Movements of Alpine newts (Mesotriton alpestris) between small aquatic habitats (ruts) during the breeding season

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Abstract

Many species with complex life cycles, such as caudate amphibians, migrate from terrestrial to aquatic habitats for reproduction. However, movements between reproductive ponds within a breeding season have rarely been studied and are usually considered to be limited. Our aim was to determine whether this pattern occurs frequently in Alpine newts (Mesotriton alpestris) inhabiting complexes of small ruts on muddy forest tracks. We analysed capture-recapture data for individually marked newts as a function of locality, sex, body condition and hydroperiod throughout the breeding season. More than one third of the newts changed their ruts. Movements occurred more often towards ruts that did not dry during the breeding season. The body condition of males that changed ponds (but not that of females) was higher compared to that of resident newts in one of the studied populations. The relatively high frequency of movements between ruts can be seen as an adaptive strategy in unpredictable habitats which have a high probability of drying. The promiscuous pattern of newts also favours low site tenacity, because few sexual partners are available in each rut. Because of the broad occurrence of this kind of habitat, future studies should take into account these movements to better understand newt population dynamics and how to apply adequate conservation measures.

Keywords: Amphibian - Habitat supplementation - Rut - Site fidelity - Temporary pond

Introduction

Most organisms must move between habitats that offer both substitutable and complementary resources for foraging, breeding and resting (Dunning, Danielson and Pulliam, 1992). Species with complex life cycles, such as many amphibians, often require both terrestrial and aquatic habitats during their lives. The extent of activities in these habitats varies greatly among species, but water and land often remain non-substitutable resources (Pilliod, Peterson and Ritson, 2002; Fellers and Kleeman, 2007). While foraging, wintering and estivating, this implies pre- and post-reproductive migrations (see, e.g., Hurlbert, 1969; Miaud, 1990; von Lindener, 1992) and also site fidelity across years due to the amphibian's sensory perception of environmental cues which help them to locate their pond every year (Gill, 1979; Joly and Miaud, 1989; Sinsch, 2006; Gamble et al., 2007).

It has been shown that amphibians, such as pond-breeding newts and salamanders, can remain in a single aquatic habitat (Blab and Blab, 1981; von Lindener, 1992; Denoël, 2003a) continuously for a long period (i.e., from weeks to months). However, there is recent evidence that newts and salamanders can disperse on land at the adult stage (Joly and Grolet, 1996; Perret et al., 2003), wander back and forth between water and land (Hurlbert, 1969; Weddeling et al., 2004), and sometimes reach other aquatic sites within the same reproductive season (Griffiths, 1984; Miaud, 1990; Wenzel, Jagla and Henle, 1995; Šusta, 1999; Denoël, Whiteman and Wissinger, 2007). Although inter-pond changes during a single breeding season seems to be limited, short distance between ponds could favour exchanges and thus allow a cluster of ponds to serve as a single aquatic unit (Miaud, 1990; Semlitsch, 2008). These movements within a pond group could be beneficial in providing higher quality resources such as food (Denoël, Whiteman and Wissinger, 2007), permanent waters (Denoël, 2003b) or sexual partners (Perret, 1996).
Most studies documenting site fidelity of newts were done in such relatively large habitats as agricultural ponds and lakes (Gill, 1979; Joly and Miaud, 1989; Miaud, 1990). In smaller habitats, such as forestry ruts, it can be expected that site fidelity would be less beneficial than in larger or permanent habitats. Moreover, individual status (sex or body condition) may have strong effect on migratory behaviour (Eggert and Guyéntant, 2003; Lodé, Holveck and Lessbarières, 2005), but these patterns are unknown for newts in such small habitats. In temperate forests of many European countries, ruts are frequently used by newts. They are often the only available water bodies within newt home range and can be inhabited by populations as large as in ponds. Despite their small size and artificial nature, ruts provide a valuable place for feeding and reproduction and are often the main habitat for newts (Babik and Rafinski, 2001; Dеноël, 2007; Dеноël and Demars, 2008). There is thus a need to focus studies at such scales to understand population functioning and provide efficient conservation measures (Semlitsch, 2002).

The aim of our study was to investigate whether newts are faithful to small aquatic habitats (ruts) during the breeding season or whether a group of these water bodies constitutes a single resource for newts. In addition, we examined the effect of sex, body condition and hydroperiod on the likelihood of animals moving between aquatic habitats. We hypothesised that the detrimental aquatic conditions (short hydroperiod, small rut size), the specific rut configuration (i.e., shorter distance between the ruts than in most previously studied systems), and the promiscuity of newts (i.e., multiple mating) favour movements between ruts.

Material and Methods

The study was carried out on Alpine newts, *Mesotriton alpestris* (Laurenti, 1768), previously known as *Triton alpestris*. This species, which is broadly distributed in Europe, needs water for courtship and egg-laying but usually spends the remaining part of the year on land. Similarly to some other newt species, it inhabits a large range of aquatic habitats, such as ponds, lakes and ruts (Moravec, 1994; Dеноël, 2003a; Dеноël, 2007). Despite the frequent use of ruts by newt species, almost no studies have focused on its relationship with this habitat (Dеноël, 2007; Kopecký and Vojar, 2007; Dеноël and Demars, 2008).

Alpine newts were surveyed at two localities, Hylváty (49°57'29"N, 16°23'53"E, elevation 355 m) and Zabitý (49°57'11"N, 16°23'54"E, elevation 500 m) near the town of Ústí nad Orlicí (Pardubice region, the Czech Republic). The two localities consist of eleven and five water-filled vehicle-track ruts that have dimensions of 0.16-1.62 m and a maximum water depth between 0.07-0.2 m (table 1: for additional details, see Kopecký and Vojar, 2007). These tracks have very low traffic, as they are almost solely used for the occasional transportation of timber. Both localities are located in spruce (*Picea abies*) forest. The nearest water bodies with presence of Alpine newts (also ruts) are at 450 m from locality Zabitý and 550 m from locality Hylváty.

Newts were captured by hand or with a net every fifth day throughout the breeding season (from 1st April to 4th July, 2005). After every capture, individuals were marked by toe-clipping (Fernter, 1979). Since amputation of one or two toes does not affect the survival or reproductive functions of newts (Arntzen, Smithson and Oldham, 1999), we cut the last two phalanxes of one or two digits. At their first capture, individuals were also measured (snout-vent length, SVL) to the nearest 0.1 mm and weighed using a Pesola scale to the nearest 0.05 g. To reduce the number of recaptures, each newt was captured. Afterwards, all animals were released back into those ruts in which they had most recently been captured.

Body condition of the newts was obtained from the residuals of log mass (g) on log snout-vent length (mm), calculated separately in males and females. In the study species, this measure reflects the lipid content (Denœl et al., 2002). The length of aquatic activity was computed as the number of days between the first capture and the last capture of a particular newt. The distance among ruts was considered to be the nearest distance between rut edges and a movement event was defined as a movement between two separate ruts by an individual newt.

Differences of counts of migrating and sedentary newts were determined by chi-square tests. *T*-tests, ANOVAs, and MANOVAs were computed to test for any effects of locality, sex, hydroperiod, and body condition on migratory variables. To fit normality, data were transformed (by square root for counts, log for other continuous data) before applying the statistical models. However, in order to show the patterns more clearly, the presented values were not transformed.

All tests were computed with Statistica 7 (Statsoft-France, 2005). Tests were two-tailed and we used α = 0.05 to evaluate statistical significance.

Results

Breeding patterns: recaptures, aquatic activity, densities, and sex ratio

Out of the 176 studied newts (101 males, 65 females), 141 (i.e., 80%) were recaptured between 1 and 11 times (mean ± SE = 2.86 ± 0.18). Locality (*F*$_{1,172}$ = 0.096, *P* = 0.71), sex (*F*$_{1,172}$ = 2.873, *P* = 0.09) and their interaction (*F*$_{1,172}$ = 0.022, *P* = 0.88) had no effect on the effect on the length of the aquatic activity of newts on the studied localities (min = 5 days, max = 75 days, mean ± SE = 19.5 ± 1.2 days).

Ruts were not similarly frequented by newts within the two localities (Hylváty: *χ*$_{2}$ = 91.027, *df* = 4, *P* < 0.001; Zabitý: *χ*$_{2}$ = 259.814, *df* = 10, *P* < 0.001). Over the course of the study there were an average of 22.6 ± 10.1 (± SE) newts per rut at Hylváty and
12.7 ± 5.5 at Zabitý ($t_{14} = 1.048, P = 0.31$). The mean number of newts per rut for a particular visit was 2.3 ± 0.8 (Table 1). The sex ratio was significantly male-biased at Hylváty (2.2:1, $\chi^2 = 9.986, df = 1, P < 0.01$) but only marginally male-biased at Zabitý (1.5:1, $\chi^2 = 3.505, df = 1, P = 0.06$).

### Table 1. Characteristics of the studied pools (ruts) during the reproductive season of newts: maximum water volume, hydroperiod, and number of newts. See fig. 1 for the relative positions of the pools.

<table>
<thead>
<tr>
<th>Rut</th>
<th>Volume</th>
<th>Hydroperiod</th>
<th>Number of newts per visit mean ± SE (max)</th>
<th>Total number of newts during the season</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hylváty</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>0.25 m$^3$</td>
<td>Temporary</td>
<td>0.6 ± 0.3 (5)</td>
<td>12</td>
</tr>
<tr>
<td>B</td>
<td>0.19 m$^3$</td>
<td>Temporary</td>
<td>0.2 ± 0.1 (2)</td>
<td>3</td>
</tr>
<tr>
<td>C</td>
<td>0.59 m$^3$</td>
<td>Temporary</td>
<td>3.5 ± 0.8 (12)</td>
<td>30</td>
</tr>
<tr>
<td>D</td>
<td>0.28 m$^3$</td>
<td>Temporary</td>
<td>0.7 ± 0.3 (5)</td>
<td>10</td>
</tr>
<tr>
<td>E</td>
<td>1.35 m$^3$</td>
<td>Permanent</td>
<td>10.9 ± 1.8 (26)</td>
<td>59</td>
</tr>
<tr>
<td>Zabitý</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>0.84 m$^3$</td>
<td>Permanent</td>
<td>6.9 ± 1.1 (16)</td>
<td>40</td>
</tr>
<tr>
<td>B</td>
<td>1.62 m$^3$</td>
<td>Permanent</td>
<td>5.4 ± 1 (11)</td>
<td>26</td>
</tr>
<tr>
<td>C</td>
<td>0.21 m$^3$</td>
<td>Permanent</td>
<td>0.3 ± 0.2 (3)</td>
<td>4</td>
</tr>
<tr>
<td>D</td>
<td>0.16 m$^3$</td>
<td>Temporary</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>E</td>
<td>0.50 m$^3$</td>
<td>Temporary</td>
<td>0.7 ± 0.3 (3)</td>
<td>9</td>
</tr>
<tr>
<td>F</td>
<td>0.26 m$^3$</td>
<td>Temporary</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>G</td>
<td>1.24 m$^3$</td>
<td>Permanent</td>
<td>5.5 ± 1.3 (19)</td>
<td>38</td>
</tr>
<tr>
<td>H</td>
<td>0.17 m$^3$</td>
<td>Temporary</td>
<td>0.4 ± 0.2 (2)</td>
<td>6</td>
</tr>
<tr>
<td>I</td>
<td>0.45 m$^3$</td>
<td>Temporary</td>
<td>0.8 ± 0.4 (4)</td>
<td>8</td>
</tr>
<tr>
<td>J</td>
<td>0.20 m$^3$</td>
<td>Temporary</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>K</td>
<td>0.24 m$^3$</td>
<td>Permanent</td>
<td>0.9 ± 0.2 (2)</td>
<td>9</td>
</tr>
</tbody>
</table>

**Figure 1.** Position of forestry ruts (i.e., pools caused by vehicle traffic) at the Hylváty and Zabitý study sites (Czech Republic). Arrows represent Alpine newt displacements between permanent (black) and temporary (grey) pools. The thickness of arrows is proportional to the percentage of movements in a given direction (1-5%, 5-10%, >10%) from all movements recorded at a study site.

**Movements of newts: locality, hydroperiod, sex, and body condition**

In total, at least 66 of the marked newts (i.e., 38% of the studied population and 47% of the newts captured more than once) moved between ruts during their breeding season (fig. 1). The proportions of newts moving between ruts differed between the localities (Hylváty = 45%, Zabitý = 30%, $\chi^2 = 4.21$, df = 1, $P < 0.05$) but not between the sexes (males = 40%, females = 31%, $\chi^2 = 1.39$, df = 1, $P = 0.24$).
Newts visited one to three ruts during the breeding season (mean ± SE = 1.42 ± 0.04). This corresponded to between 3 and 4 inter-rut movements (mean ± SE = 0.70 ± 0.07). Locality (Wilks’ λ = 0.97, F₁,₁₇₁ = 2.908, P = 0.06), sex of individuals (Wilks’ λ = 0.98, F₁,₁₇₂ = 1.607, P = 0.20) and their interaction (Wilks’ λ = 0.98, F₁,₁₇₁ = 2.036, P = 0.13) did not influence the number of visited ruts, and these also did not influence the number of movements.

The distances among ruts did not differ between the localities (Hylváty: mean ± SE = 16 ± 4.4 m, Zabity: 24.7 ± 2.5 m, t₃ = 1.403, P = 0.17). The average movement distances of newts were not different between localities (Hylváty: mean ± SE = 11.3 ± 1.6 m, Zabity: 16.5 ± 2.8 m, F₁,₆₁ = 0.03, P = 0.85), sex (F₁,₆₁ = 0.528, P = 0.47) and their interaction (F₁,₆₁ = 0.300, P = 0.59).

The newts that changed ruts had higher body condition relative to those that were not recaptured in another rut among males from locality Zabity (F₄,₄₉ = 10.386, P < 0.05), but not in males from locality Hylváty (F₄,₄₈ = 1.370, P = 0.25). Moving and non-moving females from locality Hylváty (F₄,₄₉ = 0.206, P = 0.65) and also from locality Zabity (F₄,₄₀ = 0.103, P = 0.75) did not differ in their body condition (fig. 2).

**Direction of movements**

Four out of the five ruts at Hylváty and six out of the eleven ruts at Zabity were temporary during the breeding season of newts, i.e., a desiccation event was observed at least once during the study period (fig. 1). Newts moved similarly from both permanent (n = 54 displacements) and temporary (n = 48) ruts (χ² = 0.533, df = 1, P = 0.55; fig. 1). The movements occurred more in the direction towards permanent ruts (64%) than towards temporary ruts (36%) (χ² = 7.686, df = 1, P = 0.01; fig. 1).

**Discussion**

We found that at least one third of the newts moved between ruts within a breeding season. These results confirm previous observations of inter-pond changes in amphibians in more stable, less artificial habitats (Miaud, 1990; Sinsch and Seidel, 1995; Denoël, Whiteman and Wissinger, 2007). However, the observed extent of movements shows that site fidelity is not the rule when more than one aquatic patch is available. This result suggests that not only habitat complementation (e.g., breeding in water, estivating-wintering on land) (Pilliod, Peterson and Ritson, 2002; Fellerson and Kleeman, 2007) but also habitat supplementation, i.e., a network of ponds (Dunning, Danielion and Pulliam, 1992), can be important for amphibians.

**Pond composition and configuration**

The high rate of movements in our study was most likely caused by the small size and unpredictability of ruts, which did repeatedly dry up and become unsuitable for newts’ breeding and foraging. This study represents a size extreme for aquatic habitats. The maximum water depth and volume were 0.2 m and 1.62 m³, respectively, i.e., several orders of magnitude less than the ponds and lakes studied in other systems (see, e.g., Miaud, 1990; Denoël, Whiteman and Wissinger, 2007). In such a reduced space, where environmental conditions might be sub-
best option would then be to shift habitat, and this should be facilitated in the most fitted individuals (Ims and Hjermann, 2001). Our results support partly this hypothesis in migrating males, as they exhibited higher body condition (a variable which Denoël et al., 2002 show to be correlated with stored lipids) than did those that were sedentary in one of the two studied populations.

Conclusions

Although rarely studied, small habitats such as forestry ruts are common and frequently inhabited by Alpine and other newt species (Joger, 2000). In many cases, these are the only available habitats and can allow the maintenance of large newt populations by providing them places for breeding and foraging (Denoël, 2007; Denoël and Demars, 2008). Due to historical loss of natural breeding sites, low and midland populations of Alpine newts are today primarily found in such man-made habitats as agricultural ponds, abandoned quarries, ruts caused by automobile traffic or in garden pools (Moravec, 1994; Denoël, 2007). This confirms the interest of conserving temporary wetlands to sustain amphibian populations (Semlitsch, 2002). As some of these have very short hydroperiod, the conservation of connected pools in clusters remains essential (Denoël et al., 2007; Semlitsch, 2008). The proximity between reproductive patches favours exchanges of individuals and may increase fitness in counterbalancing the local risk of drying (Jakob et al., 2003). Clusters of ruts should thus not be neglected in conservation studies, and these also represent interesting models for understanding newt ecology. Such possibly temporary habitats are valuable sites for amphibians. In such systems, newts face alternative choices that can have direct and indirect benefits. Hence, there is a need for long term integrated studies of food web ecology, environmental stochasticity and sexual behaviours on individually marked newts.

Acknowledgements

We are grateful to R. Healy, U. Sinsch and two anonymous reviewers for their constructive comments on the manuscript. M. Denoël is a Research Associate at the Fonds de la Recherche Scientifique (FNRS, Belgium) and was supported by grants FRS 1.5.013.08 and 1.5.010.09. This study was supported by grants 2007/42110/1313, 2009/42110/0001 and by the Research Project No. MSM 604607901 of the Faculty of Agrobiology, Food and Natural Resources, Czech University of Life Sciences in Prague. The study was carried out under permit number 9826/03-620/2353/03 from the Czech Ministry of the Environment.

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Received: April 22, 2009. Accepted: July 31, 2009.