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Sex-specific effect of pool desiccation on the movement of Alpine Newts, *Mesotriton alpestris* (LAURENTI, 1768), among breeding sites
(Caudata: Salamandridae)

Geschlechtsspezifische Auswirkung der Austrocknung von Tümpeln auf die Wanderbewegung von Alpenmolchen, *Mesotriton alpestris* (LAURENTI, 1768), zwischen Laichplätzen
(Caudata: Salamandridae)

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KURZFASSUNG

In unberechenbaren Lebensräumen ist es für Amphibien vorteilhaft, das Risiko wetterbedingter Nachzuchtausfälle durch Nutzung mehrerer Fortpflanzungsgebiete zu vermindern. In europäischen Laubwaldlandschaften beinhalten durch Autoverkehr verursachte Radspur-Furchen typischerweise kleine Pfützen mit variabler Hydroperiode, die im Frühling, jedenfalls aber temporär auftreten und von einigen Amphibienarten als Brutplätze benutzt werden. Bisherige Ergebnisse zeigten, daß Molche innerhalb einer Fortpflanzungsperiode zwischen Radspur-Tümpeln wechseln.

Ziel dieser Untersuchung war es, ein solches Verhalten zu charakterisieren, und zwar durch eine Fang-Wiederfang-Studie des Alpenmolchs *Mesotriton alpestris* (LAURENTI, 1768), über zwei Jahre mit unterschiedlicher Wasserverfügbarkeit. Die Bewegungsmuster unterschieden sich zwischen den Jahren je nach Geschlecht. Im Jahr, in dem die Pfützen häufiger austrockneten, wechselten mehr Weibchen die Radspur-Tümpel als im feuchteren Jahr mit stabilerer Wasserführung. Allerdings war unter ausgewachsenen Tieren, die zwischen Furchen wechselten, bei Männchen die durchschnittliche Anzahl der besuchten Wasserstellen größer. Diese Ergebnisse zeigen, daß die Geschlechter unterschiedlich auf Umweltgegebenheiten reagieren und daß Alpenmolche gut daran angepaßt sind, Netze temporärer Pfützen zu nutzen.

ABSTRACT

In unpredictable habitats, it is advantageous to amphibians to reduce the risk of weather-induced offspring mortality by utilization of several reproductive patches. In European deciduous forest landscapes, ruts caused by vehicular traffic, typically comprising small vernal or ephemeral pools with variable hydroperiod, are at times used as breeding habitats by some species of amphibians. Previous research shows that in such systems newts move between ruts within a single reproductive season.

The aim was to characterize such movements by means of a capture-mark-recapture study of the Alpine Newt *Mesotriton alpestris* (LAURENTI, 1768), during two years differing in water availability, and to detect possible sex-specific differences. Movement between ruts differed between years according to sex. In the year with higher pool drying frequency, more females changed ruts than in the year when stable conditions prevailed. Among the adults that moved between ruts, however, the mean number of aquatic patches visited was higher in males. These results show that the sexes can react differently to environmental correlates and that Alpine Newts are well adapted to utilize networks of temporary pools.

KEYWORDS

Amphibia: Caudata: Salamandridae, *Mesotriton alpestris*, Alpine Newt, amphibians, rut, site fidelity, temporary pond, desiccation, migration, reproduction, between-pool movements, mark-and-recapture method, ecology, behavior, Czech Republic

INTRODUCTION

Hydroperiod is a key variable for many organisms, such as pond-breeding amphibians (NEWMAN 1992; SEMLITSCH & SKELLY 2008). Whereas some species require water permanency to complete their life cycles, others accommodate to semi-permanent or even more temporary pools (GRIFFITHS 1997; WELLS 2007). Some species are specially adapted to desiccation risk by being able to accelerate development in the presence of such external cues as water level decrease (LAURILA & KUJASALO 1999; DENOËL 2006; MÁRQUEZ-GARCÍA et al. 2010). However, early metamorphosis at a small size, or with a low quantity of fat reserves, can be costly in the long run, e.g., in terms of a retarded onset of the first reproduction (SCOTT et al. 2007) and reduced immunocompetence (GERVASI & FOUFOPOULOS 2008).

In environments where pools are subject to drying, the selection of habitats offering the required hydroperiod is of primary importance for individual fitness (PECHMANN et al. 1989). The predictability and stability of aquatic sites are thus expected to favor site tenacity as long as all aquatic activities can be completed in a single water body (JOLY & MIAUD 1989; MIAUD 1990). Studies in individual tiger salamanders *Ambystoma tigrinum nebulosum* GEHLBACH, 1967, showed that adults can benefit from both predictable permanent waters for reproduction and unpredictable temporary ponds for feeding on transient prey (WHITEMAN et al. 1994; DENOËL et al. 2007). DENOËL (2003) found that in a lake, which splits each year into a permanent basin and a drying basin, paedomorphic Alpine Newt individuals were able to escape the drying basin by moving both on land and by using underground aquatic interstices. Alpine Newts also have been found to move between permanent breeding ponds, but those moving constituted a low percentage of recaptures (MIAUD 1990).

Alpine Newts, like many other amphibians, have also been shown to exhibit a high rate of terrestrial movements among forestry ruts, a habitat that is considered unpredictable in terms of drying (KOPECKÝ et al. 2010). Shallow pools of less than 50 cm maximum depth in southern New England were observed to have unpredictable hydroperiods (BROOKS & HAYASHI 2002). In a previous study (KOPECKÝ et al. 2010), we found an effect of pool water permanency on the movements of Alpine Newts *Mesotriton alpestris* (LAURENTI, 1768), between such ruts during a single reproductive period. Sex-specific differences were discussed, however, it remained unknown whether these effects are continuous across years. Therefore, the aim of this study was to compare previous movement data with data from another year with a different hydroperiod regime. Because males and females have different needs, particularly in terms of reproduction (TRIVERS 1972; ANDERSSON 1994), we tested for sex-specific variations in the moving behavior.

MATERIALS AND METHODS

Alpine Newts are pond-breeding amphibians, widespread in Europe. They breed in a large variety of aquatic habitats, ranging from ponds and lakes to smaller pools, such as ruts caused by traffic on forest roads (THORN & RAFFAËLLI 2001; DENOËL 2007; DENOËL & DEMARS 2008).

Alpine Newts were surveyed at Hylváty (49°57'29''N, 16°23'53''E, elevation 355 m a.s.l.), near the town of Ústí nad Orlicí (Pardubice Region, Czech Republic). This is one of two study sites where movements were recorded for our previous publication (KOPECKÝ et al. 2010). This locality consists of five water-filled vehicle-tire ruts on a muddy road with a maximum water depth of 0.2 m, and maximum volume of 1.35 m^3 (for details, see KOPECKÝ & VOJAR 2007; KOPECKÝ et al. 2010). The five ruts were close to one another (mean ± SE = 16.00 ± 4.47 m, min. – max. = 1.10 – 37.80 m; Fig. 1). The roads have very low traffic volume, as they are used almost solely for the occasional transportation of timber. During the study, there was no harvesting and transportation of timber through the locality. Despite the ruts' small size as breeding water bodies, the locality is used by newts for breeding, and eggs and larvae have been found there regularly (KOPECKÝ 2006). These ruts are likely to dry up during the breeding period due to their relatively low water volumes and their dependence on seasonal melting snow and rain.

Newts were captured by hand or with a landing net every fifth day throughout two breeding seasons – from 11 April to 26 June in 2004 and 2005, in order to have the same time period in both years. During each visit we tried to catch all newts in all ruts. Newts were found in water from the first to the last sampling days. At their first capture, in both years, newts were individually marked by toe-clipping (FERNER 1979). This technique is not detrimental to newts and is proven useful within a single reproductive season, but not for a longer time period because of toe regeneration (GUTLEB 1991; ARNTZEN et al. 1999). Consequently, only intra-year movements are analyzed in the present study. Sex determination was based on secondary sex characteristics, such as swollen cloacae and nuptial coloration in males (THORN & RAFFAËLLI 2001). During each marking session, newts were held for a maximum 5 h in plastic tanks (36 cm x 21 cm x 16 cm) filled with water from their original rut before they were put back to their original ruts.

Total rainfall from December 2003 till June 2004 was 475.6 mm. Mean temperature throughout breeding period (April-June 2004) was 12.1 °C and rainfall 186 mm. Total rainfall from December 2004 till June 2005 was 530.7 mm. Mean temperature throughout breeding period (April-June 2005) was 12.7 °C and rainfall 193 mm. Meteorological data were obtained from the meteorological station of the town Ústí nad Orlicí, located 1.5 km from the study site.

Pool availability was estimated as the proportion of time (i.e., 5-day periods) that the pools held water during the study period (80 days). Hydroperiod corresponded to the longest continuous period of time during which the ruts held water during the study.

We used *chi*-square (χ^2) tests to compare sex ratios and frequencies of moving and resident newts, and Mann-Whitney *U*-tests to compare numbers of movements between years and sexes. All tests were computed using Statistica 6 (STATSOFT INC. 2006), with α set at 0.05 to evaluate statistical significance.

RESULTS

In 2004, only one out of five ruts dried up during the breeding season, whereas four out of five dried in 2005 (Table 1). In terms of pool availability, this represented 93 ± 8 % (mean ± SE) of the visits during which pools held water in 2004, against 82 ± 8% in 2005 (Table 1). Hydroperiod (i.e., the period with continuous water during the study) was 70 ± 10 days in 2004 and 48 ± 12 days in 2005.

We captured 85 newts (57 males, 28 females) in 2004 and 72 newts (49 males, 23 females) in 2005. Of these, we recaptured 89% of the newts in 2004 and 87% in 2005. The number of captured ($\chi^2 = 1.08$, $df = 1$, $P = 0.30$) and recaptured ($\chi^2 = 0.16$, $df = 1$, $P = 0.69$) newts did not differ significantly between years. Sex ratio was significantly male-biased in both years: 2.04:1 in 2004 ($\chi^2 = 9.89$, $df = 1$, $P < 0.01$) and 2.13:1 in 2005 ($\chi^2 = 9.39$, $df = 1$, $P < 0.01$). The length of the breeding period per individual in the study site was similar for both sexes in 2004 (males, mean ± SE = 30.18 ± 2.39 days, min – max = 5 – 65; females 38.93 ± 4.17 days, 5 – 70; *U*-test, $Z = -1.82$, $P = 0.07$) and in 2005 (males, 31.83 ± 3.04 days, 5 – 70; females, 33.26 ± 4.65 days, 5 – 75; *U*-test, $Z = -1.19$, $P = 0.85$).

A higher proportion of newts moved among ruts in 2005 (33 newts, i.e. 46% of the sample) than in 2004 (23 newts, i.e. 27% of the sample) ($\chi^2 = 5.65$, $df = 1$, $P < 0.05$). Among those newts that moved, there was a lower number of movements per individual in 2004 than in 2005 (in 2004, mean ± SE = 1.35 ± 0.13, min – max = 1 – 3; in 2005, 1.88 ± 0.17, 1 – 4; *U*-test, $Z = -2.07$, $P < 0.05$).

Both sexes differed in their movement activities between the years: moving females were observed more frequently in 2005 than in 2004 (48% vs. 14%, $\chi^2 = 6.84$, $df = 1$, $P < 0.01$), whereas the proportion of resident and moving males was similar between years (45% vs. 33%, $\chi^2 = 1.49$, $df = 1$, $P = 0.22$; Fig. 2A) (χ^2 test results based on counts). In contrast, when considering only

Table 1: Hydroperiod (maximum length of time with continuous presence of water), water availability (proportion of time with water) and Alpine Newt abundances (at each visit and during whole season) in five ruts (A-E) at Hylváty, Czech Republic during the two study periods (80 days each). SE – Standard Error, (max.) – Maximum.

Tab. 1: Hydroperiode (maximale Zeitspanne mit durchgehendem Vorhandensein von Wasser), Wasserverfügbarkeit (Anteil der Zeit mit Wasser) und Alpenmolch-Häufigkeiten (bei jedem Besuch und in der ganzen Saison) in fünf Radspur-Tümpeln (A-E) in Hylváty, Tschechische Republik, während der zwei Studienperioden (jeweils 80 Tage). SE – Standardfehler, (max.) – Maximum.

Rut Radspur-tümpel	Duration of Hydroperiod (days) Dauer der Hydroperiode (Tage)	Water availability (%) Wasserverfügbarkeit (%)	Number of newts per visit mean ± SE (max.) Anzahl Molche je Begehung Mittel ± Standardabweichung (Maximum)	Total number of newts during season Gesamtzahl der Molche in der Untersuchungssaison
		2004		
A	80	100	4.8 ± 1.2 (13)	25
B	30	63	1.1 ± 0.5 (7)	9
C	80	100	5.8 ± 1.1 (13)	29
D	80	100	0.9 ± 0.2 (2)	3
E	80	100	11.2 ± 1.7 (20)	50
		2005		
A	20	63	1.1 ± 0.5 (5)	12
B	20	63	0.3 ± 0.2 (2)	3
C	60	88	4.3 ± 1.0 (12)	29
D	60	94	0.9 ± 0.4 (5)	10
E	80	100	12.8 ± 1.8 (26)	59

those individuals that changed rut, the number of recorded movements per individual was significantly different between years in males (in 2004, mean ± SE = 1.37 ± 0.20; in 2005, 2.14 ± 0.19; *U*-test, $Z = -2.65$, $P < 0.01$) but not in females (in 2004, 1.25 ± 0.25; in 2005, 1.36 ± 0.15; *U*-test, $Z = 0.26$, $P = 0.79$; Fig. 2B).

DISCUSSION

Weather conditions are a main determinant in timing of spring migration in many amphibian species (DOUGLAS 1979; PALIS 1997). Rain and humidity (BRIGGLER et al. 2004), but also air temperature (VASCONCELOS & CALHOUN 2004), are generally recognized as basic factors affecting the migration of amphibians, including European newts (CHADWICK et al. 2006), to breeding sites. In dry years, it can be expected that ruts would hold water for a shorter time. Consequently, if climate change affects rain and temperature before and during the breeding season, this may also disturb population dynamics for newts (DENOËL 2006). However, although ruts held more water in 2004 than in 2005, differences in weather conditions (rainfall, average temperature) were small. Other factors such as exposure to direct solar radiation or sedimentation, may have affected drying in the studied ruts.

Inter-pool movements of Alpine Newts can change between years, as indicated by the present results. In the wetter year 2004, when most ruts held water during the breeding season, newts were more sedentary, visiting fewer ruts, as predicted by theory (SWITZER 1993). From the studied factors characterizing the ruts, no others than pool availability and hydroperiod varied between years. The number of newts present at the study site was similar in both years, indicating that newts coped with local drying conditions by using alternative aquatic habitats instead of ending their aquatic phase. This indicates that pond fidelity can be influenced by environmental

Fig. 1: The study site: a complex of ruts in a vehicle track on a forest road at Hylváty, Czech Republic.

Abb. 1: Der Untersuchungsort: ein Komplex von Radspur-Tümpeln auf einem Waldweg bei Hylváty, Tschechische Republik.

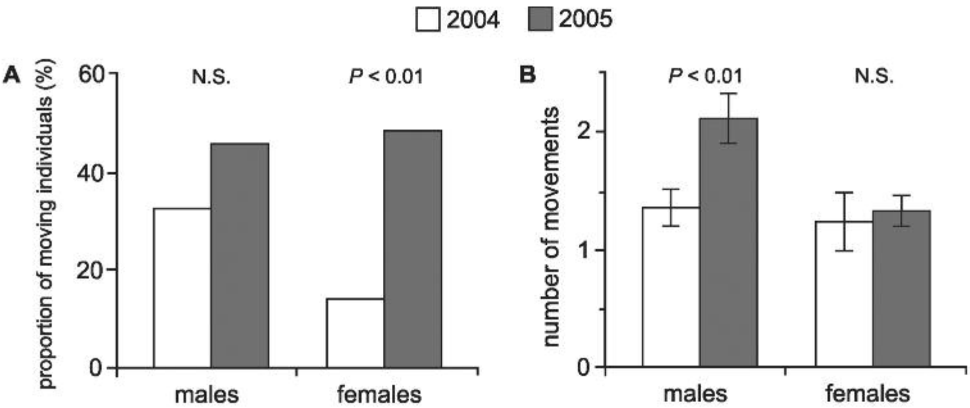

Fig. 2: Proportion of Alpine Newts moving (A) and number of movements per individual (B) among those newts, which moved, according to year and sex.
Captures 2004: 57 males and 28 females, captures 2005: 49 males and 23 females.

Abb. 2: Anteil der wandernden Alpenmolche (A) und Zahl der Wanderbewegungen (B), nach Jahr und Geschlecht, die von wandernden Individuen durchgeführt wurden.
Fänge im Jahr 2004: 57 Männchen und 28 Weibchen; Fänge im Jahr 2005: 49 Männchen und 23 Weibchen.

conditions (sensu GROSS 1996), and that experimental work could provide insight toward determining the proximate mechanisms. Previous evidence of site tenacity in permanent ponds may thus be a consequence of water permanency. However, pond isolation seems also to be a determining factor. In agricultural landscapes, Alpine Newts have been shown to be particularly faithful to their ponds when these were more isolated (MIAUD 1991), although intra-generational dispersal has been observed for distant ponds (SCHMIDT et al. 2006). The ruts at our study site are very close to one another, making terrestrial inter-pool movements less costly (KOPECKÝ et al. 2010) than between typical farm ponds (MIAUD 1990; SCHMIDT et al. 2006). On the other hand, inter-individual variation in site tenacity exists and could explain variation within and among sites (PERRET et al. 2003).

Among sexes, movement activities were different, albeit in a complex way: the newts reacted to pond instability in 2005, when more drying events occurred, in that the percentage of moving females (but not males) increased significantly. Among the moving individuals, however, the males (but not the females) exhibited a significantly higher number of moves between ruts in the drier year 2005. Such differences might find their basis in inherent intersexual differences (ANDERSSON 1994), but such hypothetical explanations need to be tested experimentally. Because of the lowest sexual responsiveness of females during the egg-laying period, males can have more sexual partners than females and, thus, may be advantaged in visiting a higher number of ruts. On the other hand, once they picked up the spermatophore, females stay in the water for a longer period of time, as they lay their eggs sequentially, one by one (MIAUD 1993; GALLOY & DENOËL 2010). Details of the spatial egg-laying strategies were not analyzed in our study, but it can be expected that laying eggs into more than one water body could be advantageous particularly in a place with a high probability of drying. Development of newts can be accelerated in the presence of higher temperatures, but several weeks of aquatic larval stage are required for completing metamorphosis (THORN & RAFFAËLLI 2001; D'AMEN et al. 2007; GALLOY & DENOËL 2010). The consequences of inadequate pond selection may thus be detrimental to the newt population.

In contrast to our results, PERRET et al. (2003) found no sex differences in dispersal at the adult stage, but they hypothesized that female moving behavior could depend on the cost of dispersal. The closer vicinity of ruts in the present study makes it less costly than in the study of PERRET et al. (2003) and may also imply other mechanisms. Inter-pool change and dispersal can be due to different selective pressures. Despite differences between both studies, it can be hypothesized that costs of short-range movements are lower than those of long-range movements, thus, facilitating the former ones.

Considering each rut separately gives a low number of breeders, but, as all ruts were connected by frequent newt movements, the total number is within a range typical of a medium-sized, viable Alpine Newt population (VON LINDEINER 1992; SCHMIDT et al. 2006; DENOËL 2007). Although remaining up to two months in the ruts, newts stayed there for only one month on average, which time is shorter than in bigger wetlands (FASOLA & CANOVA 1992; VON LINDEINER 1992; FABER 1994).

Most of our knowledge of the behavioral ecology of Alpine Newts is based only on studies of isolated aquatic habitats. Thus, it is important also to consider networks of complementary patches in order to fully understand the success of Alpine Newts in clusters of ponds.

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REFERENCES

ANDERSSON, M. (1994): Sexual selection; Princeton (Princeton University Press), pp. 599.

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, St. Louis; 33: 567-576.

BRIGGLER, J. T. & JOHNSON, J. E. & RAMBO D. D. (2004): Demographics of a ringed salamander (*Ambystoma annulatum*) breeding migration.- Southwestern Naturalist, Austin; 49: 209-217.

BROOKS, R. & HAYASHI, M. (2002): Depth-area-volume and hydroperiod relationships of ephemeral (vernal) forest pools in southern New England.- Wetlands: journal of the Society of Wetland Scientists, Dordrecht; 22: 247-255.

CHADWICK, E. A & SLATER, F. M. & ORMEROD, S. J. (2006): Inter- and intraspecific differences in climatically mediated phenological change in coexisting *Triturus* species.- Global Change Biology, Oxford; 12: 1069-1078.

D'AMEN, M. & VIGNOLI, L. & BOLOGNA, M. A. (2007): The effects of temperature and pH on the embryonic development of two species of *Triturus* (Caudata: Salamandridae).- Amphibia-Reptilia, Leiden; 28: 295-300.

DENOËL, M. (2003): How do paedomorphic newts cope with lake drying?- Ecography, Oxford; 26: 405-410.

DENOËL, M. (2006): Seasonal variation of morph ratio in facultatively paedomorphic populations of the palmate newt *Triturus helveticus*.- Acta Oeco - logica, Paris; 29: 165-170.

DENOËL, M. (2007): Le Triton alpestre, *Triturus alpestris* (LAURENTI, 1768); pp. 62-71. In: JACOB, J. P. & PERCSY, C. & DE WAVRIN, H. & GRAITSON, E. & KINET, T. & DENOËL, M. & PAQUAY, M. & PERCSY, N. & REMACLE, A. (Eds.): Amphibiens et reptiles de Wallonie; Namur (Centre de Recherche de la Nature, des Forêts et du Bois), pp. 384.

DENOËL, M. & DEMARS, B. (2008): The benefits of heterospecific oophagy in a top predator.- Acta Oecologica, Paris; 34: 74-79.

DENOËL, M. & WHITEMAN, H. H. & WISSINGER, S. A. (2007): Foraging tactics in alternative heterochronic salamander morphs: trophic quality of ponds matters more than water permanency.- Freshwater Biology, Oxford; 52: 1667-1676.

DOUGLAS, M. E. (1979): Migration and sexual selection in *Ambystoma jeffersonianum*.- Canadian Journal of Zoology, Ottawa; 57: 2303-2310.

FABER, H. (1994): Jahresaktivitätsmuster des Bergmolches (*Triturus alpestris*) in Kleingewässern der subalpin-alpine Höhenstufe.- Abhandlungen und Berichte für Naturkunde, Magdeburg; 17: 135-142.

FASOLA, M. & CANOVA, L. (1992): Residence in water by the newts *Triturus vulgaris*, *T. cristatus* and *T. alpestris* in a pond in northern Italy.- Amphibia-Reptilia, Leiden; 13: 227-233.

FERNER, J. W. (1979): A review of marking techniques for amphibians and reptiles.- Herpetological Circular, Lawrence; 9: 1-41.

GALLOY, V. & DENOËL, M. (2010): Detrimental effect of temperature increase on the fitness of an amphibian (*Lissotriton helveticus*).- Acta Oecologica, Paris; 36: 179-183.

GERVASI, S. S. & FOUFOPOULOS, J. (2008): Costs of plasticity: responses to desiccation decrease post-metamorphic immune function in a pond-breeding amphibian.- Functional Ecology, Oxford; 22: 100-108.

GRIFFITHS, R. A. (1997): Temporary ponds as amphibian habitats.- Aquatic Conservation : Marine and Freshwater Ecosystems, New York; 7: 119-126.

GROSS, M. R. (1996): Alternative reproductive strategies and tactics: diversity within sexes.- Trends in Ecology and Evolution, Amsterdam; 11: 92-98.

GUTLEB, B. (1991): Phalangengeneration und eine neue Methode zur Individualerkennung bei Bergmolchen, *Triturus alpestris* (LAURENTI, 1768) (Caudata: Salamandridae).- Herpetozoa, Wien; 4: 117-125.

JOLY, P. & MIAUD, C. (1989): Fidelity to the breeding site in the Alpine newt *Triturus alpestris*.- Behavioural Processes, Amsterdam; 19: 47-56.

KOPECKÝ, O. (2006): Migrace čolka horského ve vodní fázi a některé související jevy; Olomouc (BSc. thesis, Palacký University), pp. 76.

KOPECKÝ, O. & VOJAR, J. (2007): Které vlastnosti vodních biotopů ovlivňují početnost čolků horských (*Mesotriton alpestris*) za nestálých podmínek prostředí?- Sborník severočeského muzea, Přírodní vědy, Liberec; 25: 131-139.

KOPECKÝ, O. & VOJAR, J. & DENOËL, M. (2010): Movements of alpine newts (*Mesotriton alpestris*) between small aquatic habitats (ruts) during the breeding season.- Amphibia-Reptilia, Leiden; 31: 109-116.

LAURILA, A. & KUJASALO, J. (1999): Habitat duration, predation risk and phenotypic plasticity in common frog (*Rana temporaria*) tadpoles.- Journal of Animal Ecology, Oxford; 68: 1123-1132.

MÁRQUEZ-GARCÍA, M. & CORREA-SOLÍS, M. & MÉNDEZ, M. A. (2010): Life-history trait variation in tadpoles of the warty toad in response to pond drying.- Journal of Zoology, London; 281: 105-111.

MIAUD, C. (1990): La dynamique des populations subdivisées: étude comparative chez trois amphibiens urodèles (*Triturus alpestris*, *T. helveticus* et *T. cristatus*). Villeurbanne (Claude Bernard Lyon I University), pp. 158.

MIAUD, C. (1991): Essai de synthèse sur les caractéristiques demographiques des tritons du genre *Tri - turus*.- Bulletin de la Société Herpétologique de France, Paris; 59: 1-18.

MIAUD, C. (1993): Predation on newt eggs (*Triturus alpestris* and *T. helveticus*): identification and protective role of oviposition behaviour.- Journal of Zoology, London; 231: 575-582.

NEWMAN, R. A. (1992): Adaptive plasticity in amphibian metamorphosis.- Bioscience, Berkeley; 42: 671-678.

PALIS, J. G. (1997): Breeding migration of *Ambystoma cingulatum* in Florida.- Journal of Herpetology, Athens; 31: 71-78.

PECHMANN, J. H. K. & SCOTT, D. E. & WHITFIELD GIBBONS, J. & SEMLITSCH, R. D. (1989): Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians.- Wetlands Ecology and Management, Dordrecht; 1: 3-11.

PERRET, N. & PRADEL, R. & MIAUD, C. & GROLET, O. & JOLY, P. (2003): Transience, dispersal and survival rates in newt patchy populations.- Journal of Animal Ecology, Oxford; 72: 567-575.

Schmidt, P. & Weddeling, K. & Thomas, M. & Rottscheidt, R. & Tarkhnishvili, D. N. & Hachtel, M. (2006): Dispersal of *Triturus alpestris* and *T. vulgaris* in agricultural landscapes – comparing estimates from allozyme markers and capture-mark-recapture analysis; pp. 139-143. In: Vences, M. & Köhler, J. & Ziegler, T. & Böhme W. (Eds.): Herpetologia Bonnensis II. Proceedings of the 13th Congress of the Societas Europaea Herpetologica; Bonn, Germany, 27 September – 2 October 2005 (Societas Europaea Herpetologica).

Scott, D. E. & Casey, E. D. & Donovan, M. F. & Lynch, T. K. (2007): Amphibian lipid levels at metamorphosis correlate to post-metamorphic terrestrial survival.- Oecologia, Berlin; 153: 521-532.

Semlitsch, R. D. & Skelly, D. K. (2008): Ecology and conservation of pool-breeding amphibians; pp. 127-147. In: Calhoun, A. J. K. & deMaynadier, P. G. (Eds.): Science and conservation of vernal pools in northeastern North America., Boca Raton, FL (CRC Press), pp. 363.

Statsoft Inc. (2006): Electronic Statistics Textbook; Tulsa (StatSoft), pp. 453.

Switzer, P. V. (1993): Site fidelity in predictable and unpredictable habitats.- Evolutionary Ecology, London; 7: 533-555.

Thorn, R. & Raffaëlli, J. (2001): Les Salamandres de l'Ancien Monde; Paris (Editions N. Boubée), pp. 449.

Trivers, R. L. (1972): Parental investment and sexual selection; pp. 136-179. In: Campbell, B. (Ed.): Sexual selection and the descent of man, 1871-1971. Chicago (Aldine), pp. 378.

Vasconcelos, D. & Calhoun, A. J. K. (2004): Movement patterns of adult and juvenile *Rana sylvatica* (LeConte) and *Ambystoma maculatum* (Shaw) in three restored seasonal pools in Maine.- Journal of Herpetology, New Haven; 38: 551-561.

von Lindeiner, A. (1992): Untersuchungen zur Populationsökologie von Berg-, Faden- und Teichmolch (*Triturus alpestris* L., *T. helveticus* Razoumowski, *T. vulgaris* L.) an ausgewählten Gewässern im Naturpark Schönbuch (Tübingen).- Jahrbuch für Feldherpetologie / Beihefte, Duisburg; 3: 1-117.

Wells, K. D. (2007): The ecology and behavior of amphibians; Chicago (The University of Chicago Press), pp. 1148.

Whiteman, H. H. & Wissinger, S. A. & Bohonak, A. J. (1994): Seasonal movement patterns in a sub-alpine population of the tiger salamander, *Ambystoma tigrinum nebulosum*.- Canadian Journal of Zoology, Ottawa; 72: 1780-1787.

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