



## Terrestrial ecology of juvenile great crested newts (*Triturus cristatus*) in a woodland area

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The great crested newt *Triturus cristatus* is declining in many parts of its range. Although the aquatic ecology of this species is well known, the terrestrial ecology of great crested newts remains poorly understood, especially that of juveniles. This study examined the terrestrial ecology of juvenile great crested newts from March to October, 2008 to 2011 over four years within Epping Forest, UK. Sixty-three cover objects (logs and stones) were sampled weekly. While 28% of juveniles were only encountered once, 72% were observed for between one and seven months per year, often exhibiting a pattern of repeated presence and absence. This suggests that juveniles may remain within small home ranges close to natal ponds to feed and grow. Body Condition Index (BCI) scores varied significantly with seasons, with the highest values in spring and the lowest values in summer. BCI scores were highest after milder winters. Apparent monthly survival of juveniles varied between 0.12 and 1.00 while the estimated number of juveniles present under refuges ranged between three and 50. Findings from this study increase our understanding of the ways in which juveniles utilise cover objects and demonstrate that estimates of body condition and monthly survival vary between March and October over a four year period.

*Key words:* amphibian, body condition, capture-recapture, juvenile, terrestrial, *Triturus cristatus*

### INTRODUCTION

The great crested newt (*Triturus cristatus*) has a widespread distribution across northern and central Europe, with native populations in 25 countries (Sillero et al., 2014). Despite this, populations are declining throughout its range (Kuzmin et al., 1996; Edgar & Bird, 2006; Denoël, 2012) due to urban development, modern farming practices and lack of management (Clemons, 1997; Jehle et al., 2011). Many studies have examined the ecology of this species during the aquatic phase (e.g., Joly & Giacoma, 1992; Griffiths et al., 1994; Miaud, 1995; Baker, 1999; Jehle et al., 2001; Denoël & Ficetola, 2008) such that the requirements of great crested newts whilst at breeding ponds are largely understood. However, relatively few studies have examined great crested newt behaviour and ecology during the terrestrial phase (Oldham et al., 2000; Malmgren, 2007), for which our understanding lags far behind that of the aquatic phase (Oldham et al., 2000; Schabetsberger et al., 2004; Malmgren, 2007).

Observations of adult great crested newts whilst on land have shown that individuals favour a range of habitats which include rank grass, deciduous woodland and soil (Langton et al., 1994; MacGregor, 1995; Latham & Oldham, 1996; Jehle & Arntzen, 2000; Gustafsen et al., 2011). Radio-tracking studies on adults of the

related Italian crested newt (*T. carnifex*) have shown that individuals utilise a wide range of terrestrial habitats including burrows of rodents, cavities under rocks, rotting tree stumps from depths 5–80 cm (Schabetsberger et al., 2004; see also review in Jehle et al., 2011). Adult *T. cristatus* may move up to 1290 m from ponds in one year (Jehle & Arntzen, 2000) whilst juveniles may move up to 860 m from natal ponds within one year of metamorphosis (Kupfer & Kneitz, 2000). These findings have aided in the provision and protection of suitable terrestrial habitat for great crested newts such as scrub, long vegetation and loose soil around breeding ponds. In addition, provision of artificial 'hibernacula', consisting of piles of stones and soil, and cover objects, such as logs, have been suggested in conservation advice (Langton et al., 2001). Immature amphibians may have different terrestrial requirements compared to adults due to differences in their size and ecology (Semlitsch, 2000; Stevens et al., 2004), and these differences should be considered when managing habitats for different life stages (Roznik et al., 2009). However, studying the terrestrial ecology of juveniles is difficult because of their small size and elusive behaviour (Popescu & Hunter, 2011).

Here I present the results from a four-year investigation of terrestrial juvenile *T. cristatus* in an area of deciduous woodland in Epping Forest, UK. The aims of this study were to: (1) assess the patterns of terrestrial cover

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object use by juveniles; (2) calculate body condition indices (BCI) of juveniles over four years and examine how temperature and rainfall may influence BCI; (3) use capture-mark-recapture models to estimate apparent monthly survival and capture probability of juveniles whilst on land.

## MATERIALS AND METHODS

### Location of terrestrial refuges

The study was conducted within the grounds of Epping Forest Field Centre in Epping Forest, UK (51°39'47" N, 0°2'35" E) comprising 2.2 ha in area (including buildings) and two ponds. The ponds were between 200 and 300 m<sup>2</sup> in area and approximately 26 m apart, with deciduous woodland within 5 m of both ponds extending for several hundred metres in all directions, providing terrestrial habitat in the form of loose soil, dead leaves, scrub and decaying wood. There was a third, larger breeding pond (area c. 400 m<sup>2</sup>) just over 400 m to the northeast of these two ponds surrounded by further extensive deciduous woodland. The next nearest ponds were greater than 1 km away.

A total of 63 refuges located between 10 and 50 m from the two adjacent breeding ponds were utilised for this study and comprised all the logs and concrete slabs which could be lifted or rolled over. The field centre is surrounded by deciduous woodland comprising mainly common beech (*Fagus sylvatica*), silver birch (*Betula pendula*) and pedunculate oak (*Quercus robur*). Deciduous woodland continued for several hundred metres in all directions. The refuges were lying on natural substrate, usually leaf litter, soil or grass in small rings or lines. Forty-eight refuges were natural logs varying in size between 25 cm length (L) x 22 cm diameter (D) and 121 cm L x 20 D cm. Six of the refuges were flattened stones, 34 cm x 31 cm in size, while the remaining nine refuges were concrete slabs (69 cm x 60 cm x 5 cm). Due to their location within the grounds (i.e. secluded or protected areas) refuges were unlikely to have been disturbed by members of the public.

### Sampling methodology

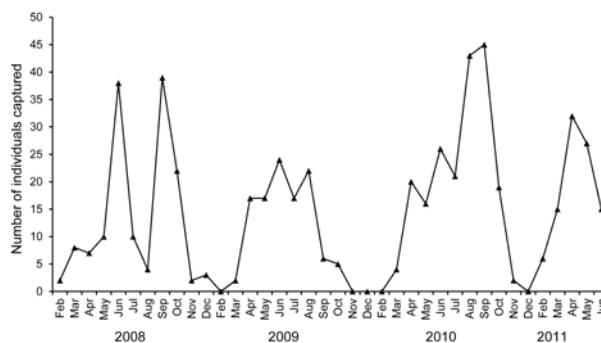
Refuges were lifted or rolled weekly between 1000 and 1200 hours to determine the presence of great crested newt juveniles. Sampling was not conducted more frequently as this may have affected the newts' behaviour and site fidelity (Marsh & Goicochea, 2003). The snout-vent length (SVL) was measured to the nearest 0.5 mm using callipers. Individuals were classed as juveniles if they were between 36 and 59 mm and lacked features of sexually mature adults, i.e. a vestigial crest and enlarged cloaca in a male or swelling in the abdomen indicating presence of eggs in a female. Juveniles with a SVL <40 mm and with the presence of gill slits on the head were classed as metamorphs, i.e. metamorphosed from larvae during the year of capture. Body mass was recorded to the nearest 0.01 g using digital pocket scales. Individual adult great crested newts have a unique ventral pattern marking (Arntzen et al., 1999) which meant that digital photograph recognition could be used to identify

individuals (Griffiths et al., 2010). All great crested newts were returned to their points of capture immediately after taking measurements and photographs. Weather data were collected from an on-site meteorological station, managed by the Meteorological Office, UK.

### Data analysis

Linear regression analysis was used to determine whether the number of juveniles captured in each month was affected by mean monthly minimum air temperature and total monthly rainfall. The body condition index (BCI) of each juvenile was calculated by taking the residuals ( $y$ ) from a Modell II regression of mass against SVL after log transformation:  $BCI = (\text{Log}_{10} \text{SVL}) / (\text{Log}_{10} \text{mass})^y$  (Green, 2001). Juveniles were divided into size classes of 10 mm intervals (30 to 39 mm, 40 to 49 mm and 50 to 59 mm) prior to body condition analysis, as the proportion of stored energy changes depending on size (Peig & Green, 2010). An unbalanced two-way analysis of variance using the general linear model (GLM) facility in Minitab was used to determine whether there was a significant difference in BCI among seasons and years; analysis was restricted to BCI data collected between 2008 and 2010. Linear regression was used to analyse the relationship between mean minimum air temperature and total non-aquatic period rainfall on mean BCI of juveniles in spring of each year. Mean air temperature was taken as the mean minimum air temperature across the winter period, from December to February each year. Total non-aquatic period rainfall refers to the rain falling during the non-breeding (non-aquatic) period and was calculated as the total rain falling in the preceding August to February for each year.

Apparent monthly survival ( $\Phi$ ) and capture probability ( $p$ ) were calculated in the period March to October, 2008 to 2011, using the live-recapture Cormack-Jolly-Seber model which uses Akaike's Information Criterion (AIC) to build and select models (Burnham & Anderson, 2002) in program MARK (White & Burnham, 1999). No juveniles were captured outside of this period. Since sexual maturation (Thomson et al., 2009) and death may be confounded by permanent emigration (Mazerolle et al., 2007), the term apparent survival is used (Pledger et al., 2003). The information-theoretic approach was utilised to create models with varying numbers of parameters based on  $\Phi$  and  $p$ . The global model with the largest number of parameters was:  $\{\Phi(\text{time}), p(\text{time})\}$  i.e. both apparent monthly survival and capture probabilities vary



**Fig. 1.** Incidence of capture of juvenile great crested newts, February 2008 to June 2011.

**Table 1.** CJS model selection for monthly juvenile survival and capture probability 2008 to 2011 based upon  $\Delta\text{QAICc}$  in program MARK.  $\Phi$ =survival,  $p$ =capture probability, (t)=parameter varies with time, (.)=parameter constant with time, QAICc=quasi Akaike's Information Criteria for small sample sizes,  $\Delta\text{QAICc}$ =delta quasi Akaike Information Criteria for small sample sizes adjusted using  $\hat{c}$ . NP=number of parameters used in each model.

| Year | Model               | QAICc  | $\Delta\text{QAICc}$ | QAICc weights | NP |
|------|---------------------|--------|----------------------|---------------|----|
| 2008 | $\{\Phi(.), p(.)\}$ | 48.971 | 0.000                | 0.957         | 2  |
|      | $\{\Phi(t), p(.)\}$ | 55.578 | 6.607                | 0.035         | 8  |
|      | $\{\Phi(.), p(t)\}$ | 58.579 | 9.608                | 0.008         | 8  |
|      | $\{\Phi(t), p(t)\}$ | 58.579 | 21.772               | 0.000         | 13 |
| 2009 | $\{\Phi(.), p(t)\}$ | 54.389 | 0.000                | 0.694         | 7  |
|      | $\{\Phi(t), p(.)\}$ | 56.477 | 2.088                | 0.244         | 7  |
|      | $\{\Phi(.), p(.)\}$ | 59.272 | 4.883                | 0.060         | 2  |
|      | $\{\Phi(t), p(t)\}$ | 67.307 | 12.917               | 0.001         | 11 |
| 2010 | $\{\Phi(t), p(.)\}$ | 81.012 | 0.000                | 0.857         | 8  |
|      | $\{\Phi(.), p(t)\}$ | 84.729 | 3.717                | 0.134         | 8  |
|      | $\{\Phi(.), p(.)\}$ | 90.404 | 9.392                | 0.008         | 2  |
|      | $\{\Phi(t), p(t)\}$ | 93.817 | 12.805               | 0.001         | 13 |
| 2011 | $\{\Phi(.), p(.)\}$ | 32.426 | 0.000                | 0.918         | 2  |
|      | $\{\Phi(.), p(t)\}$ | 38.365 | 5.939                | 0.047         | 5  |
|      | $\{\Phi(t), p(.)\}$ | 39.010 | 6.584                | 0.034         | 5  |
|      | $\{\Phi(t), p(t)\}$ | 48.822 | 16.396               | 0.000         | 7  |

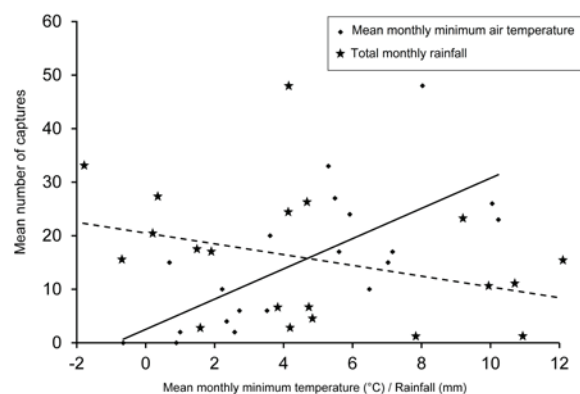
with time. Models with fewer parameters were then derived from this global model. Goodness-of-fit to the global model was performed by parametric bootstrapping of 1000 iterations. AIC corrected for small sample size (AICc) was used to perform model selection. QAICc, an adjustment of AICc taking into account the  $\hat{c}$  value, was calculated and the  $\Delta\text{QAICc}$  was used to give a measure of the fit of each model relative to the best fitting model. The variance inflation factor,  $\hat{c}$  was applied to model selection to correct for over-dispersion in the data. This was calculated by dividing the deviance of the global model from that of the mean of the bootstrap models (White & Cooch, 2012). Models ranked with the lowest  $\Delta\text{QAICc}$  were considered to have the best support for the data (Burnham & Anderson, 2002). Values for  $\Delta\text{QAICc} < 2.0$  were regarded as having considerable support.  $\Delta\text{QAICc}$  values between 3.0 and 7.0 had little support and values  $> 10.0$  were unlikely to support the data (Burnham & Anderson, 2002). In cases where lower ranking models had a  $\Delta\text{QAICc} > 2.0$ , model averaging was performed whereby the parameter estimate and standard error were averaged across all supporting models (Burnham & Anderson, 2002). The estimated number of juveniles under refugia in each month was estimated by dividing the number of individuals captured at a particular pond in a given month by the capture probability for that month (Griffiths et al., 2010).

## RESULTS

### Patterns and incidence of capture

A total of 149 individual juvenile great crested newts were captured 556 times in the period March 2008 to June 2011. Juveniles frequently shared the same refuge

and did not appear territorial. Only 9 individual adults were recorded in the same time period. Patterns of capture varied with season and year (Fig. 1). Captures were zero in the period December to February. In each year, numbers rose through the spring (March to April) and peaked in the summer (June and July) and early autumn (September and October) before rapidly dropping off in late November. In 2008 there were two peaks in abundance, the first of which occurred in June with 48 individuals and then a second in late September of 42 individuals. In the period February to June there was a significant positive relationship between the mean monthly minimum air temperature and the mean monthly captures of juveniles ( $R^2=0.49$ ,  $F_{1,19}=17.36$ ,  $p<0.001$ ; Fig. 2). There was no significant relationship between the number of juveniles captured and total monthly rainfall ( $R^2=0.11$ ,  $F_{1,19}=2.34$ ,  $p=0.14$ ; Fig. 2),



**Fig. 2.** Multiple regression showing the relationship between mean monthly minimum air temperature and total monthly rainfall with number of juveniles captured.

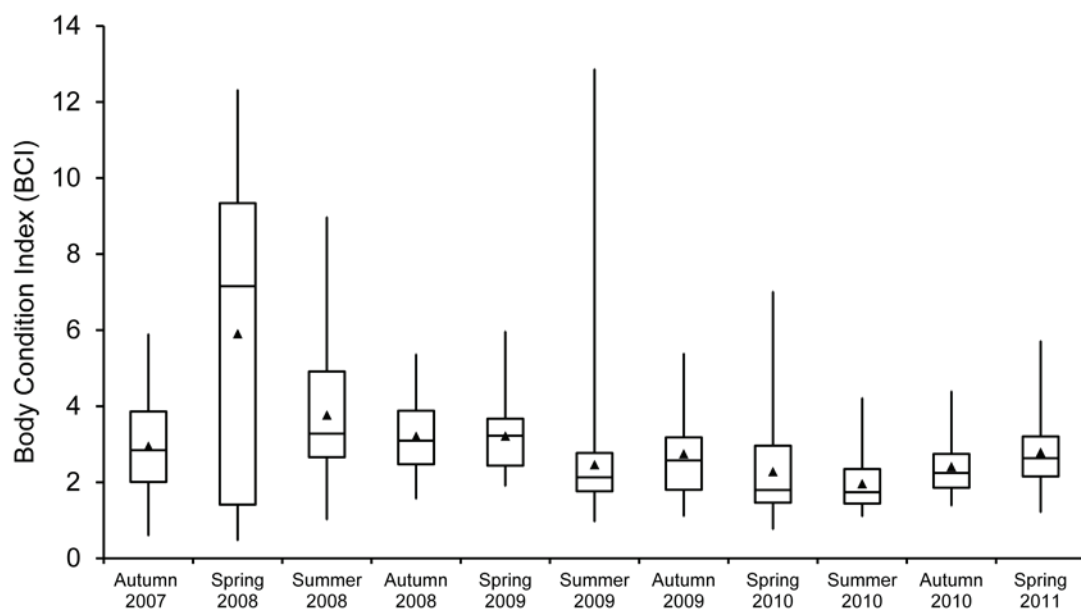
**Table 2.** Survival and capture probability for the models with the highest rank for each year 2008 to 2011. SE=standard error,  $\Phi$ =survival estimate;  $p$ =capture probability estimate, N/A=not applicable; value constant with time for the months analysed.

| Year | Model                     | Parameter | Month | Estimate | SE       |
|------|---------------------------|-----------|-------|----------|----------|
| 2008 | { $\Phi(\cdot)p(\cdot)$ } | 1: $\Phi$ | N/A   | 0.564    | 0.081    |
|      |                           | 2: $p$    | N/A   | 0.888    | 0.100    |
| 2009 | { $\Phi(\cdot)p(t)$ }     | 1: $\Phi$ | N/A   | 0.783    | 0.062    |
|      |                           | 2: $p$    | Mar   | 0.564    | 1376.809 |
|      |                           | 3: $p$    | Apr   | 0.564    | 1376.809 |
|      |                           | 4: $p$    | May   | 0.668    | 0.194    |
|      |                           | 5: $p$    | Jun   | 0.946    | 0.030    |
|      |                           | 6: $p$    | Jul   | 0.827    | 0.144    |
|      |                           | 7: $p$    | Aug   | 0.831    | 0.196    |
|      |                           | 8: $p$    | Sep   | 0.465    | 0.182    |
|      |                           | 9: $p$    | Oct   | 0.251    | 0.030    |
| 2010 | { $\Phi(t)p(\cdot)$ }     | 1: $\Phi$ | Mar   | 0.450    | 0.000    |
|      |                           | 2: $\Phi$ | Apr   | 1.000    | 0.000    |
|      |                           | 3: $\Phi$ | May   | 0.705    | 0.208    |
|      |                           | 4: $\Phi$ | Jun   | 0.497    | 0.181    |
|      |                           | 5: $\Phi$ | Jul   | 0.788    | 0.189    |
|      |                           | 6: $\Phi$ | Aug   | 1.000    | 0.000    |
|      |                           | 7: $\Phi$ | Sep   | 0.763    | 0.151    |
|      |                           | 8: $\Phi$ | Oct   | 0.118    | 0.079    |
|      |                           | 9: $p$    | N/A   | 0.893    | 0.070    |
| 2011 | { $\Phi(\cdot)p(\cdot)$ } | 1: $\Phi$ | N/A   | 0.775    | 0.183    |
|      |                           | 2: $p$    | N/A   | 0.691    | 0.211    |

indicating that individuals were no more likely to be present in wetter compared to drier conditions.

Forty-two (28%) individuals were captured only once. Just over half (57%) of these were metamorphs located under refuges <10 m away from a pond. The remaining 72% of individuals were captured between two and 19 times, often on consecutive sampling occasions. These

individuals often returned to the same refuge and remained there for between one and seven months per year (Table 2). During the winter months (December to February) 24 individuals (16%) disappeared from refuges and then re-appeared under the same slab the next spring. Only one individual (0.7%) was encountered for more than two consecutive years.



**Fig. 3.** Box and whisker plot showing body condition index (BCI) for each season from autumn 2007 to spring 2011. Spring=March to May; summer=June to August; autumn=September to November. Boxes denote 1<sup>st</sup> and 3<sup>rd</sup> quartiles, horizontal lines and crosses denote median and mean values respectively. Whiskers show maximum and minimum BCI.

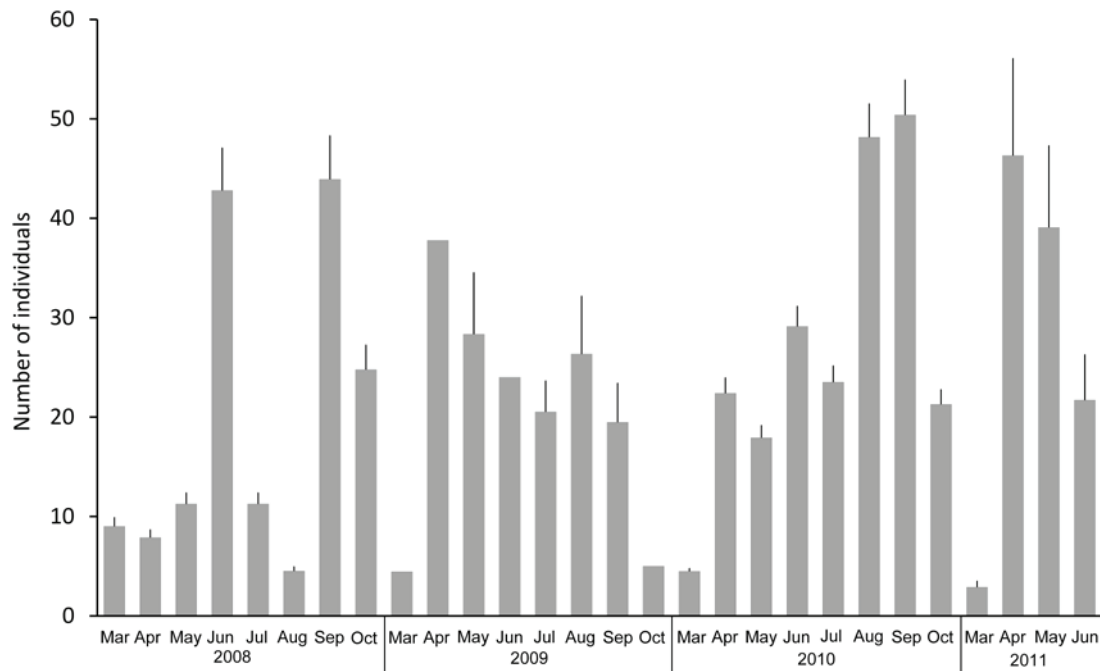


Fig. 4. Population estimates with standard error for juveniles, March to October 2008 to 2011.

#### Body condition

There were significant differences in juvenile body condition among years ( $F_{2,343}=47.48$ ,  $p<0.001$ ) and seasons ( $F_{2,343}=13.35$ ,  $p<0.001$ ) with a significant interaction indicating that seasonal variation in BCI depended on year ( $F_{4,343}=6.36$ ,  $p<0.001$ ). Annual mean BCI scores were highest in 2008 (3.86, SE=0.24) before falling to 2.70 (SE=0.12) and 2.20 (SE=0.12) in 2009 and 2010, respectively. Body condition index scores rose slightly at the start of 2011 to 2.78 (SE=0.17). The highest seasonal BCI score was in spring 2008 at 5.91 (SE=1.21) and lowest in summer 2010 at 1.97 (SE=0.09) (Fig. 3). Body condition was low in the summers of 2009 and 2010, followed by a rise in autumn. However, this trend was not evident in 2008. The summer (June to August) of 2008 was cool with a mean minimum air temperature of 9.53°C compared to 11.74°C and 11.78°C in 2009 and 2010 respectively. Linear regression showed no significant relationship between mean monthly winter temperature (December to February) and the body condition of juveniles the following spring ( $R^2=0.67$ ,  $F_{1,3}=4.15$ ,  $p=0.18$ ), and mean BCI score of juveniles and total non-aquatic period rainfall ( $R^2=0.02$ ,  $F_{1,3}=0.04$ ,  $p=0.86$ ).

#### Estimation of monthly survival and capture probability

The highest ranking model varied in each year of study (Table 1) and model averaging was only required in 2009. Estimates for apparent monthly survival were constant in three out of the four years (Table 1). The lowest estimates were 0.56 in 2008 and highest at 0.78 in both 2009 and 2011 (Table 2). This indicates relatively high monthly survival in the period March to October in all three years. In 2010, estimates of apparent monthly survival varied between each month ranging from 0.12 in October to 1.00 in April and August (Table 2). Capture probability was also constant between months in three out of the four years, ranging between 0.69 and 0.89 (Table 2).

This indicates a high likelihood of finding juveniles under cover objects in these years. Capture probabilities varied by month in 2009, ranging between 0.25 in October to 0.95 in June (Table 2).

The estimated number of juveniles present under refuges varied between month and year ranging from three individuals in March 2011 to 50 in September 2010 (Fig. 4). In March of all four years, estimated numbers of juveniles were low. Peak estimates were in June and September in 2008, April in 2009, August and September in 2010 and April in 2011.

## DISCUSSION

#### Utilisation of terrestrial cover objects

The provision of terrestrial cover objects to aid in the conservation of amphibians during their terrestrial phase has been recognised for many years (Langton et al., 2001; Roznik & Johnson, 2009). However, the degree to which individuals, especially juveniles, utilise such refuges under field conditions remains largely unknown (Malmgren, 2007). Results from this study suggest that juvenile great crested newts readily utilise cover objects such as logs and concrete slabs which surround breeding ponds. These may provide shelter for juveniles and reduce the risk of predation and desiccation (Denton & Beebee, 1993; Heuring & Mathis, 2014). Adults were rarely encountered under refuges, implying that they were either utilising different habitats or were at lower densities than juveniles. The study site was within dense deciduous woodland, which includes microhabitats used by both adults and juveniles (Jehle & Arntzen, 2000; Marty et al., 2005). However, further research is required to determine how the habitat preferences of adults and juveniles vary (Semlitsch, 2008).

Juveniles were found under cover objects in all months except between December and February, when

individuals probably migrated into the soil to avoid the cold winter temperatures (Griffiths, 1984). Peaks in abundance of juveniles under refuges in spring corresponding to increases in temperature may reflect rises in activity levels after the winter, as has been noted in adults migrating to breeding ponds (Verrell & Halliday, 1985; Andreone & Giacoma, 1989; Latham & Oldham, 1996; Gravel et al., 2012). The lack of significant relationship between monthly rainfall and juvenile movement is similar to that observed in adult newts in the UK (Griffiths, 1984; Verrell & Halliday, 1985; Reading, 2007), but contrary to populations of amphibians in southern European (e.g., Andreone & Giacoma, 1989; Miaud et al., 2000; Ribéron & Miaud, 2000; Mazerolle, 2001) and North America (Vasconcelos & Calhoun, 2004) where both temperature and rainfall appear important predictors of activity. The numbers of juveniles encountered under refuges often peaked in the autumn, which coincided with emigration of metamorphs from ponds and thus reflected high abundance in the terrestrial habitat (Daverson et al., 2012). Therefore provision and availability of terrestrial cover objects may be at its most crucial for juvenile great crested newts between August and October.

Juveniles appeared to exhibit two types of behaviour in relation to the use of cover objects. First, individuals would reside under a refuge for a short time, (less than one week) before moving to alternative habitats and remaining undetected for the duration of the study. This behaviour was recorded in individual juveniles found under the majority of refuges examined and suggests that many cover objects in this site were used in this way, especially if they were close to breeding ponds. This single-use of cover objects may reflect that individuals were seeking new foraging areas and hibernacula (Müllner, 2001; Bonato & Fracasso, 2003). Immediately after metamorphosis and leaving ponds, juveniles may exhibit a series of exploratory movement patterns. Initially, juveniles disperse rapidly and are least responsive to habitat quality (Pittman et al., 2014). Following this, individuals move more slowly, with increased path sinuosity, and select more suitable microhabitats (Patrick et al., 2008; Pittman et al., 2014). The juveniles that were observed to spend less than one week under cover objects in this study may have been in an initial dispersal phase when they were at their most mobile, moving away from ponds and least likely to settle in one location for a prolonged period (Perret et al., 2003; Pittman et al., 2014).

A second behaviour exhibited by juveniles was that of utilising cover objects as a stable, semi-permanent refuge as has been noted in other terrestrial amphibians (Daverson et al., 2012; Connet & Semlitsch, 2013; Pittman et al., 2014). In the study area a row of six, large concrete refuges were used by 72% of juveniles. Individuals using these refuges exhibited extended periods of repeated presence and absence. This suggests that these juveniles (no metamorphs were recorded here) were utilising nearby habitats for foraging and feeding. It is possible that juveniles were returning to ponds to feed as noticed by Verrell & Halliday (1985), since the nearest breeding

pond was only 50 m away. In addition, juveniles may have been utilising terrestrial habitats within a local, known home range, as has been recorded in European species of terrestrial salamander (Schulte et al., 2007). Provided the surrounding terrestrial habitat is of suitable quality, these home ranges may only be between 1 and 2 m<sup>2</sup> in terrestrial salamanders (Pittman et al., 2014). However home range size between individuals may vary (Schulte et al., 2007) and the home range size for juvenile great crested newts remains to be determined. The specific behaviour of returning to known refuges has been noted by Griffiths (1984) and Ribéron & Miaud (2000) for other European urodeles, and Jehle (2000) showed that adult *T. cristatus* will return to similar terrestrial locations after translocation. In addition, after displacement of 35 m, terrestrial North American salamanders, *Plethodon shermani* and *P. chatahoochee*, are capable of returning to specific refuges (Connet & Semlitsch, 2013). This study is the first to document repeated use of the same cover object by juvenile great crested newts in the UK. Site fidelity such as this may be an adaptive strategy, allowing individuals to forage and return to a known, safe refuge (Müllner, 2001). In this study only 0.7% of juveniles were found in more than two consecutive years suggesting that after two years, juveniles had moved away from the refuges and utilised alternative microhabitats, perhaps returning to ponds to breed (Baker, 1999). The exact mechanisms which amphibians use to return to known terrestrial refuges remain unknown, but previous research suggests that amphibians may use a combination of visual, olfactory and magnetic cues when returning to breeding ponds (Fischer et al., 2001; Diego-Rasilla et al., 2005; Sinsch, 2006). In terrestrial habitats, spotted salamanders (*Ambystoma maculatum*) have been observed to use landmarks to identify foraging patches (Heuring & Mathis, 2014). It is therefore likely that when travelling short distances to and from terrestrial refuges that juvenile great crested newts use a combination of visual and olfactory cues (Popescu & Hunter, 2011). However, this remains to be tested and further research is required to determine how this species navigates to and from the same terrestrial refuge.

#### Body condition indices

The body condition of juveniles was, on average, highest in the spring, following winter hibernation. Previous studies have indicated that adult common toads (*Bufo bufo*) and yellow bellied toads (*Bombina variegata*) emerge from winter hibernation with higher body condition after cooler winters (Tomasevic et al., 2007; Băncilă et al., 2010). The higher body condition of juveniles in this study in spring compared to later in the year may therefore indicate conservation of fat reserves during the winter. However, in this study, there was no observed relationship between winter temperature and body condition of juveniles the following spring. This may be due to the relatively short four-year duration of this study. More data are required to determine whether this relationship occurs in juveniles over a longer time period. The body condition indices of juveniles were low in the summers of 2009 and 2010 before rising again in the

autumn. Lower BCI values at this time of year may reflect drying of the soil and surrounding microhabitats, resulting in fewer feeding opportunities (Reading & Clarke, 1995), and greater utilisation of fat reserves. However, drier conditions may also result in reduced body condition due to lower levels of body hydration. Long, dry summers may negatively impact on the condition of juveniles which due to their smaller size may be more prone to desiccation compared to adults (Rothermel, 2004; Roznik & Johnson, 2009). Provision of suitable microhabitats, such as cover objects, damp soil or thick vegetation may help mitigate this risk. The recorded rising of body condition in the autumn months in 2009 and 2010 may reflect the return of cooler, damper conditions and greater opportunities to forage and feed in preparation for winter. The rise in body condition may also have been due to an increase in body hydration levels. The distinction between changes in body condition as a result of water loss compared to loss of fat reserves could not be determined in this study and therefore changes in body condition may be due to a combination of both these factors. In 2008, body condition scores showed the opposite trend to 2009 and 2010, with scores being higher in the summer than the autumn. In this year summer temperatures were cooler than 2009 and 2010, which may have resulted in lower desiccation risk and thus higher body condition. However, the link between weather conditions, behaviour and body condition index was not directly demonstrated in this study and further research is required involving long term field data on juveniles, such as that carried out by Griffiths et al. (2010) on adults. However, findings from my study suggest that varying climatic conditions affect the body condition of juveniles and that monitoring body condition is important in amphibian conservation (Băncilă et al., 2010).

#### **Apparent monthly survival**

Apparent monthly survival of great crested juveniles varied between years, being constant in the period March to October in 2008, 2009 and 2011 but varying with each month in 2010. In the years when estimates of apparent monthly survival were constant, values ranged between 0.56 and 0.78. These estimates are similar to the value of 0.59 previously recorded for annual survival by Baker (1999); however this estimate was based on counts from aquatic environments rather than in terrestrial habitats. Survival rates of newly metamorphosed juveniles are likely to be influenced by various factors in the terrestrial habitat, such as predator abundance or the density and arrangement of refuges (Roznik & Johnson, 2009). Previous studies have indicated that adult annual survival is generally higher than that of juveniles (Arntzen & Teunis, 1993; Baker, 1999; Griffiths et al., 2010), probably because adults are less vulnerable to factors including predation, lack of food, microhabitat type and microclimate (Earl & Semlitsch, 2015), although the degree to which these factors affect individuals may vary depending on the time of year (Earl & Semlitsch, 2015). Results from this study suggest that, in some years, monthly survival in the period March to October may be as high as annual survival in adults. However the

range in monthly estimates for juveniles in this study indicates a high variability in survival in different years. This has been confirmed by other studies (Arntzen & Teunis, 1993; Kupfer & Kneitz, 2000) which show high variability in annual survival in juveniles. Estimates of apparent survival cannot distinguish between permanent emigration and death, resulting in potentially incorrect estimates of survival (Schmidt et al., 2007). Therefore any permanent emigration by juveniles to alternative sites would have resulted in a biased estimate for monthly survival. Across several years juveniles may also have undergone temporary emigration before returning as adults (Kendall et al., 1997; Malmgren, 2001; Schmidt et al., 2002; Bailey et al., 2004a, 2004b; Schaub et al., 2004;) and may bias estimates of survival. However, since this study examined survival across a relatively short time period this reduces errors caused by potential temporary emigration.

The estimated number of juveniles under refuges varied between month and year which may be due to differential survival and emigration of juveniles. The low estimates in March of all years may indicate that individuals were emerging from hibernation and due to the cold weather were not active. The high estimated number of juveniles under refuges in September probably reflected the emergence of metamorphs from ponds (Jehle et al., 2011). Estimates were particularly high in 2008 and 2010 which may indicate good recruitment of juveniles to the population in these years. The high numbers of juveniles present in the September of one year were followed by high estimates the following spring. This may indicate high survival of metamorphs over the winter, although it may have just reflected the high number of metamorphs emerging during the autumn. It was not possible to estimate apparent survival of metamorphs over the winter since metamorphs could not be uniquely identified due to a lack of belly pattern markings.

#### **Conclusions**

Results from this four-year study of the terrestrial ecology of juvenile great crested newts indicate that individuals may utilise cover objects in one of two ways. Firstly, juveniles may use cover objects as a temporary refuge, usually less than one week, whilst dispersing from breeding ponds. Alternatively, individuals may utilise refuges for several months of each year, exhibiting patterns of repeated presence and absence. This suggests that some juveniles may occupy a small home range, returning to the same refuge to shelter. During this period they may be utilising surrounding habitats for foraging. These findings therefore suggest that providing cover objects between 10 m and 50 m from great crested newt breeding ponds will provide areas of refuge for juveniles that will be important not only in the autumn during emergence from ponds but also throughout the year, except in the winter, when individuals move to alternative microhabitats. The body condition of juveniles, along with estimates of monthly survival, varied across the four years of study, which suggests that juveniles are vulnerable to changing environmental conditions (e.g., temperature and rainfall), predation

and desiccation. The presence of local cover objects may therefore help mitigate these risks by providing a stable refuge for juveniles.

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## REFERENCES

- Andreone, F. & Giacoma, C. (1989). Breeding dynamics of *Triturus carnifex* at a pond in northwestern Italy (Amphibia, Urodela, Salamandridae). *Holarctic Ecology* 12, 219–223.
- Arntzen, J.W., Smithson, A. & Oldham, R.S. (1999). Marking and tissue sampling effects on body condition and survival in the newt *Triturus cristatus*. *Journal of Herpetology* 33, 567–576.
- Arntzen, J.W. & Teunis, S.F.M. (1993). A six year study on the population dynamics of the crested newt (*Triturus cristatus*) following colonization of a newly created pond. *Herpetological Journal* 3, 99–100.
- Bailey, L.L., Simons, T.R. & Pollock, K.H. (2004a). Spatial and temporal variation in capture probability of Plethodon salamanders using the robust capture-recapture design. *Journal of Wildlife Management* 68, 14–24.
- Bailey, L.L., Simons, T.R. & Pollock, K.H. (2004b). Estimating detection probability parameters for Plethodon salamanders using the robust capture-recapture design. *Journal Wildlife Management* 68, 1–13.
- Baker, J.M.R. (1999). Abundance and survival rates of great crested newts (*Triturus cristatus*) at a pond in central England: monitoring individuals. *Herpetological Journal* 9, 1–8.
- Băncilă, R. I., Hartel, T., Plăiașu, R., Smuts, J. & Cogălniceanu, D. (2010). Comparing three body condition indices in amphibians: a case study of yellow bellied toad *Bombina variegata*. *Amphibia-Reptilia* 31, 558–562.
- Bonato, L. & Fracasso, G. (2003). Movements, distribution pattern and density in a population of *Salamandra atra aurorae* (Caudata: Salamandridae). *Amphibia-Reptilia* 24, 251–260.
- Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multimodal Inference: a practical information-theoretic approach*. 2<sup>nd</sup> Edition. Springer Science, USA.
- Clemons, J. (1997). Conserving Great Crested Newts. *British Society of Herpetology Bulletin* 59, 2–5.
- Connette, M. & Semlitsch, R.D. (2013). Context-dependent movement behavior of woodland salamanders (*Plethodon*) in two habitat types. *Zoology* 116, 325–330.
- Daversa, D.R., Muths, E. & Bosch, J. (2012). Terrestrial movement patterns of the common toad (*Bufo bufo*) in Central Spain reveal habitat conservation importance. *Journal of Herpetology* 46, 658–664.
- Denoël, M. (2012). Newt decline in Western Europe: highlights from relative distribution changes within guilds. *Biodiversity Conservation* 21, 2887–2898.
- Denoël, M. & Ficetola, G.F. (2008). Conservation of newt guilds in an agricultural landscape of Belgium: the importance of aquatic and terrestrial habitats. *Aquatic Conservation: Marine and Freshwater Ecosystems* 18, 714–728.
- Denton, J. & Beebee, T.J.C. (1993). Summer and winter refugia of natterjacks (*Bufo calamita*) and common toads (*Bufo bufo*) in Britain. *Herpetological journal* 3, 90–94.
- Diego-Rasilla, F.J., Luengo, R.M. & Phillips, J.B. (2005). Magnetic compass mediates nocturnal homing by the alpine newt, *Triturus alpestris*. *Behavioural Ecology and Sociobiology* 58, 361–365.
- Earl, J.E. & Semlitsch, R.D. (2015). Importance of forestry practices relative to microhabitat and microclimate changes for juvenile pond-breeding amphibians. *Forest Ecology and Management* 357, 151–160.
- Edgar, P. & Bird, D.R. (2006). *Action Plan for the Conservation of the Crested Newt Triturus cristatus Species Complex in Europe*. Convention on the conservation of European wildlife and natural habitats. Standing Committee meeting, Strasbourg, 27–30<sup>th</sup> November 2006.
- Fischer, J.H., Freaque, M.J., Borland, S.C. & Phillips, J.B. (2001). Evidence for the use of magnetic map information by an amphibian. *Animal Behaviour* 62, 1–10.
- Gravel, M., Mazerolle, M.J. & Villard, M.A. (2012). Interactive effects of roads and weather on juvenile amphibian movements. *Amphibia-Reptilia* 33, 113–127.
- Green, A.J. (2001). Mass/length residuals: measures of body condition or generators of spurious results? *Ecology* 82, 1473–1483.
- Griffiths, R.A. (1984). Seasonal behaviour and intrahabitat movements in an urban population of smooth newts, *Triturus vulgaris* (Amphibia: Salamandridae). *Journal of Zoology* 203, 241–251.
- Griffiths, R.A., Wijer P. de, & May, R.T. (1994). Predation and competition within an assemblage of larval newts (*Triturus*). *Ecography* 17, 176–181.
- Griffiths, R.A., Sewell, D. & McCrea, R. (2010). Dynamics of a declining amphibian metapopulation: Survival, dispersal and the impact of climate. *Biological Conservation* 143, 485–491.
- Gustafsen, D.H., Malmgren, J.C. & Mikusiński, G. (2011). Terrestrial habitat predicts use of aquatic habitat for breeding purposes – a study on the great crested newt (*Triturus cristatus*). *Annales Zoologici Fennici* 48, 295–307.
- Heuring L. & Mathis, A. (2014). Landmark learning by juvenile salamanders (*Ambystoma maculatum*). *Behavioural Processes* 108, 173–176.
- Jehle, R. & Arntzen, J.W. (2000). Post-breeding migrations of newts (*Triturus cristatus*) and (*T. marmoratus*) with contrasting ecological requirements. *Journal of Zoology, London* 251, 297–306.
- Jehle, R., Arntzen, J.W., Burke, T., Krupa, A.P. & Hödl, W (2001). The annual number of breeding adults and the effective population size of syntopic newts (*Triturus cristatus*, *T. marmoratus*). *Molecular Ecology* 10, 839–850.



- Jehle, R., Thiesmeier B. & Foster, J. (2011). *The Crested Newt – A Dwindling Pond Dweller*, Laurenti-Verlag, Bielefeld, Germany.
- Joly, P. & Giacoma, C. (1992). Limitation of similarity and feeding habits in three syntopic species of newts (*Triturus*, Amphibia). *Ecography* 15, 401–411.
- Kendall, W.L., Nichols, J.D. & Hines, J.E. (1997). Estimating temporary emigration using capture-recapture data with Pollock's Robust Design. *Ecology* 78, 563–578.
- Kupfer, A. & Kneitz, S. (2000). Population ecology of the great crested newt (*Triturus cristatus*) in an agricultural landscape: dynamics, pond fidelity and dispersal. *Herpetological Journal* 10, 165–172.
- Kuzmin, S.L., Bobrov, V.V. & Dunaev, E.A. (1996). Amphibians of Moscow Province: distribution, ecology and conservation. *Zeitschrift für Feldherpetologie* 3, 19–72.
- Langton, T.E.S., Beckett, C.L., Morgan, K. & Dryden, R.C. (1994). Translocation of a crested newt *Triturus cristatus* population from a site in Crewe, Cheshire, to a newly receptor site. In: *Conservation and management of great crested newts: Proceedings of a symposium held on 11<sup>th</sup> January 1994 at Kew Gardens, Richmond, Surrey*. Eds T. Gent and R. Bray. English Nature Science Report No. 20. English Nature, Peterborough.
- Langton, T.E.S., Beckett, C.L., & Foster, J.P. (2001). *Great Crested Newt Conservation Handbook*, Froglife, Halesworth.
- Latham, D.M. & Oldham, R.S. (1996). Woodland management and conservation of the great crested newt (*Triturus cristatus*). *Aspects of Applied Biology* 44, 451–459.
- MacGregor, H.C. (1995). Crested Newts – ancient survivors. *British Wildlife* 7, 1–8.
- Malmgren, J.C. (2001). Allometry for sexual size dimorphism in newts of the genus *Triturus* (Caudata: Salamandridae). *Evolutionary Ecology of Newts*, PhD thesis, University of Örebro.
- Malmgren, J.C. (2007). Modelling terrestrial interactions and shelter use in great crested newts (*Triturus cristatus*). *Amphibia-Reptilia* 28, 205–215.
- Marsh, D.M. & Goicochea, M.A. (2003). Monitoring terrestrial salamanders: biases caused by intense sampling and choice of cover objects. *Journal of Herpetology* 37, 460–466.
- Marty, P., Angélibert, S., Giani, N. & Joly, P. (2005). Directionality of pre- and post- breeding migrations of a marbled newt population (*Triturus marmoratus*): implications for buffer zone management. *Marine and Freshwater Ecosystems* 15, 215–225.
- Mazerolle, M.J. (2001). Amphibian activity, movement patterns, and body size in fragmented peat bogs. *Journal of Herpetology* 35, 13–20.
- Mazerolle, M.J., Bailey, L.L., Kendall, W.L., Royale, A., Converse, S.J. & Nichols, J.D. (2007). Making great leaps forward: accounting for detection probability in herpetological field studies. *Journal of Herpetology* 41, 672–689.
- Miaud, C. (1995). Oviposition site selection in three species of European newts (Salamandriidae) genus *Triturus*. *Amphibia-Reptilia* 16, 265–272.
- Miaud, C., Sanuy, D., and Avrillier, J. (2000). Terrestrial movements of the natterack toad *Bufo calamita* (Amphibia, Anura) in a semi-arid, agricultural landscape. *Amphibia-Reptilia* 21, 357–369.
- Müllner, A. (2001). Spatial patterns of migrating Great Crested Newts and Smooth Newts: The importance of the terrestrial habitat surrounding the breeding pond. In: *Der Kammmolch (Triturus cristatus) Verbreitung, Rana Sonderheft 4*. Ed. Andreas Krone, Biologie, Ökologie und Schutz. Natur & Text, Germany.
- Oldham, R.S., Keeble, J., Swan, M.J.S. & Jeffcote, M. (2000). Evaluating the suitability of habitat for the great crested newt (*Triturus cristatus*). *Herpetological Journal* 10, 143–155.
- Patrick, D.A., Harper, E.B., Hunter Jr, M.L. & Calhoun, A.J.K. (2008). Terrestrial habitat selection and strong density-dependent mortality in recently metamorphosed amphibians. *Ecology* 89, 2563–2574.
- Peig, J. & Green, A.J. (2010). The paradigm of body condition: a critical reappraisal of current methods based on mass and length. *Functional Ecology* 24, 1323–1332.
- Perret, N., Pradel, R., Miaud, C., Grolet, O. & Joly, P. (2003). Transience, dispersal and survival rates in newt patchy populations. *Journal of Animal Ecology* 72, 567–575.
- Pittman, S.E., Osbourn, M.S. & Semlitsch, R.D. (2014). Movement ecology of amphibians: A missing component for understanding population declines. *Biological Conservation* 169, 44–53.
- Pledger, S., Pollock, K.H., & Norris, J.L. (2003). Open capture-recapture models with heterogeneity: I. Cormack-Jolly-Seber model. *Biometrics* 59, 786–794.
- Popescu, V.D. & Hunter, Jr, M.L. (2011). Clear-cutting affects habitat connectivity for a forest amphibian by decreasing permeability to juvenile movements. *Ecological Applications* 21, 1283–1295.
- Reading, C.J. (2007). Linking global warming to amphibian declines through its effects on female body condition and survivorship. *Oecologia* 151, 125–131.
- Reading, C.J. & Clarke, R.T. (1995). The effects of density, rainfall and environmental temperature on body condition and fecundity in the common toad, *Bufo bufo*. *Oecologia* 102, 453–459.
- Regosin, J.V., Windmiller, B.S. & Reed, J.M. (2003). Terrestrial habitat use and winter densities of the wood frog (*Rana sylvatica*). *Journal of Herpetology* 37, 390–394.
- Ribéron, A. & Miaud, C. (2000). Home range and shelter use in *Salamandra lanzai*. *Amphibia-Reptilia* 21, 255–260.
- Rothermel, B.B. (2004). Migratory success of juveniles: a potential constraint on connectivity for pond-breeding amphibians. *Ecological Applications* 14, 1535–1546.
- Roznik, E.A. & Johnson, S.A. (2009). Burrow use and survival of newly metamorphosed gopher frogs (*Rana capito*). *Journal of Herpetology* 43, 431–437.
- Schabetsberger, R., Jehle, R., Maletzky, A., Pesta, J. & Sztatecsny, M. (2004). Delineation of terrestrial reserves for amphibians: post breeding migrations of Italian crested newts (*Triturus c. carnifex*) at high altitude. *Biological Conservation* 117, 95–104.
- Schaub, M., Gimenez, O., Schmidt, B.R. & Pradel, R. (2004). Estimating survival and temporary emigration in the multistate capture-recapture framework. *Ecology* 85, 2107–2113.
- Schmidt, B.R., Schaub, M. & Anholt, B.R. (2002). Why you should use capture-recapture methods when estimating survival and breeding probabilities: on bias, temporary emigration and overdispersion in common toads. *Amphibia-Reptilia*

- 23, 375–388.
- Schmidt, B.R., Schaub, M. & Steinfartz, S. (2007). Apparent survival of the salamander *Salamandra salamandra* is low because of high migratory activity. *Frontiers in Zoology* 4, 19–25.
- Schulte, U., Küsters, D., and Steinfartz, S. (2007). A PIT tag based analysis of annual movement patterns of adult fire salamanders (*Salamandra salamandra*) in a middle European habitat. *Amphibia-Reptilia*, 28, 531–536.
- Semlitsch, R.D. (2000). Principles for management of aquatic breeding amphibians. *Journal of Wildlife Management* 64, 615–631.
- Semlitsch, R.D. (2008). Differentiating migration and dispersal processes for pond-breeding amphibians. *Journal of Wildlife Management* 72, 260–267.
- Sillero, N., J. Campos, A. Bonardi, C. Corti, R. et al. (2014). Updated distribution and biogeography of amphibians and reptiles of Europe. *Amphibia-Reptilia* 35, 1–31.
- Sinsch, U. (2006). Orientation and navigation in Amphibia. *Marine and Freshwater Behaviour and Physiology* 39, 65–71.
- Sinsch, U., Schäfer, R., Sinsch, A. (2006). The homing behaviour of displaced smooth newts *Triturus vulgaris*. In: M. Vences, J. Köhler, T. Ziegler, W. Böhme (eds): *Herpetologia Bonnensis II. Proceedings of the 13th Congress of the Societas Europaea Herpetologica*. pp. 163–166.
- Stevens, V.M., Polus, E., Wesselingh, R.A., Schtickzelle, N., & Baguette, M. (2004). Quantifying functional connectivity: experimental evidence for patch-specific resistance in the Natterjack toad (*Bufo calamita*). *Landscape Ecology* 19, 829–842.
- Thomson, D.L, Conroy, M.J., Anderson, D.R., Burnham, K.P., et al. (2009). Standardising terminology and notation for the analysis of demographic processes in marked populations. In: D.I. Thomson, E.G., Cooch & M.J. Conroy (Eds.): *Modeling demographic processes in marked population*. Springer.
- Tomašević, N., Cvetković, D., Aleksić, I. & Crnobrnja-Isailović, J. (2007). Effect of climatic conditions on post-hibernation body condition and reproductive traits of *Bufo bufo* females. *Archives of Biological Sciences, Belgrade* 59, 51-52.
- Vasconcelos, D. & Calhoun, A.J.K. (2004). Movement patterns of adult and juvenile *Rana sylvatica* (Le conte) and *Ambystoma maculatum* (Shaw) in three reforested seasonal pools, Maine. *Journal of Herpetology* 38, 551–561.
- Verrell, P. & Halliday, T. (1985). The population dynamics of the crested newt *Triturus cristatus* at a pond in southern England. *Holarctic Ecology* 8, 151–156.
- White, G.C. & Burnham, K.P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Suppl. 1), S120–S139.
- White, G.C. & Cooch, E. Eds. (2012). *Program MARK: a gentle introduction, 11<sup>th</sup> edition*, Available from: <<http://www.phidot.org/software/mark/docs/book/>>.

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