Short Note

Sampling efficiency, bias and shyness in funnel trapping aquatic newts

Jan W. Arntzen*, Annie Zuiderwijk

Abstract. A lightweight, collapsible funnel trap designed for crayfish was furnished with a smaller mesh and then used to study adult breeding populations of five species of newts in five ponds in France. Observations were made in spring, at the peak of breeding activity, over an 11-year period. Annual experiments involved on average 7.7 traps and 5.3 overnight sampling sessions at 2.0 day intervals. In 95 out of 171 experiments (56%) the probability for an individual to go undetected was $<1\%$. A trend was observed for catchability to increase with body size (*Lissotriton* $<$ *Ichthyosaura* $<$ *Triturus*). The two *Triturus* species involved were frequently exhaustively sampled in a single overnight session. In spite of their smaller size, *L. helveticus* males were more readily captured than females, presumably reflecting breeding associated locomotor activity. The numbers captured decreased over time suggesting ‘trap shyness’ to operate. We noted some predation by diving beetles (family Dytiscidae) affecting *L. helveticus* males in particular.

Keywords: catchability, detectability, France, *Ichthyosaura*, *Lissotriton*, mortality, predation, *Triturus*.

Surveying and monitoring are essential components to the study of wildlife for conservation and research. Amphibian surveys over larger areas are mostly carried out with the traditional dip-net, yielding data per visit instantaneously. The monitoring of aquatic amphibians is increasingly carried out with traps. However, the use of traps requires at least two visits, for positioning and for inspection, with the trade-off that experiments are more readily standardized and results better comparable than with dip-nets. Early studies with aquatic traps are those by Calef (1973), van Gelder (1973) and Bell (1977). By now a substantial literature exists on the design and performance of traps, from which it is apparent that they generally perform well (Skelly and Richardson, 2010; Kronshage et al., 2014). However, for research into demography and population processes, high sampling efficiencies are advantageous. For example, to

unambiguously identify adults that skip one or more annual breeding opportunities requires that all animals that engage in breeding are actually observed, over a range of years. We here describe the functioning and sampling efficiency of lightweight, collapsible funnel traps that we use to study European newts. The traps were originally designed for catching crayfish, but are for amphibian monitoring manufactured with a smaller, 4×4 mm mesh. The traps consist of a framework of one large semi-circular (diameter 48 cm) and three smaller circular metal loops (diameter 29 cm), to which the funnel and the collection chamber are attached (fig. 1). The actual funnel is cone-shaped, 30 cm deep and has the apex removed to create a funnel opening of 7×7 cm. A rectangular 45×97 cm extension leading towards the trap opening enlarges the catchment area. The total length of the traps is 207 cm and the weight is ca. 600 g. The traps were purchased at Casa Galo, Avenida Palomares 26, 41100, Coria del Rio, Sevilla, Spain.

The study was carried out in the French ‘departments’ Pas-de-Calais (pond 1, located near

Naturalis Biodiversity Center, Leiden, The Netherlands

*Corresponding author;

e-mail: pim.arntzen@naturalis.nl

Figure 1. Funnel trap used to capture newts during the breeding season. Traps were positioned with the diagonal of the semi-circular funnel flat to the pond bottom. The position of the narrow opening in between the two chambers is indicated by line 'a'. Line 'b' indicates the section of the trap that stays above the water surface, if so needed with the help of a polystyrene floater. The anterior chamber can be opened for inspection at position 'c'. The iron poles at either side are M10 threaded rods, so that the tension applied to the cords is easily adjusted. The sheet of paper is of A4 size. One functional difference with most other funnel traps is the extension at the front that enlarges the catchment area.

the village Ambleteuse) and Mayenne (ponds 2-5, located around the village Jublains). Ponds 1-4 are small sized field ponds used for watering cattle and pond 5 is a disused sand quarry. Sizes and depths in spring vary from ca. 60-300 m² and 50-150 cm. Locally, up to five newt species can be found in syntopy (Arntzen and de Wijer, 1989), namely *Ichthyosaura alpestris* (Laurenti, 1768), *Lissotriton helveticus* (Razoumovsky, 1789), *L. vulgaris* (Linnaeus, 1758), *Triturus cristatus* (Laurenti, 1768) and *T. marmoratus* (Latreille, 1800). Observations on *T. cristatus* * *T. marmoratus* F₁ hybrids (Arntzen et al., 2009; Cogălniceanu, Stănescu and Arntzen, 2019) and juvenile *T. cristatus* were ignored. The number of overnight sampling sessions ranged from three to nine (average 5.3) and the number of installed funnel traps ranged from four to 13 (average 7.7). When moved from one pond to the other, the traps were disinfected with a 1% (w/v) solution of Virkon® to prevent possible cross-contamination of e.g. chytrid fun-

gus (Johnson et al., 2003; Dejean, Miaud and Schmeller, 2010).

Small- (genus *Lissotriton*) and medium-sized newts (genus *Ichthyosaura*) were marked by clipping one finger. Large-bodied newts in the genus *Triturus* were either toe-clipped or PIT-tagged (Perret and Joly, 2002) but to maintain comparability among species, the individual recaptures were dealt with as batch mark recaptures. The annual median date for observations was April 29 and the average time between subsequent sampling sessions was 2.0 days. Because our monitoring was restricted to adult newts and each year carried out over a relatively short (1-2 week) period coinciding with the summit of the breeding period, we consider the study populations 'closed' for the duration of the experiment. Applying batch marks in a closed population amounts to (virtual) removal sampling (Chao and Huggins, 2005). To analyze the data (recaptures excluded), we applied the likelihood methods of Moran (M) and Schnute

(S) as implemented in FSA software (Ogle, 2016). The Moran method estimates a constant probability of capture across all sampling sessions (p_M), whereas the Schnute method accounts for a different probability of capture for the first sample (p) and a constant probability of capture for all ensuing samples (p_{1S}). The S-method was preferred over the M-method if catchability significantly differed between the first sample and the other samples, as determined from negative log-likelihoods by the chi-square test statistic (Ogle, 2016). The parameters p_M , p_S and p_{1S} are catchabilities at the first (p) and subsequent visits (p_1) for the Moran (p_M) and Schnute methods (p_S and p_{1S}). For analyses across the data set p_M was used to ensure the comparability of the results. The overall probability of being detected (and not being missed in an annual experiment) is detectability (D), which here is the number of different animals encountered (N_{diff}) divided by the estimated population size ($\hat{N}$). Ninety-five percent confidence intervals (CI95) are derived from $\hat{N}$ and based on likelihood ratio theory as described in Schnute (1983). Experiments with $N_{\text{diff}} < 5$ were not analyzed and results with CI95 covering the zero to unity range were ignored. A special case are capture histories such as (x, 0, 0, etc.) that have x individuals caught at the first sampling session and none at two or more sessions afterwards. Such data are not accommodated by the Moran and Schnute methods and results were interpreted as $x = N_{\text{diff}} = \hat{N}$, with p_M and D at unity. This type of analysis we refer to as the count method (c). Population parameters were estimated per pond, year and species for either sex in the period 2009-2019. The number of study years was one for pond 1, three for pond 5 and 11 for ponds 2, 3 and 4. Data statistical analysis was with SPSS (IBM SPSS v. 20, 2016).

The total number of observations was 22 161 (numbers irrespective of marking status). The default M-method was applied most frequently (128 experiments, 75%). The S-method was preferred in 29 experiments (17%), mostly for *L. helveticus* (21 times), or the other species

when samples were large ($N_{\text{diff}} > 30$, six times). Experiments with $p_S > p_{1S}$ and $p_S < p_{1S}$ were about equally frequent, suggesting no particular tendency for a decrease or increase in the catchability of unmarked animals over time. The c-method was applied in 14 experiments (8%) and only to *Triturus*, suggesting that these two species were frequently exhaustively sampled in a single overnight sampling session. We generally achieved high yields with $D \geq 0.90$ in 135 experiments (79%) and $D \geq 0.99$ in 95 experiments out of 171 (56%; table 1). Across the study catchability p_M was significantly higher for males than for females in the small bodied species (related samples Wilcoxon signed rank test: *L. helveticus*, $n = 33$, $W = 479.5$, $P < 0.0001$; *L. vulgaris*, $n = 7$, $W = 28$, $P < 0.05$) and not in the large bodied species (*T. cristatus*, $n = 22$, $W = 100$, $P > 0.05$; *T. marmoratus*, $n = 20$, $W = 90$, $P > 0.05$). Overall, catchability was markedly higher for syntopic *T. marmoratus* and *T. cristatus* than for *L. helveticus* and *L. vulgaris* (supplementary table S1). Among congeneric species differences were not significant (*Lissotriton*: $n = 17$, $W = 97$, $P > 0.05$; *Triturus*: $n = 21$, $W = 135$, $P > 0.05$). In the species studied body length increases in the order *L. helveticus* – *L. vulgaris* – *I. alpestris* – *T. marmoratus* – *T. cristatus* (Griffiths, 1996; Arntzen, 2000) and we note that catchability increases in approximately the same order, but to further test this apparent relationship more data are required on *I. alpestris*. A decrease with body size highlights the position of *L. helveticus*, in which males are smaller than females, yet they have higher catchability.

In the literature, a male capture bias and no capture bias have both been reported, frequently however without reference to total population size (e.g. Griffiths, 1985). The statistical analysis of Trevor Beebee's data, with population sizes known (Beebee, 1990), reveals a male bias for *T. cristatus* (G -test for independence, $G = 10.3$, $P < 0.01$) and no bias for *L. vulgaris* ($G = 1.05$, $P > 0.05$). The study also shows a higher catchability for *T. cristatus* than for *L. vulgaris* ($G = 17.5$, $P \leq 0.001$). The data by

Table 1. Probability of being detected (D) in annual experiments for male (M) and female (F) newts in the french departments Pas-de-Calais (pond 1) and Mayenne (ponds 2-5). 95CI is the 95% confidence interval. Methods used in the process are c (count), M (Moran) and S (Schnute); for details see text. Empty cells denote experiments for which the number of different individuals encountered was <5.

Locality	Year	Number		Sex	D (95CI), method			
		Capture sessions	Funnel traps		<i>Lissotriton helveticus</i>	<i>Lissotriton vulgaris</i>	<i>Ichthyosaura alpestris</i>	<i>Triturus cristatus</i>
Pond 1	2012	4	5	M	0.42 (0.33-0.68), M 0.33 (0.00-0.62), S	0.51 (0.33-0.86), M 0.33 (0.33-0.92), S	0.83 (0.63-0.94), M	
				F			0.33 (0.00-0.60), M	
				<i>Triturus marmoratus</i>				
Pond 2	2009	5	8	M	0.40 (0.33-0.65), M 0.33 (0.33-0.64), M		1.00 (0.94-1.00), M 0.45 (0.33-1.00), M	
				F				
	2010	6	5	M	1.00 (0.96-1.00), M 0.99 (0.91-1.00), M		1.00 (0.95-1.00), M 1.00, c	
				F				
	2011	5	6	M	0.99 (0.95-1.00), S 0.99 (0.95-1.00), M		1.00 (0.35-1.00), M	
				F				
	2012	4	8	M	0.95 (0.75-0.99), S 0.97 (0.92-1.00), S		1.00, c	
				F				
	2013	5	6	M	0.93 (0.81-0.98), S 0.87 (0.65-0.95), S		1.00 (0.86-1.00), M 1.00 (0.65-1.00), M	
				F				
	2014	6	8	M	0.94 (0.84-0.99), S 0.91 (0.77-0.98), S		1.00 (0.85-1.00), M	
				F				
	2015	4	10	M	0.88 (0.81-0.94), M 0.94 (0.84-0.98), S		1.00, c 1.00, c	
				F				
	2016	4	9	M	0.92 (0.33-0.97), S 0.92 (0.86-0.97), M		1.00 (0.95-1.00), M 1.00, c	
				F				
	2017	4	6	M	0.86 (0.73-0.94), M 0.66 (0.42-0.81), M		1.00 (0.86-1.00), M	
				F				
	2018	5	9	M	0.97 (0.93-0.99), S 0.93 (0.85-0.98), S		1.00 (0.99-1.00), M 1.00 (0.96-1.00), M	
				F				
	2019	4	6	M	0.97 (0.93-0.99), S 0.96 (0.91-0.99), M		1.00 (0.74-1.00), M 1.00 (0.96-1.00), M	
				F				
Pond 3	2009	8	10	M		0.87 (0.33-1.00), M	1.00 (0.33-1.00), M	
				F			1.00 (0.57-1.00), M	1.00 (0.74-1.00), M
	2010	6	4	M	1.00 (0.70-1.00), M 1.00 (0.83-1.00), M	1.00 (0.95-1.00), M 1.00 (0.85-1.00), M	1.00 (0.89-1.00), M 1.00 (0.95-1.00), M	
				F				1.00, c
	2011	4	7	M		1.00 (0.88-1.00), M	1.00 (0.98-1.00), M	
				F			U	1.00 (0.92-1.00), M
	2012	6	10	M	1.00 (0.87-1.00), M 1.00 (0.87-1.00), M		1.00 (0.92-1.00), M 0.99 (0.89-1.00), M	
				F				1.00 (0.85-1.00), M
	2013	5	6	M	0.78 (0.33-1.00), M 0.92 (0.33-1.00), M	1.00 (0.88-1.00), M 1.00 (0.60-1.00), M	1.00 (0.85-1.00), M 1.00 (0.97-1.00), M	
				F				0.82 (0.33-1.00), M
	2014	8	7	M	0.71 (0.33-0.90), M 0.33 (0.33-0.68), M	U 0.33 (0.00-0.75), S	0.77 (0.42-0.94), M	
				F				0.99 (0.81-1.00), M
	2015	6	6	M	0.90 (0.64-1.00), M 0.54 (0.00-0.94), S	0.90 (0.60-1.00), M 0.79 (0.33-1.00), M	U	
				F				1.00 (0.96-1.00), S
	2016	6	9	M	0.98 (0.91-1.00), M 0.80 (0.38-0.97), M	1.00 (0.99-1.00), S 0.88 (0.40-1.00), M	0.95 (0.84-1.00), M	
				F				0.69 (0.33-0.93), M
	2017	6	6	M	0.88 (0.33-1.00), M 0.75 (0.33-0.99), S	0.97 (0.63-1.00), M	0.94 (0.83-1.00), M	
				F				U
	2018	5	9	M	0.99 (0.94-1.00), M 0.97 (0.88-1.00), M	0.95 (0.60-1.00), M	0.99 (0.85-1.00), S	
				F				

Table 1. (Continued.)

Locality	Year	Number		Sex	D (95CI), method			
		Capture sessions	Funnel traps		<i>Lissotriton helveticus</i>	<i>Lissotriton vulgaris</i>	<i>Triturus marmoratus</i>	<i>Triturus cristatus</i>
Pond 4	2019	4	8	M	0.85 (0.52-0.99), M	1.00 (0.94-1.00), M		0.99 (0.93-1.00), M
				F	0.87 (0.60-0.99), M	0.97 (0.95-1.00), M		1.00 (0.94-1.00), S
	2009	6	8	M	1.00 (0.98-1.00), M		1.00 (0.91-1.00), S	1.00 (0.96-1.00), S
				F	0.97 (0.89-1.00), M		0.88 (0.33-1.00), M	0.99 (0.86-1.00), M
	2010	6	6	M	0.98 (0.93-1.00), M		1.00 (0.99-1.00), M	1.00 (0.98-1.00), M
				F	0.92 (0.81-0.98), M		1.00, c	1.00 (0.99-1.00), M
	2011	5	6	M	U		1.00 (0.91-1.00), M	1.00 (0.87-1.00), M
				F	0.86 (0.56-0.98), M		0.97 (0.50-1.00), M	1.00 (0.94-1.00), M
	2012	5	4	M	NS		1.00 (0.63-1.00), M	0.94 (0.40-1.00), M
				F	NS		0.74 (0.33-1.00), M	1.00 (0.67-1.00), M
	2013	9	7	M	1.00 (0.96-1.00), M		0.99 (0.75-1.00), M	1.00 (0.90-1.00), M
				F	0.33 (0.33-0.75), M		1.00 (0.60-1.00), M	0.33 (0.00-0.88), M
	2014	9	8	M	0.99 (0.95-1.00), M		1.00 (0.97-1.00), M	0.92 (0.43-1.00), M
				F	0.93 (0.84-0.98), M		1.00 (0.82-1.00), M	1.00 (0.90-1.00), M
	2015	4	13	M	0.99 (0.33-1.00), S		1.00, c	1.00 (0.97-1.00), M
				F	0.99 (0.97-1.00), M		1.00, c	1.00 (0.90-1.00), M
	2016	6	10	M	0.90 (0.33-0.95), S		1.00 (0.87-1.00), M	0.98 (0.59-1.00), M
				F	0.86 (0.78-0.92), M		1.00 (0.79-1.00), M	1.00 (0.95-1.00), M
2017	5	8	M	0.98 (0.91-1.00), S		1.00, c	1.00 (0.96-1.00), M	
			F	0.94 (0.82-0.99), S			1.00 (0.95-1.00), M	
2018	6	13	M	1.00 (0.99-1.00), M		1.00, c	1.00 (0.94-1.00), M	
			F	0.91 (0.78-0.97), S		1.00, c	1.00 (0.98-1.00), M	
2019	5	13	M	1.00 (0.99-1.00), S		1.00 (0.98-1.00), M	1.00 (0.96-1.00), M	
			F	0.91 (0.81-0.97), M		1.00, c	1.00, c	
Pond 5	2010	3	6	M	0.90 (0.51-0.90), M		0.98 (0.97-0.98), M	
				F	0.92 (0.55-0.94), M		0.99 (0.98-0.99), M	
	2011	3	6	M	U		0.97 (0.77-1.00), M	
				F	0.37 (0.00-0.99), M		1.00 (0.96-1.00), M	
	2016	5	8	M	NS		1.00 (0.94-1.00), M	
				F	NS		0.93 (0.72-1.00), M	

NS – Not studied.

U – Undetermined because the 95% confidence interval covers the zero to unity range.

Ortmann et al. (2005), with a population size estimate available, indicate a significant male bias for *T. cristatus* in one year ($G = 28.9$, $P < 0.001$) and not the other year ($G = 1.42$, $P > 0.05$).

We also investigated if newt numbers captured would be higher at early than at late sessions within the annual experiment, irrespective of marking status. Consistently lower capture numbers at later sessions might indicate ‘trap shyness’ (or conversely ‘trap addiction’). Trap shyness is the alteration of an animal’s pattern of behavior after it has been caught for the first

time (Seber, 1982). Accordingly, in the case of four or five sessions (see table 1) the pooled samples of sessions 1 and 2 were compared with pooled samples for the last two sessions; with six or seven sessions sets of three were compared, etc. Because the funnel traps were mostly up over a period confined to 1-2 weeks at the peak of the breeding season, so after immigration and prior to emigration, effects of phenology will be minor (Arntzen, 2002 and see discussion below). Across ponds we observed a significant decline in the numbers of newts captured from early to late funnel trap sessions

Figure 2. Numbers of adult newts caught in early (vertical axis, y) versus late (horizontal axis, x) funnel trap sessions across ponds, years and species. Note the logarithmic scale. The solid line shows $x = y$. With 58 observations falling above the line, 23 below the line and one at the line the difference between 'early' and 'late' is statistically significant (G -test for equal proportions, $G = 15.12$, $df = 1$, $P < 0.001$). For species specific results and discussion see text.

(fig. 2). This observation supports the hypothesis of trap shyness. For individual species, significant reductions were observed for *L. helveticus* (paired t -test on log-transformed numbers, $t = 4.65$, $df = 31$, $P < 0.0001$) and *T. marmoratus* ($t = 2.52$, $df = 20$, $P < 0.05$) and marginal insignificant differences for *L. vulgaris* ($t = 1.99$, $df = 8$, $0.05 < P < 0.10$) and *T. cristatus* ($t = 1.95$, $df = 19$, $0.05 < P < 0.10$). More work is required to test if trap-shy individuals hide in the pond or perhaps temporarily leave the pond. Alternatively, premature emigration of the breeding site on account of the experiment cannot be excluded, especially for *T. marmoratus* which species has the shortest annual aquatic period of ca. two months, versus e.g. five months for *T. cristatus* (Arntzen, 2003; Wielstra et al., 2019). However, to study pond emigration would require additional work, e.g. with terrestrial pitfall traps (Bouton, 1986) or involve the radio-tracking of individuals (Jehle, 2000; Jehle and Arntzen, 2000).

Over the course of the study 25 males and one female *L. helveticus*, two male and one female *L. vulgaris*, one *T. cristatus* female and three male and three female *T. marmoratus* were

found dead inside the traps. The *L. helveticus* were invariably laterally injured, at a position just in front of the insertion of a hind leg. Injuries of this kind were not observed in the other species or outside the traps. Prime candidates for the assaults are predatory diving beetles of the family Dytiscidae. Species identified were *Agabus bipustulatus* (Linnaeus, 1767) and *Dytiscus marginalis* Linnaeus, 1758. Fish are absent in the ponds we studied and fish predation reported elsewhere (e.g. Swartz and Miller, 2018) is not an issue. Food intake by trapped newts was not studied, but some elevated predation by *Triturus* on *Lissotriton* is likely, as is the feeding by newts on larvae of the early breeding amphibian species *Rana dalmatina* Fitzinger, 1839, *Rana temporaria* Linnaeus, 1758 and *Salamandra salamandra* (Linnaeus, 1758). The hibernating tadpoles of *Alytes obstetricans* (Laurenti, 1768) are too large to be eaten and *Bufo* tadpoles (*Bufo bufo* (Linnaeus, 1758) in Pas-de-Calais and *Bufo spinosus* Daudin, 1803 in Mayenne) are considered unpalatable (Heusser, 1971; Peterson and Blaustein, 1991). In pond 3 some *Rana dalmatina* tadpoles were found dead inside the funnel traps at a spell of high temperature. Accordingly, we recommend caution in using the funnel traps later in the season and we wonder if not cases of accidental trap injury and mortality are underreported in the literature (but see Klemish, Engbrecht and Lannoo, 2013 and references therein). The very high sampling efficiency of the funnel traps here described is probably mostly achieved through their large size and large catchment area. Practical assets of the traps are their low weight and small volume when collapsed, facilitating handling and storage.

Addendum

Annie Zuiderwijk passed away on January 27, 2020. In herpetology she will be best remembered for her biogeographical work (Schoorl and Zuiderwijk, 1980; Zuiderwijk, 1980; Bergmans and Zuiderwijk, 1986), observations on

Figure 3. Annie Zuiderwijk searching a French farm pond for amphibians using the traditional dip-net.

newt courtship behaviour (Zuiderwijk and Sparreboom, 1986; Zuiderwijk, 1990) and for her involvement with the Mapping Committee of the SEH. Annie also initiated the reptile monitoring program in the Netherlands (e.g. Kery et al., 2009), that is now operated by the NGO RAVON (Reptile, Amphibian and Fish Research in the Netherlands). Annie retired from her appointment as a member of the research staff at the Zoological Museum, University of Amsterdam in 2008, yet remained keen and active in herpetological research (fig. 3, see also van Diepenbeek, 2011; Evrard, 2017). A more comprehensive In Memoriam on Annie will shortly be published by her closest colleagues in the RAVON journal.

Acknowledgements. We thank R. Butôt, D. Cogalniceanu, R. Jehle, M. de Jong, N. Madden, W. Meilink and G. Wallis for help in the field, D. Bardou, S. Cornu, D. Laurent and

C. Tranquille for access to their properties. The work was carried out under permission of departmental authorities. Open access of this publication was made possible by the ‘Stichting ter Bevordering van Natuurwetenschappelijk Onderzoek’.

Supplementary material. Supplementary material is available online at:

<https://doi.org/10.6084/m9.figshare.11897142>

References

- Arntzen, J.W. (2000): A growth curve for the newt *Triturus cristatus*. *J. Herpetol.* **34**: 227-232. DOI:10.2307/1565419.
- Arntzen, J.W. (2002): Seasonal variation in sex ratio and asynchronous presence at ponds of male and female *Triturus* newts. *J. Herpetol.* **36**: 30-35. DOI:10.2307/1565798.
- Arntzen, J.W. (2003): *Triturus cristatus* superspecies – Kammolch-Artenkreis (*Triturus cristatus* (Laurenti, 1768) – Nördlicher Kammolch, *Triturus carnifex* (Laurenti, 1768) – Italienischer Kammolch, *Triturus dobrogicus* (Kiritzescu, 1903) – Donau-Kammolch, *Triturus karelinii* (Strauch, 1870) – Südlicher Kammolch). In: *Handbuch der Reptilien und Amphibien Europas*, Schwanzlurche IIA, p. 421-514. Grossenbacher, K., Thiesmeier, B., Eds, Aula-Verlag, Wiebelsheim, Germany.
- Arntzen, J.W., de Wijer, P. (1989): On the distribution of the palaearctic newts (genus *Triturus*) including the description of a five species pond in western France. *Br. Herpetol. Soc. Bull.* **30**: 6-11.
- Arntzen, J.W., Jehle, R., Bardakci, F., Burke, T., Wallis, G.P. (2009): Asymmetric viability of reciprocal-cross hybrids between crested and marbled newts (*Triturus cristatus* and *T. marmoratus*). *Evolution* **63**: 1191-1202. DOI:10.1111/j.1558-5646.2009.00611.x.
- Beebee, T.J.C. (1990): Crested newt rescues: how many can be caught. *Br. Herpetol. Soc. Bull.* **32**: 12-14.
- Bell, G. (1977): The life of the smooth newt (*Triturus vulgaris*) after metamorphosis. *Ecological Monogr.* **47**: 279-299. DOI:10.2307/1942518.
- Bergmans, W., Zuiderwijk, A. (1986): *Atlas van de Nederlandse Amfibieën en Reptielen en hun Bedreiging*. Koninklijke Nederlandse Natuurhistorische Vereniging, Zeist, The Netherlands.
- Bouton, N. (1986): Données sur la migration de *Triturus cristatus* et *T. marmoratus* (Urodela, Salamandridae) dans le Département de la Mayenne (France). *Bull. Soc. Herpétologique Fr.* **40**: 43-51.
- Calef, G.W. (1973): Natural mortality of tadpoles in a population of *Rana aurora*. *Ecology* **54**: 741-758. DOI:10.2307/1935670.
- Chao, A., Huggins, R.M. (2005): Modern closed-population capture-recapture models. In: *Handbook of Capture-Recapture Analysis*, p. 58-87. Amstrup, S.C., McDonald, T.L., Manly, B.F., Eds, Princeton University Press, Princeton, New Jersey, USA.

- Cogălniceanu, D., Stănescu, F., Arntzen, J.W. (2019): Testing the hybrid superiority hypothesis in crested and marbled newts. *J. Zool. Syst. Evol. Res.* **58**: 275-283. DOI:10.1111/jzs.12322.
- Dejean, T., Miaud, C., Schmeller, D. (2010): Protocole d'hygiène pour limiter la dissémination de la Chytridiomycose lors d'interventions sur le terrain. *Bull. Soc. Herpétologique Fr.* **134**: 47-50.
- Evrard, P. (2017): Rencontre avec Pim Arntzen et Annie Zuiderwijk. *L'Echo Herpéto, Feuille de Liaison des Herpétologues des Pays de la Loire* **3**: 2-5.
- Griffiths, R.A. (1985): A simple funnel trap for studying newt populations and an evaluation of trap behavior in smooth and palmate newts, *Triturus vulgaris* and *Triturus helveticus*. *Herpetol. J.* **1**: 5-10.
- Griffiths, R.A. (1996): *Newts and Salamanders of Europe*. Poyser, London, United Kingdom.
- Heusser, H. (1971): Differenzierendes Kaulquappen-Fressen durch Molche. *Experientia* **27**: 475-476. DOI:10.1007/BF02137323.
- IBM SPSS (2016): *Statistical Package for the Social Sciences*. SPSS Inc., Chicago, USA.
- Jehle, R. (2000): The terrestrial summer habitat of radio-tracked great crested newts (*Triturus cristatus*) and marbled newts (*T. marmoratus*). *Herpetol. J.* **10**: 137-142.
- Jehle, R., Arntzen, J.W. (2000): Post-breeding migrations of newts (*Triturus cristatus* and *T. marmoratus*) with contrasting ecological requirements. *J. Zool.* **251**: 297-306. DOI:10.1017/S0952836900007032.
- Johnson, M.L., Berger, L., Philips, L., Speare, R. (2003): Fungicidal effects of chemical disinfectants, UV light, desiccation and heat on the amphibian chytrid *Batrachochytrium dendrobatidis*. *Diseases Aq. Org.* **57**: 255-260. DOI:10.3354/dao057255.
- Kery, M., Dorazio, R.M., Soldaat, L., van Strien, A., Zuiderwijk, A. (2009): Trend estimation in populations with imperfect detection. *J. Appl. Ecol.* **46**: 1163-1172. DOI:10.1111/j.1365-2664.2009.01724.x.
- Klemish, J.L., Engbrecht, N.J., Lannoo, M.J. (2013): Positioning minnow traps in wetlands to avoid accidental deaths of frogs. *Herpetol. Rev.* **44**: 241-242.
- Kronshage, A., Schlüppmann, M., Beckmann, M., Weddeling, K., Geiger, A., Haaks, A., Böll, S. (2014): Empfehlungen zum Einsatz von Wasserfallen bei Amphibienerfassungen. In: *Wasserfallen für Amphibien – praktische Anwendung im Artenschutz*. Abhandl. Westfälischen Mus. Naturk. **77**, p. 293-358. Kronshage, A., Glandt, D., Eds.
- Ogle, D.H. (2016): *Introductory Fisheries Analyses With R*. Chapman and Hall/CRC, Boca Raton, USA.
- Ortmann, D., Hachtel, M., Sander, U., Schmidt, P., Tarkhnishvili, D., Weddeling, K., Böhme, W. (2005): Standardmethoden auf dem Prüfstand–Vergleich der Effektivität von Fangzaun und Unterwassertrichterfallen bei der Erfassung des Kammmolches, *Triturus cristatus*. *Zeitschr. Feldherpetologie* **12**: 197-209.
- Perret, N., Joly, P. (2002): Impacts of tattooing and PIT-tagging on survival and fecundity in the Alpine newt (*Triturus alpestris*). *Herpetologica* **58**: 131-138. DOI:10.1655/0018-0831(2002)058[0131:IOTAPO]2.0.CO;2.
- Peterson, J.A., Blaustein, A.R. (1991): Unpalatability in anuran larvae as a defense against natural salamander predators. *Ethol. Ecol. Evol.* **3**: 63-72. DOI:10.1080/08927014.1991.9525389.
- Schnute, J. (1983): A new approach to estimating populations by the removal method. *Can. J. Fish. Aquat. Sci.* **40**: 2153-2169. DOI:10.1139/f83-250.
- Schoorl, J., Zuiderwijk, A. (1980): Ecological isolation in *Triturus cristatus* and *Triturus marmoratus* (Amphibia: Salamandridae). *Amph.-Rept.* **1**: 235-252. DOI:10.1163/156853881X00357.
- Seber, G.A.F. (1982): *The Estimation of Animal Abundance and Related Parameters*, 2nd Edition. Griffin, London, United Kingdom.
- Skelly, D.K., Richardson, J.L. (2010): Larval sampling. In: *Amphibian Ecology and Conservation: a Handbook of Techniques*, p. 55-70. Dodd, C.K., Ed., Oxford University Press, New York, USA.
- Swartz, T.M., Miller, J.R. (2018): Trapping amphibians and their predators: tradeoffs in trap design and performance. *Herpetol. Rev.* **49**: 238-243.
- van Diepenbeek, A. (2011): Annie van de atlas, Annie van de monitoring. *RAVON tijdschrift* **13** (41): 78-83. <http://natuurtijdschriften.nl/download?type=document&docid=407365>.
- van Gelder, J.J. (1973): Ecological observations on Amphibia in the Netherlands II. *Triturus helveticus* Razoumowski: migration, hibernation and neoteny. *Neth. J. Zool.* **23**: 86-108. DOI:10.1163/002829673X00210.
- Wielstra, B., McCartney-Melstad, E., Arntzen, J.W., Butlin, R.K., Shaffer, H.B. (2019): Phylogenomics of the adaptive radiation of *Triturus* newts supports gradual ecological niche expansion towards an incrementally aquatic lifestyle. *Mol. Phylogen. Evol.* **133**: 120-127. DOI:10.1016/j.jmpev.2018.12.032.
- Zuiderwijk, A. (1980): Amphibian distribution patterns in western Europe. *Contr. Zool.* **50**: 52-72. <http://www.repository.naturalis.nl/document/547972>.
- Zuiderwijk, A. (1990): Sexual strategies in the newts *Triturus cristatus* and *Triturus marmoratus*. *Contr. Zool.* **60**: 51-64. DOI:10.1163/26660644-06001003.
- Zuiderwijk, A., Sparreboom, M. (1986): Territorial behaviour in crested newt *Triturus cristatus* and marbled newt *T. marmoratus* (Amphibia, Urodela). *Contr. Zool.* **56**: 205-213. DOI:10.1163/26660644-05602002.

Submitted: September 16, 2019. Final revision received: February 21, 2020. Accepted: February 24, 2020.
Associate Editor: Guillermo Velo-Antón.