Lv	−1.365	0.491	0.255
Zone 1 versus 3	0.846	0.37	2.330
Zone 2 versus 3	0.35	0.367	1.419
Cover 1 versus 3	−1.471	0.517	0.230
Cover 2 versus 3	−1.314	0.824	0.269
Age 1 versus 3	−0.865	0.491	0.421
Age 2 versus 3	0.368	0.96	1.445
2010 versus 2011	−0.843	0.141	0.430
Canopy	−0.001	0.006	0.999
Log fence lenght	0.825	0.188	2.282
Tc × zone 1	−0.047	0.4	0.954
Tc × zone 2	−0.332	0.425	0.717
Tc × 2010	−0.418	0.202	0.658
Tc × cover 1	−1.216	0.68	0.296
Tc × cover 2	0.247	0.923	1.280
Canopy × Tc	0.022	0.005	1.022
Tc × age 1	0.634	0.476	1.885
Tc × age 2	0.884	1.047	2.421
Zone 1 × age 1	−0.608	0.516	0.544
Zone 1 × age 2	0.617	0.524	1.853
Zone 2 × age 1	−0.134	0.524	0.875
Zone 2 × age 2	−0.099	0.551	0.906
Tc × zone 1 × age 1	1.275	0.547	3.579
Tc × zone 1 × age 2	−1.031	0.571	0.357
Tc × zone 2 × age 1	0.714	0.594	2.042
Tc × zone 2 × age 2	0.162	0.622	1.176
Tc × age 1 × cover 1	2.408	0.797	11.112
Tc × age 2 × cover 1	−0.717	1.245	0.488
Lv × age 1 × cover 1	1.809	0.657	6.104
Lv × age 2 × cover 1	0.384	1.063	1.468

Cover, shelter-providing understory cover; Canopy, cover of the
dominating canopy cover

Smooth newts (Fig. 6b) were captured most frequently
from the old forest sites with high ground cover vegetation
(>63 % cover). Captures from these favored sites differed
significantly from the old sites with low ground cover
($p = 0.012$) and from the young sites with high ground
cover ($p = 0.024$). Among the youngest sites, intermediate
ground cover had significantly lower capture rates compared with low ($p = 0.019$) and high ground cover classes
($p = 0.037$). Among the intermediate ground cover class,
the amount of captured smooth newts increased significantly ($p = 0.004$) from the youngest to middle-aged sites.

Among the youngest sites, great crested newts clearly
favored sites with high shelter-providing vegetation compared to smooth newts ($p = 0.006$). In medium-aged sites
with low ground-covering vegetation, smooth newts outnumbered great crested newts ($p = 0.018$). Within the
oldest sites, more of both species were captured when
ground cover increased from the lowest to the highest
level.

In addition to the above-mentioned variables, also the
canopy cover was included in the model. In the case of the
great crested newt, the coefficient of canopy cover had a
value of 0.022 ($p < 0.001$), meaning that an increase in
canopy cover of one unit (%) will result a 2.1 % increase
($0.999 \times 1.022 = 1.021$) in great crested newts per fence
compared with the smooth newt.

Discussion

Our main aim was to compare a common and a rare newt
species, to see whether their ecological characteristics
differ and whether these differences can help in managing
and conserving populations. We found that surroundings of
the breeding ponds have a major influence on the occurrence of both the species. Understory shelter is decisive but

Fig. 6 a Great crested and
b smooth newt captures (±SE)
in different shelter-providing
understory cover and age
classes
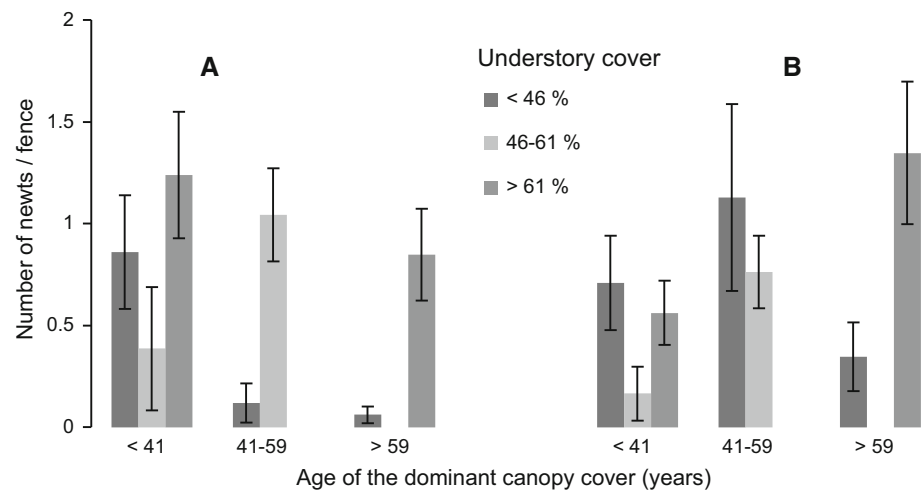
also forest age matters. We also found that the longer the distance from the breeding pond, the more selective the species become in their habitat choice. The rare species, in particular, seemed always to require sheltering understory vegetation but not necessarily old forest.

The importance of forest structure and shelter-providing vegetation on understory

Shelter-providing vegetation on the understory provides protection against water loss and thermal stress (Mazerolle and Desrochers 2005). It is, thus, probably highly important for ectothermic salamanders. In our results, too, the importance of ground cover was clearly visible within all the distance classes separately and we did not capture any great crested newts from treeless clear-cut areas. The combination of age and ground cover together revealed essential interactions; the greatest difference in newt captures was found in old forests between low and high vegetation cover. This suggests that the age or canopy cover of the forest alone is not an adequate factor to determine the quality of the terrestrial habitat of newts. More important is the cover of vegetation which provides direct shelter on the forest floor. Newts have been found to use ground-covering objects such as grass tussocks, logs, or burrows as land refuges. Newts return to these refuges during the day after nightly movements or they are used for estivation and overwintering (Jehle 2000; Jehle and Arntzen 2000; Malmgren et al. 2007; Schabetsberger et al. 2004).

Originally, we anticipated that newts would avoid recently clear-cut areas and would be found more frequently with increasing age of the forest, peaking among the oldest forests. Clear-cuts were devoid of great crested newts, as we expected, but, surprisingly, we found a decreasing trend in great crested newt captures with increasing age, while smooth newts clearly favored

intermediate and old sites. Notably, however, smooth newts did not show any difference in captures in clear-cuttings compared with all the other sites. This supported the hypothesis of the rare species being mote intolerant compared with the common one.

According to our results, 10 years after clear-cut the sites were already used frequently by the newts. Ash (1997) found that salamanders returned to clear-cut areas after 4–6 years together with rapid growth of understory vegetation, which creates favorable microclimatic conditions on the forest floor (Brooks and Kyker-Snowman 2008). In spite of the relatively low canopy covers, these young sites probably have enough ground layer to provide shelter to newts (for cover data, see Lakka and Kouki 2009).

Buffer zones around the ponds

The distance from the pond has a major effect on the newt abundance. In our study, the number of captures in the vicinity of the ponds was more than double compared with captures 50–75 m away from the shoreline. This is in accordance with Jehle and Arntzen (2000) who studied post-breeding migrations of 14 great crested newts by radio tracking and found that they migrated on average 28.5 m (±7.9) from the pond (range 2.1–99.5 m). Only three (all females) of the studied 14 individuals passed 25 m (Jehle and Arntzen 2000). Also Jehle (2000) found that 95 % of all summer refuges were within 63 m of one pond. It is evident that also the newts in our study clearly preferred to stay in the vicinity of the ponds.

Since the terrestrial habitats around the ponds are often inhabited by the newts and since they have a clear preference for specific habitats, our results support the maintenance of buffer zones around the breeding ponds. The greatest amounts of smooth newts were found in old forests, with a dense field layer vegetation of herbs and grasses. These

conditions are best met if forests are not intensively managed and, in particular, if clear-cuttings are avoided. However, the maintenance of a herbaceous field layer may require small-scale gap formation, to avoid too dense canopy coverage. Generally, the understory vegetation is influenced by the dominant tree canopy cover composition and structure via modifications of resource availability like light, water, and soil nutrients together with the physical characteristics of the litter layer (Barbier et al. 2008). Single-tree selection has been shown to maintain mixed multi-storied stands with more diverse understory vegetation (Duguid and Ashton 2013; Smith et al. 2008; Zenner et al. 2011). Instead of planting spruce monocultures in the vicinity of the breeding ponds, it may be worth considering the use of single-tree selection as a forest-harvesting method to improve the quality of the terrestrial habitats.

In addition to habitat type, the width of the buffer zone is a matter of importance too. This zone should extend far enough to include all habitats at different life stages (Semlitsch and Bodie 2003). In our study, the interaction of distance and understory cover showed that the occurrence patterns of great crested newts were not similar in all zones. To facilitate movement of the newts, clear-cuts should not be applied within the buffer zone. Furthermore, soil scarification would likely be extremely harmful for the great crested newts because it destroys the protective ground vegetation.

Differences between the rare and the common species

Though difference in their commonness, the species pair in this study has been shown to share similar responses to environment (Denoel et al. 2013). The interspecific interactions between these two species are considered weak due to their different feeding habits and microhabitats (Griffiths et al. 1994; Griffiths and Mylotte 1987). According to our results, rare species seemed to have more restricted habitat use than common species, especially at sites with low vegetation cover. Great crested newts clearly avoided these sites, while smooth newts were found to be more evenly distributed with respect to the vegetation cover. This might be explained by the species' size difference: The great crested newt, being a larger species, is easily detected in sparse vegetation. The different behavior might be also due to the availability of different prey species, which was not studied here. Nor can we totally exclude the possibility that smooth newts could show some avoidance of the habitats with abundant great crested newt populations.

The effect of forest management in terms of canopy age was opposite to our predictions. It was the common species which avoided the young age classes created by loggings and the rare one which favored them. The reason for this different behavior cannot be directly deducted from our

data and was somewhat unexpected. Behind the pattern might lie differences in food resources, humidity, or avoidance of the same habitats by the smooth newts in the presence of great crested newts. Probably, other factors than canopy age determine the terrestrial habitat use of great crested newts.

From the conservation viewpoint, the requirement of understory shelter is more critical to the great crested newt. Even though it could live and migrate through younger forests, too, the lack of sheltering vegetation may be critical. This may have some implications on how well the species can colonize new sites and maintain viable populations regionally. The narrow habitat selection together with long inter-patch distances would indicate that the rare species has relatively good dispersal ability (Rosenzweig and Lomolino 1997). The knowledge about great crested newt's long-distance dispersal is unfortunately limited, but the dispersal ability of amphibians is generally underestimated (Smith and Green 2005). It is also possible that we still have not seen the impact of isolation at its' full scale (for extinction debt, see Tilman et al. 1994) due to relatively recent land use change by drainage of mires for forestry purposes, which has destroyed breeding habitats by desiccation, overgrowing, and fish dispersion (Vuorio et al. 2015). The rare species has faced these land use threats only in the last 50 years, so it could be regarded as newly rare species, which is expected to have a greater risk of extinction, compared with species with a longer history of rarity (Gaston and Kunin 1997a).

The species pair shows differences also in the use of aquatic habitats, which were not covered in our study. The better capability of the smooth newt to breed in ponds with fish (Skei et al. 2006) and lower pH (Griffiths and Dewijer 1994) provides it substantially more potential breeding sites. The larger number of potential breeding sites associated with the greater tolerance to dispersal matrix might explain the commonness of smooth newt.

Conclusions

We found that the combination of tall trees and high understory cover forms the most attractive habitat structure for the newts in the forested landscape. Thus, to facilitate movement in terrestrial habitats, the maintenance of protective vegetation around the breeding ponds is essential. If natural canopy openings are rare due to planted monocultures, small-scale habitat restoration or selective cuttings may be needed to maintain a diverse herbaceous layer that provides ground-level shelter.

We also found that there are notable differences between the two newt species. It appeared that the rare species—the great crested new—seemed to be less tolerant to changes in

sheltering vegetation. At long-distances from the breeding ponds, the species almost exclusively occurred on sheltered sites only, whereas the smooth newt was still quite common in exposed habitats. This observation suggests that facilitation of the dispersal of the rare species requires careful attention to be paid to forest structure between ponds. It is quite likely that species cannot disperse over long-distances if sheltering vegetation is absent. Unfortunately, it is quite difficult to give general management recommendations because, for example, forest structure and distances between ponds are so variable (Baldwin et al. 2006) and because our study was still rather limited in its spatial scale. Although fixed-width buffers are administratively simple to implement and monitor, our results suggest that site-specific consideration of wider buffer zones with continuous understory cover would benefit the newts.

Conflict of interest The authors declare that they have no conflict of interest.

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