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Short Note

On the aquatic phenology of sympatric crested and marbled newts (genus *Triturus*)

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Abstract. The large-bodied newts *Triturus cristatus* and *T. marmoratus* possess ranges that overlap in western France where they frequently share breeding ponds. I test the hypothesis that the aquatic phenology differs between them, as associated with a more aquatic and terrestrial life style respectively. Total adult population sizes were determined in spring in 13 experiments by the capture-mark-recapture methodology, followed by equivalent experiments in summer. Population sizes dropped by an order of magnitude on average whereas species frequencies changed in favour of *T. cristatus*, suggesting that *T. marmoratus* leaves the breeding site earlier than *T. cristatus*. Interspecies hybrids behaved like *T. marmoratus*. Descriptions are provided of other features (in ecology, morphology, demography, and colouration pattern) that support the different, aquatic versus terrestrial life styles of *T. cristatus* and *T. marmoratus*.

Keywords: breeding population size, capture-mark-recapture, hybrids, population size estimates, species frequencies, syntopy.

Introduction

The large bodied newts *Triturus cristatus* and *T. marmoratus* form an attractive system for comparative research because their ranges overlap over a wide area in the west of France. Within this area that covers ca. 28% of continental France, the species frequently share breeding ponds where they occasionally hybridize (Vallée, 1959; Arntzen et al., 2021; Arntzen, 2024b). Other than for most two-species systems that have mutually exclusive ranges (Arntzen, 2023a), species characteristics can often be directly compared in syntopy. To investigate the possibly different phenology of *T. cristatus* and *T. marmoratus* suggested in the literature (Bouton, 1986; Arntzen, 2003; Wielstra et al., 2019), I estimated population sizes in 'spring' and in 'summer' for ten ponds with both species, for a total of 26 experiments and 13 seasonal comparisons.

Materials and methods

Research was carried out in and around the municipality of Jublains in the département (dept.) Mayenne in the west of France. All study localities were field ponds intended for cattle water supply except for pond 10 that is an abandoned sand quarry. Captures were made with the dipnet (20 experiments), with funnel traps (one experiment), by using a fence and pitfall system (one experiment) or by torching shallow ponds with transparent water (four experiments). For the equipment used see the literature (Arntzen et al., 1995; Arntzen and Zuiderwijk, 2020). Funnel traps were not used in summer because of the high risk of death

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for amphibian larvae. Animal marking was done by batch-mark toe clipping, except for individual marking in some small populations (Woodbury, 1956), or recognition from the ventral (*T. cristatus*) or lateral coloration pattern (*T. marmoratus*) (Hagström, 1973; Arntzen et al., 2004). For batch mark data sets estimates of the adult *Triturus* population size ($\hat{N}$) were made by capture-mark-recapture analysis with approaches that go back to Schnabel (1938) and Schumacher and Eschmeyer (1943) that are implemented in the software FSA (Ogle, 2016). Methods were chosen on account of the precision they provided. For experiments with individually recognized newts the 'closed captures under full likelihood p and c' was used in software MARK (White and Cooch, 2001; White, 2008). When capture efforts could be assumed to be equal among sampling sessions, such as with funnel traps, estimates were based on depletion of the number of unmarked individuals, analysed with FSA's 'removal' routine. Hybrids were taken to show the presence of both species. Juveniles (that are not part of the breeding population) were observed for *T. cristatus* only and not taken into further consideration.

Results

Population sizes and species frequencies in spring varied widely among ponds (table 1). Total adult population sizes declined into summer in 13 out of 13 seasonal comparisons along with a 13/13 relative increase of *T. cristatus* ($P < 0.001$, binomial tests) (fig. 1). This phenomenon is sharply illustrated by observations for pond 10 that show the largest recorded population size and lowest *T. cristatus* capture frequency in spring (0.6%; four *T. cristatus* out of $N = 622$) and the lowest estimated population size and high *T. cristatus* capture frequency in summer (23.1%; three *T. cristatus* out of $N = 13$). The frequency of *T. cristatus* × *T. marmoratus* F_1 hybrids across the ponds averaged at 2.2% in spring and 1.1% in summer. The relative number of hybrids decreases from spring to summer compared to *T. cristatus* (G-test of independence, $df = 1$, $G = 23.53$, $P < 0.0001$) but not *T. marmoratus* ($G = 0.211$, $P > 0.05$).

Discussion

Within their wide zone of range overlap *T. cristatus* and *T. marmoratus* are rarely equally frequent (Vallée, 1959; Schoorl and Zuiderwijk, 1981). This gives rise to a mosaic distribution in which the one or the other species predominates. Regions with a preponderance of *T. cristatus* are mostly flat and open whereas *T. marmoratus* areas are hilly and forested (Schoorl and Zuiderwijk, 1981; Arntzen, 2023a,b). Yet, ponds with both species are not infrequent. Such syntopic populations allow the direct comparison of species attributes. Decreasing aquatic population sizes show that both species leave the pond from spring to summer. Species frequencies however suggest that *T. marmoratus* pond emigration is in advance of *T. cristatus*. Numbers on hybrids are low but on aggregate indicate that they behave more like *T. marmoratus* than like *T. cristatus*.

The marked ecological differentiation of the species and their different phenology here demonstrated indicate that they are differently adapted to aquatic versus terrestrial life styles. Features in support of this observation are that

i. *Triturus cristatus* reaches maturity in two years whereas *T. marmoratus* takes three or four years (Francillon-Vieillot et al., 1990; Cogălniceanu et al., 2020). Whereas *T. cristatus* juveniles may be found in the water, *T. marmoratus* and hybrid juveniles are strictly terrestrial.
ii. The species differ in general built, most clearly expressed in the number of vertebrae that is three units higher in the slender *T. cristatus* than in the robust *T. marmoratus* (Vallée, 1959). Across *Triturus* species, higher numbers have been associated with a lengthier aquatic lifestyle (Arntzen, 2003; Wielstra et al., 2019).
iii. The vivid orange ventral colouration observed in crested newts classifies as 'hidden aposematism' (Ferreira et al., 2019). Colours may be shown in water and on land, but are only exposed to would-be predators on encounter (Beebee, 1980; Telea et al., 2021; Loeffler-Henry et al., 2023). In the variety of crested newt species, an association appears to exist between colouration and

Table 1. Overview of logistics and results on the capturing of *Triturus* newts in the dept. Mayenne in the west of France. Symbol N̂ represents the estimated adult population size and CI stands for confidence interval. Capturing methods are a fences/pitfall system (barrier, B), dipnet (D), funnel traps (F) and torching (T). Population sizes were estimated for 13 'spring' (A) and 'summer' (B) experiments with the 'Schnabel' (S), 'Schumacher and Eschmeyer' (SE) and 'Removal' (R) methods in FSA software (Ogle, 2016), or with the 'Closed captures under full likelihood p and c' (Cc) option in the programme MARK. For the selected models (M_0, M_b, M_t), see Lukacs (2024).

Pond / year	Experiment	Temporal window	Capturing method	Number of sessions	Numbers observed[#]			*T. cristatus* (%)°	Population size estimates			Data courtesy[φ]
					T. cristatus	*T. marmoratus*	Hybrids		Method	N̂	95% CI	
1 /	1A	1-28/5	D	4	33	98	5	26.1	SE	114	100-134	
1981	1B	5-31/7	D	7	47	32	3	59.1	SE	45	38-55	
1 /	2A	15/3-27/7	B	2	2	85	0	2.3	SE	96	60-164	NB
1986	2B	4-8/8	D	3	3	32	0	8.6	Cc M_b	20	20-20	
2 /	3A	3/3-11/6	D	4	28(2)	31	0	47.5	Cc M_t	46	40-62	
1981	3B	15/7-25/8	D	3	9	2	0	81.8	SE	8	3-20	
3 /	4A	20/3-29/6	T	8	8	47	13	21.3	S	163	92-309	
1981	4B	8-27/7	T	4	11	11	0	50.0	S	39	16-96	
4 /	5A	23/3-26/5	D	6	48	8	5	82.8	S	102	61-180	
1981	5B	1/7-28/7	D	5	44	4	0	91.7	S	85	45-171	
5 /	6A	4/3-27/5	D	4	31	16	0	66.0	S	136	97-197	
1981	6B	5/7-1/8	D	5	61(2)	21	2	73.8	S	115	76-180	
6 /	7A	13/3-28/5	D	7	123(1)	1	4	97.7	Cc M_b	205	192-247	
1981	7B	18-28/7	D	6	110	0	1	99.5	Cc M_0	66	59-111	
7 /	8A	10/4-2/6	T	5	68(6)	4	2	93.2	S	75	50-117	
1981	8B	4/7-20/7	T	3	54	2	0	96.4	S	47	25-95	
8 /	9A	26/3-24/4	D	3	14	14	2	50.0	S	70	28-172	
1981	9B	20/5-8/7	D	3	10	2	1	80.8	S	11	4-27	
9 /	10A	15/4-30/5	D	6	12(2)	80	0	13.0	S	95	67-139	
1981	10B	1/7-1/8	D	7	15	20	0	41.2	SE	21	18-26	
9 /	11A	16/3-25/6	D	12	43	192	0	18.3	S	185	167-208	NB
1986	11B	4-9/8	D	3	27	41	0	39.7	Cc M_b	53	51-66	
9 /	12A	5-22/4	D	4	25	179	0	12.2	SE	164	127-233	
1989	12B	22-27/6	D	3	20	13	0	60.6	SE	21	18-26	PB
10 /	13A	17/4-5/5	F	18	4	608	10	1.4	R	461	427-495	
2024	13B	24-28/6	D	4	3	10	0	23.1	SE	8	5-14	

[#]Recaptures included. Number of juveniles in brackets.

°Hybrids counted half *T. cristatus* and half *T. marmoratus*.

[φ]AZ – Annie Zuiderwijk, JS – Jaap Schoorl, NB – Niels Bouton and PB – Pieter Bouma.

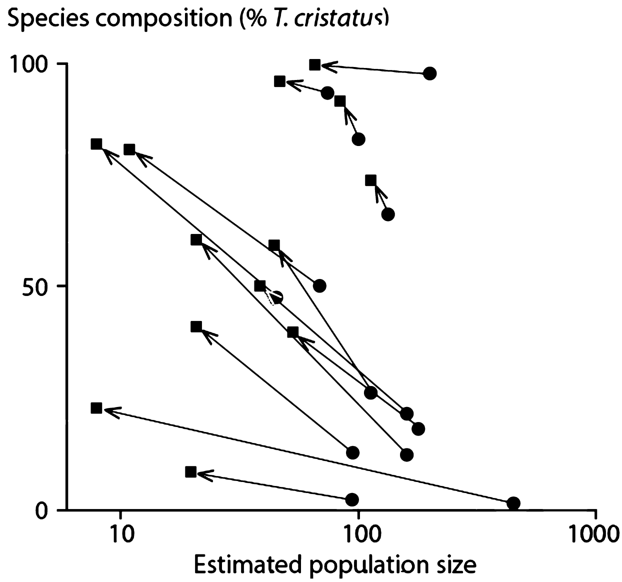

Figure 1. The percent frequency of *Triturus cristatus* (vertical axis) plotted against the estimated total aquatic population size of adult *Triturus* newts (horizontal axis on a logarithmic scale), with population sizes estimates in spring (round symbols) and in summer (square symbols). The correlated change of population size and species composition is highlighted by arrows. For the underlying data, see table 1.

body shape and duration of the aquatic phase. Colours range from yellow venters in stocky species (*T. karelinii*, *T. carnifex*) to deep red in the slender *T. dobrogicus* (see e.g., illustrations in Fahrbach and Gerlach, 2018), suggesting that the ventral colouration intensifies with the length of the aquatic phase. Conversely, the green and black blotched dorso-lateral colouration of adult *T. marmoratus* is to assist camouflage, mostly serving on land. Perpendicular to this scheme, juvenile *T. marmoratus* are equipped with a near-fluorescent bright orange and green dorsal colouration over black (see e.g., Fig. 2C in Arntzen, 2024a) that classifies as 'exposed aposematism' (as in the terrestrial *Salamandra salamandra*). With the notion that life style and colour pattern are correlated, the genus *Triturus* may contribute to an evolutionary analysis over a wide range of organisms.

It may be wondered to what extend the results and conclusions are dependent on uncertainties associated with field work and data analysis. Foremost, experiments in summer are only feasible if the pond keeps water, such as in the particularly wet years 1981 and 2024. Drying up inevitably forces all post-metamorphs to land whatever the species. As for species frequencies, most individuals were captured by dipnet, which has been shown to be unbiased for newts (Arntzen, 2002). Funnel traps show possibly a slightly higher efficiency towards *T. marmoratus* than *T. cristatus* (Arntzen and Zuiderwijk, 2020), perhaps achieved through escapes by the latter, aquatically versatile species. As for species numbers, spring and summer population size estimates were made in similar ways and the difference is by an order of magnitude on average. Some experiments took place over long periods and the assumption of a 'closed population' is unlikely to have been met. However, the strong signals received are likely to override shortcomings associated with data gathering and analysis. Despite the heavy work load, the 95% confidence intervals are often large. However, these intervals frequently encompass the minimum population size as known from the number of different individuals observed (nine cases out of 26, 35%, data not shown), suggesting that they are overly wide, at least at the lower end. In practical terms the data show that inventories after the breeding season bias the outcome towards *T. cristatus* because this is the more aquatic species that stays at the breeding site for longer.

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