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.

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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 Lindeiner, 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 Lindeiner, 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 Guyétant, 2003; Lodé, Holveck and Lesbarréres, 2005), but these patterns are unknown for newts in such small habitats. In temperate forests in 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; Denoël, 2007; Denoël 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 *Triturus 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; Denoël, 2003a; Denoël, 2007). Despite the frequent use of ruts by this species, almost no studies have focused on its relationship with this habitat (Denoël, 2007; Kopecký and Vojar, 2007; Denoël 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 m³ 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 in 2005, a total of 20 sampling dates at each locality). The chance of capture was high in both localities, due to the small water vo-

lumes, the clear water in the ruts, and the absence of water plants (Kopecký, 2006; Kopecký and Vojar, 2007). Both localities are used by newts for breeding, because eggs and larvae have been found there (Kopecký, 2006). Some ruts in both localities are threatened by desiccation during the breeding period due to their relatively low water volumes and their dependence on rainfall (grey patches in fig. 1). They are referred to in the text as temporary. Other ruts on both localities held water over the whole study period (black patches in fig. 1).

For the time when newts were being measured and marked, the newts from each rut were placed separately in plastic tanks filled with water from their original ruts. Each newt captured for the first time was individually marked by toe-clipping (Ferner, 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. In order to be able to detect movement of a newt between ruts, we always identified the rut where 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 (Denoël 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 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: $\chi2 = 91.027$, df = 4, $P < 0.001$; Zabitý: $\chi2 = 259.814$, 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

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.

| Rut	Volume	Hydroperiod	Number of newts per visit mean ± SE (max)	Total number of newts during the season
Hylváty				
A	0.25 m³	Temporary	0.6 ± 0.3 (5)	12
B	0.19 m³	Temporary	0.2 ± 0.1 (2)	3
C	0.59 m³	Temporary	3.5 ± 0.8 (12)	30
D	0.28 m³	Temporary	0.7 ± 0.3 (5)	10
E	1.35 m³	Permanent	10.9 ± 1.8 (26)	59
Zabitý				
A	0.84 m³	Permanent	6.9 ± 1.1 (16)	40
B	1.62 m³	Permanent	5.4 ± 1 (11)	26
C	0.21 m³	Permanent	0.3 ± 0.2 (3)	4
D	0.16 m³	Temporary	0	0
E	0.50 m³	Temporary	0.7 ± 0.3 (3)	9
F	0.26 m³	Temporary	0	0
G	1.24 m³	Permanent	5.5 ± 1.3 (19)	38
H	0.17 m³	Temporary	0.4 ± 0.2 (2)	6
I	0.45 m³	Temporary	0.8 ± 0.4 (4)	8
J	0.20 m³	Temporary	0	0
K	0.24 m³	Permanent	0.9 ± 0.2 (2)	9
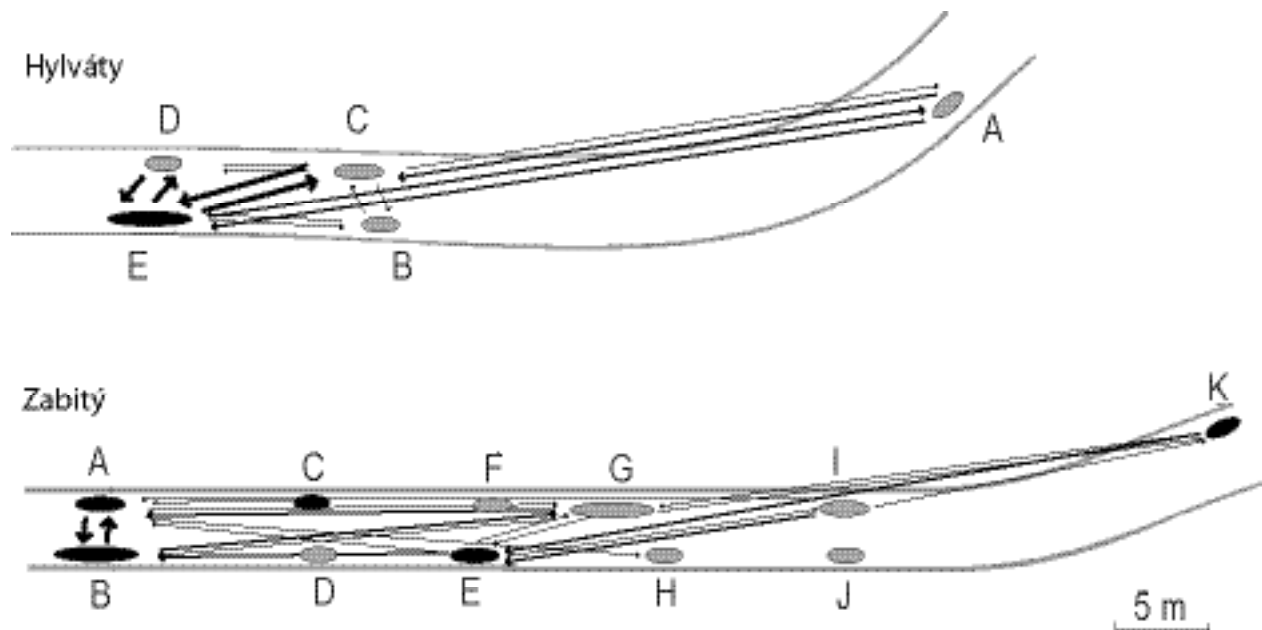
Figure 1. Position of forestry ruts (i.e., pools caused by vehicle traffic) at the Hylváty and Zabitý study sites (Czech Republic). Arrows represent Alpine newt displacements between permanent (black) and temporary (grey) pools. The thickness of arrows is proportional to the percentage of movements in a given direction (1-5%, 5-10%, >10%) from all movements recorded at a study site.

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, $\chi2 = 9.986$, df = 1, $P < 0.01$) but only marginally male-biased at Zabitý (1.5:1, $\chi2 = 3.505$, df = 1, $P = 0.06$).

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%, $\chi2 = 4.21$, df = 1, $P < 0.05$) but not between the sexes (males = 40%, females = 31%, $\chi2 = 1.39$, df = 1, $P = 0.24$).

Newts visited one to three ruts during the breeding season (mean $\pm$ SE = 1.42 $\pm$ 0.04). This corresponded to between 0 and 4 inter-rut movements (mean $\pm$ SE = 0.70 $\pm$ 0.07). Locality (Wilks' λ = 0.97, $F_{2,171}$ = 2.908, P = 0.06), sex of individuals (Wilks' λ = 0.98, $F_{2,171}$ = 1.607, P = 0.20) and their interaction (Wilks' λ = 0.98, $F_{2,171}$ = 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 $\pm$ SE = 16 $\pm$ 4.4 m, Zabitý: 24.7 $\pm$ 2.5 m, t_{63} = 1.403, P = 0.17). The average movement distances of newts were not different between localities (Hylváty: mean $\pm$ SE = 11.3 $\pm$ 1.6 m, Zabitý: 16.5 $\pm$ 2.8 m, $F_{1,61}$ = 0.03, P = 0.85), sex ($F_{1,61}$ = 0.528, P = 0.47) and their interaction ($F_{1,61}$ = 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 Zabitý ($F_{1,49}$ = 10.386, P < 0.05), but not in males from locality Hylváty ($F_{1,48}$ = 1.370, P = 0.25). Moving and non moving females from locality Hylváty ($F_{1,21}$ = 0.206, P = 0.65) and also from locality Zabitý ($F_{1,40}$ = 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 Zabitý 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 ($\chi2$ = 0.353, df = 1, P = 0.55; fig. 1). The movements occurred more in the direction towards permanent ruts (64%) than towards temporary ruts (36%) ($\chi2$ = 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; Fellers and Kleeman, 2007) but also habitat supplementation, i.e., a network of ponds (Dunning, Danielson 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 su-

boptimal, it would be advantageous to spread reproductive investments among more aquatic habitats, in a perspective of mortality risk for eggs and larvae in drying ponds (Griffiths, 1997). Our field study supports this hypothesis, as most movements occurred in directions to permanent ponds. Also mesocosm experiments and field surveys have shown that newts are able to move to new water bodies in the event of drying (Denoël, 2003b). However, newts left the permanent ruts as much as they left the temporary ones. The unpredictability of studied aquatic sites that have a high drying probability (63% during the studied season) may explain the movement pattern of newts. Such behaviour can be seen as a within-generation risk-spreading strategy (Hopper, 1999).

It can be expected that inter-pond movements, migrations and dispersal are costly behavioural patterns. Newts need humidity, particularly after their yearly adaptation to the aquatic reproductive period (Hourdry and Beaumont, 1985). On land, in particular, they could suffer from desiccation (Jehle and Arntzen, 2000). Although newts are sometimes able to migrate over long distances (Vilter and Vilter, 1962; Jehle and Sinsch, 2007), their movements can be limited by landscape composition and configuration and by their morpho-functional possibilities (Joly et al., 2001). In support of these hypotheses, radio-telemetric studies have shown that displacements dropped by 50% at about 100 m from the breeding pond (Semlitsch, 2008), whereas capture-mark-recapture surveys have pointed out that inter-pond movement is dependent on the distance between ponds (Dolmen, 1981; Griffiths, 1984; Miaud, 1990; Wenzel, Jagla and Henle, 1995). Our results show that in a close configuration of pools, which is typical of ruts on unpaved roads, a higher rate of migration is prevalent. The ruts investigated in our study were on an average 20 m apart, in contrast to distances of several hundred meters between ponds in agricultural systems (Denoël and Lehmann, 2006; Denoël and Ficetola, 2008). In our study, moreover, the pools were connected by an unpaved forestry track, which could function as a corridor and thus facilitate exchanges as it has been shown for terrestrial salamanders (Denoël, 1996).

Sex and body condition

The consequences of site fidelity can be different for males and for females. Both sexes need to find prey and partners for mating (Stephens and Krebs, 1986; Arnqvist and Rowe, 2005). Newts are promiscuous, and thus each individual can reproduce with more than one mate during a single reproductive season, but males usually have more partners than females (Gabor and Halliday, 1997; Denoël, 1999; Osikowski and Rafinski, 2001). After their first copulation, females can improve their own fitness by multiple mating (Osikowski and Rafinski, 2001) and by becoming less receptive and more selective (Gabor and Halliday, 1997), which reduces the success of their future mates. On the other hand, females need to lay eggs in a habitat that will retain water throughout larval development. Consequently, the detrimental conditions of ruts (i.e., high probability of desiccation) can increase the movement rate of females. In contrast to studies on more mobile amphibians such as toads (Sinsch, 1992), however, we did not find any effect of sex on movement patterns in the Alpine newt. This may be due to the very low densities and male-biased sex ratio, which may have also constrained males to move among ruts more often (cf. mating competition). In such habitats, the
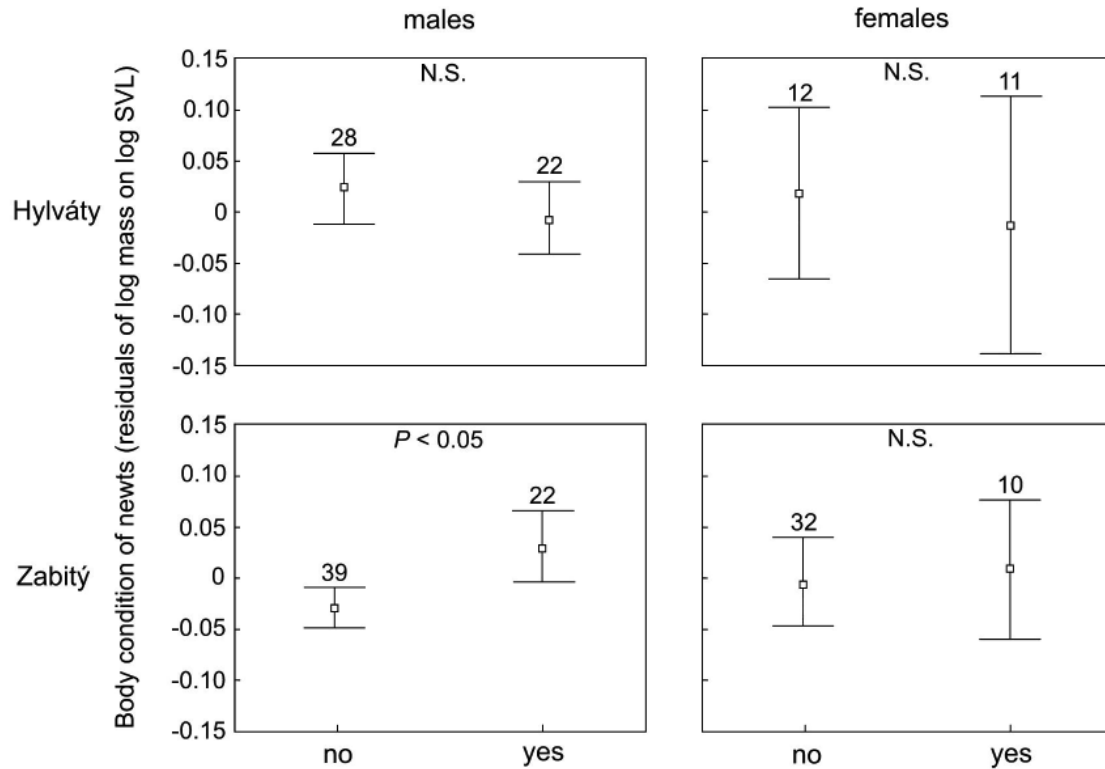
Figure 2. Body condition of Alpine newt for each sex and locality separately as a function of movement pattern (F -test).

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

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