



BRILL

Coexistence of two newt species in a transition zone of range overlap

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Abstract

Theory suggests that spatial segregation of similar, co-occurring species may be driven by alternative innate life history and dispersal strategies, and that it operates through catastrophic events. An inventory of the evolutionary closely related small-bodied newts *Lissotriton helveticus* and *L. vulgaris* in the northwest of France demonstrated the species' spatial partitioning, with *L. vulgaris* dominating in two pond-rich and historically disturbed coastal areas and *L. helveticus* prevailing inland where ponds are sparser. Population numbers were followed over several decades (1975–2021) in a pond within the narrow (ca. 2000 m wide) species transition zone. Early in the temporal survey (1986) a massive die-off was observed of two-third of the *L. helveticus* breeding population from a late frost event. Yet, the contribution of *L. helveticus* to the newt assemblage was more or less stable around 60%, even though the total population size fluctuated by an order of magnitude. *Lissotriton vulgaris* and a third species, *Ichthyosaura alpestris*, made up ca. 30% and 10% of the total till 1993, after which date their relative contributions reversed. These data suggest that a state shift may have occurred among the latter two species and that the assumed two-species dynamics of *Lissotriton* underlying the study has been an oversimplification. The local decline of *L. vulgaris* is paralleled by the loss of well-vegetated ponds from the wider agricultural terrain that affects this species more than *L. helveticus* and *I. alpestris*.

Keywords

competitive exclusion – dispersal – ecological separation – *Lissotriton* – niche shift – population size estimates – syntopy – sympatry

Introduction

The competitive exclusion principle asserts that, when resources are in short supply, no two non-hybridizing species can exploit the environment in exactly the same way and coexist. Syntopic species will therefore differ along one or more niche dimensions (Hardin, 1960; Mueller, 2019). When it was shown that coexistence rather than exclusion of closely related species is the rule, this principle gradually changed into the 'competitive niche shift principle' (den Boer, 1986). Whether the strict or more lenient perspective is taken, to further test and document the principle, it would be advantageous to select a study system that covers a wide array of environmental conditions and to not be restrained by dimensions of time or space. The European small-bodied smooth and palmate newts (*Lissotriton vulgaris* and *L. helveticus*) provide an appropriate research system, because they are morphologically similar and closely related species with widely overlapping ranges. They breed in discrete aquatic habitats (mostly ponds) where they are usually abundant and frequently co-occur. In two pioneering papers, Griffiths (1986, 1987) reported on the overlapping niche dimensions of adult newts during their aquatic breeding phase and concluded that there was no evidence for resource partitioning in the species' temporal, micro-habitat or feeding profiles, suggesting that population regulation occurred during another phase of life. In newts this may be the larval stage, or the terrestrial juvenile and adult stages. Resource partitioning in the aquatic larval stage remains to be studied and not much is known about the species' terrestrial habitat preferences, though *L. helveticus* may be prevailing at higher altitudes than *L. vulgaris* (Cooke & Ferguson, 1975; Feldmann, 1981), in forested areas, on heathland and sandy soils (van Gelder, 1972; Geraeds, 2009)

and in nutrient-poor and acidic environments, possibly related to geology (Cooke & Frazer, 1976; Denton, 1991).

I here investigate the long-standing issue of a differential habitat utilization of smooth and palmate newts along wide spatial and temporal axes. This work demonstrates the importance of long-term research on populations in order to understand the drivers of population trends. As newts seem to be at the mercy of catastrophic and density-independent factors (e.g., freezing and drying ponds), the observed patterns are highly stochastic. Yet, this study suggests that the species do possess different life histories and dispersal strategies and respond differently to environmental perturbations and it shows how intrinsic and environmental factors can differentially affect the abundance of coexisting species.

Materials and methods

Amphibian survey data for the western, coastal part of the département (department, dept.) Pas de Calais in the northwest of France were obtained over the 1974–2021 period (see e.g., Zuiderwijk, 1980; Arntzen et al., 2017). The data were recompiled to obtain the frequency (F) of *Lissotriton helveticus*, the palmate newt ($F_h = N_h / (N_h + N_v)$) and *L. vulgaris*, the smooth newt ($F_v = 1 - F_h$) in ca. 400 ponds across the landscape. For 105 ponds (this excludes the 'focal' pond described below) sample sizes were over the $N_h + N_v = 9$ threshold that was considered the minimum to conduct a meaningful analysis. A contour map of F_v was produced with MyStat software (Systat Inc., 2008), with the logarithm of $(N_h + N_v)$ as a weighing factor to give more emphasis to larger samples. An indication of pond density was obtained by calculating the average Euclidian distance of the pond under consideration to the other nearest

one to ten ponds (Ponddist1 – Ponddist10). Hardness and salinity of pond water were determined with a Hach DR/3 Photometer as Ca^{2+} in mg/l (58 observations) and Cl^{-} in mg/l (28 observations).

The inventory revealed a marked spatial separation of *Lissotriton helveticus* and *L. vulgaris* (see results below). To investigate the species' long-term population dynamics under conditions of syntopy, a study pond was selected located at the transition of *L. vulgaris* to *L. helveticus* dominated areas. Additional selection criteria were permission to access, small pond size and substantial newt populations, to provide sample sizes with sufficient statistical power to analyse rigorously. The selected pond with coordinates 50.820 N and 1.604 E is located in rough pasture between the villages Ambleteuse and Audresselles adjacent to the Selles brook. The surrounding area was initially communal land and classified as a nature reserve since 2012 (Réserve naturelle régionale du pré communal d'Ambleteuse). Aerial photography available at <https://remonterletemps.ign.fr> reveals that the study pond was created in between July 14, 1971 and January 1, 1972, possibly for the purpose of sand extraction (supplementary fig. S1). Dimensions were ca. 15 × 20 m. The pond was detected as a site for amphibian reproduction in 1975 and followed up to the present day. A further newt species surveyed at the pond alongside *L. vulgaris* and *L. helveticus* was the alpine newt, *Ichthyosaura alpestris*, whereas the northern crested newt, *Triturus cristatus*, was seen just once.

Observed pond depth in spring varied from 90 to zero cm (i.e., dry). Pond half-life in the area has been estimated at 20 years on average (Curado et al., 2011) so that the chance for a randomly selected pond to survive the study period of 47 years was about one in five. Natural succession reduced pond size and depth, and it was further

diminished by the dumping of debris from the beach and construction waste in 1993–1994. Encroachment by shrubs and trees fully shaded the pond within a local spinney (diameter 40 m) by 2003 (supplementary fig. S2). In spring 2021 pond size was down to ca. 9 × 14 m with a depth of 35 cm. In 1975, 1979–1981, 1984 and 2021 adult newts were sampled in spring or early summer to determine species composition. In spring 1987 the pond was dry and in 1983, 1986, 1988–1995 and 2012 population size estimates were made through a multiple capture procedure of marked and unmarked individuals, by either using funnel traps (in 2012) or dip nets (the other years). Batch marking was applied by the clipping of a single finger. Population size estimates (\hat{N}) were made in the breeding period for the entire newt population of three species, i.e., *L. helveticus*, *L. vulgaris* and *I. alpestris*, on the – substantiated – assumption of equal catchability of species (Arntzen, 2002; Arntzen & Zuiderwijk, 2020). The pooling of species was deemed necessary because it is tedious to estimate small population sizes with an acceptable level of confidence. Immigration and emigration were assumed to be absent, amounting to a 'closed' population. Recaptured individuals were taken into account with the 'weighted mean' method (\hat{N}_{WM} ; Begon, 1979), or excluded from the calculations for the 'removal' method (\hat{N}_R , Pollock & Otto, 1983, as implemented in the Capture program by Rexstad & Burnham (1991), accessible at <https://www.mbr-pwrc.usgs.gov/software/capture.html>). The results on $\log \hat{N}_{WM}$ and $\log \hat{N}_R$ correlate ($r = 0.84$, $df = 12$, $P < 0.01$), with the tendency that $\log \hat{N}_{WM}$ would exceed $\log \hat{N}_R$ by a factor 1.05 on average (range 0.997–1.180) (for details see the Results section). I here utilize the more conservative \hat{N}_R estimates that come with a 95% confidence interval (CI95).

Capture efficiency is defined as the number of different individuals observed in an annual sampling period divided by \hat{N}_R .

Females of both *Lissotriton* species have similar appearance (Veith & Dorr, 1985; Arntzen et al., 1998), with one of the differences being that *L. helveticus* females appear a little heavier than *L. vulgaris* females. Because different volumes may indicate different fecundities (see Verrell, 1986), I counted the number of yolked oocytes in females of both species in early spring, i.e., before the onset of oviposition. These females were found dead in the focal pond directly after a freezing incident just prior to the annual breeding period (see below).

Statistical analyses were done with SPSS 28 (IBM SPSS, 2021).

Results

Species distribution

A total of 17,537 adult *Lissotriton* captures was made (average sample size per pond 167.0, range 10–2162) with more *L. helveticus* (74%) than *L. vulgaris* (26%) (table 1). *Lissotriton vulgaris* was the more numerous species in and around the coastal zones ‘Dunes de la Slack’ and the so-called ‘bomb crater area’ south of Cap Griz Nez, whereas *L. helveticus* was more numerous inland (fig. 1). The contour plot of species frequencies describes the transition in species composition from $0.4 < F_v < 0.6$ over a distance of ca. 2000 m. At all localities with large sample sizes ($N_h + N_v > 200$ in 20 ponds) both species were found. *Lissotriton vulgaris* was rare ($F_v < 0.05$) in six of these localities whereas *L. helveticus* was never rare.

Correlations of F_v and chemical parameters were marginally insignificant for hardness of the pond water (Spearman's correlation coefficient, $r_s = -0.249$, $N = 58$, $P < 0.10$) and for salinity ($r_s = -0.336$, $N = 28$, $P < 0.10$). The data are presented in supplementary table S1.

Species composition F_v was significantly negatively correlated with the average distance to other ponds for Ponddist3–Ponddist10 but not for Ponddist1 and Ponddist2, indicating that *L. vulgaris* is more numerous when ponds are close together (supplementary table S2).

Species numbers in the focal pond – early observations

Dip-netting the focal pond in 1975 yielded 31 *L. helveticus* and ten *L. vulgaris* ($F_v = 0.24$) which is in line with the pond's location in the species transition zone (fig. 1). In early March 1986 the combination of a low water table in combination with a ‘false spring’ was fatal for a large cohort of newts, presumably through freezing or suffocation in ca. 20 cm of ice, water and mud. On March 12 and 13, the ice had largely melted and 505 *L. helveticus* (280 males, 225 females), eight *L. vulgaris* (four males, four females) and one *I. alpestris* male were observed dead. It is unclear if the casualties had been hibernating in the pond or that they were early immigrants. Found alive were three males and five females of *L. helveticus*. The population size estimates later in the season suggested that the incident affected the breeding population of *L. helveticus* (505 dead out of $\hat{N} = 721$, 70%) more strongly than the other species (*L. vulgaris* – eight dead out of $\hat{N} = 274$, 3%; *I. alpestris* one dead out of $\hat{N} = 27.4$ %) and further suggests that the latter two species arrived at the pond later in the season, after the catastrophic event had occurred. Also found dead were 94 presumably aquatically hibernating *Rana temporaria* juveniles, along with one adult male and five juveniles alive. All corpses were without signs of decomposition. They were collected by hand, preserved in ethanol for later storage at the Naturalis Biodiversity Center, with collection numbers ZMA.RENA.7819–7823. The average number of yolked oocytes (\hat{N}_{oo}) was counted in 12 *L. helveticus* ($\hat{N}_{oo} = 242.4$,

TABLE 1 Numbers of adult *Lissotriton* newts observed over 105 ponds in the western part of the department Pas de Calais in the 1974 to 2021 period. $F_v = L_v / (L_h + L_v)$

Pond number	Coordinates		Sample size for species		F_v
	Northern latitude	Eastern longitude	<i>Lissotriton helveticus</i> (N)	<i>Lissotriton vulgaris</i> (N)	
1	50.770	1.772	21	1	0.05
2	50.871	1.617	194	175	0.47
3	50.902	1.679	223	9	0.04
4	50.901	1.678	126	7	0.05
5	50.870	1.606	580	24	0.04
6	50.902	1.680	233	6	0.03
7	50.869	1.608	34	1	0.03
8	50.869	1.609	20	0	0.00
9	50.875	1.656	26	2	0.07
10	50.855	1.666	410	149	0.27
11	50.854	1.664	188	96	0.34
12	50.839	1.672	108	10	0.08
13	50.837	1.675	29	5	0.15
14	50.820	1.631	65	41	0.39
15	50.858	1.630	26	6	0.19
16	50.861	1.610	92	34	0.27
17	50.860	1.606	43	0	0.00
18	50.849	1.597	186	87	0.32
19	50.853	1.595	27	11	0.29
20	50.866	1.608	107	46	0.30
21	50.844	1.590	104	76	0.42
22	50.844	1.598	26	16	0.38
23	50.844	1.599	83	66	0.44
24	50.845	1.599	812	182	0.18
25	50.845	1.599	45	16	0.26
26	50.845	1.599	53	40	0.43
27	50.845	1.599	86	35	0.29
28	50.845	1.600	41	16	0.28
29	50.845	1.600	79	33	0.29
30	50.845	1.600	70	17	0.20
31	50.845	1.601	51	45	0.47
32	50.846	1.600	1712	450	0.21
33	50.845	1.600	576	152	0.21
34	50.846	1.603	10	10	0.50
35	50.849	1.598	4	6	0.60
36	50.861	1.591	31	61	0.66
37	50.860	1.586	113	244	0.68

TABLE 1 Numbers of adult *Lissotriton* newts observed over 105 ponds in the western part of the department Pas de Calais in the 1974 to 2021 period. $F_v = L_v / (L_h + L_v)$ (cont.)

Pond number	Coordinates		Sample size for species		F_v
	Northern latitude	Eastern longitude	<i>Lissotriton</i> <i>helveticus</i> (N)	<i>Lissotriton</i> <i>vulgaris</i> (N)	
38	50.860	1.583	72	347	0.83
39	50.857	1.664	36	2	0.05
40	50.864	1.616	18	4	0.18
41	50.865	1.602	82	24	0.23
42	50.855	1.664	112	35	0.24
43	50.832	1.626	19	12	0.39
44	50.844	1.593	19	12	0.39
45	50.850	1.582	1	10	0.91
46	50.819	1.611	17	4	0.19
47	50.818	1.608	35	35	0.50
48	50.822	1.600	11	3	0.21
49	50.823	1.602	618	159	0.20
50	50.821	1.619	14	10	0.42
51	50.823	1.623	25	10	0.29
52	50.819	1.617	45	7	0.13
53	50.820	1.598	32	15	0.32
54	50.821	1.599	31	10	0.24
55	50.797	1.626	24	68	0.74
56	50.795	1.627	3	11	0.79
57	50.800	1.623	14	27	0.66
58	50.799	1.622	0	11	1.00
59	50.784	1.617	16	33	0.67
60	50.797	1.619	4	66	0.94
61	50.797	1.621	3	34	0.92
62	50.798	1.613	17	295	0.95
63	50.791	1.621	21	110	0.84
64	50.799	1.615	5	12	0.71
65	50.797	1.616	0	12	1.00
66	50.799	1.618	0	131	1.00
67	50.797	1.624	1	15	0.94
68	50.799	1.628	2	18	0.90
69	50.793	1.625	7	6	0.46
70	50.791	1.624	9	3	0.25
71	50.808	1.667	8	14	0.64
72	50.826	1.668	19	4	0.17
73	50.851	1.723	148	2	0.01
74	50.855	1.700	68	1	0.01

TABLE 1 Numbers of adult *Lissotriton* newts observed over 105 ponds in the western part of the department Pas de Calais in the 1974 to 2021 period. $F_v = L_v / (L_h + L_v)$ (cont.)

Pond number	Coordinates		Sample size for species		F_v
	Northern latitude	Eastern longitude	<i>Lissotriton</i> <i>helveticus</i> (N)	<i>Lissotriton</i> <i>vulgaris</i> (N)	
75	50.863	1.692	405	1	0.00
76	50.823	1.722	118	27	0.19
77	50.822	1.722	302	302	0.50
78	50.822	1.721	91	78	0.46
79	50.851	1.759	36	4	0.10
80	50.850	1.758	66	10	0.13
81	50.854	1.701	22	0	0.00
82	50.819	1.718	302	218	0.42
83	50.805	1.699	77	0	0.00
84	50.805	1.700	28	0	0.00
85	50.831	1.821	20	0	0.00
86	50.844	1.783	42	27	0.39
87	50.833	1.775	50	14	0.22
88	50.833	1.778	558	46	0.08
89	50.832	1.776	13	3	0.19
90	50.832	1.774	42	8	0.16
91	50.832	1.776	47	4	0.08
92	50.830	1.775	20	2	0.09
93	50.831	1.773	20	12	0.38
94	50.837	1.800	7	5	0.42
95	50.800	1.689	13	14	0.52
96	50.789	1.691	1883	6	0.00
97	50.778	1.679	66	1	0.01
98	50.779	1.659	13	0	0.00
99	50.771	1.666	327	3	0.01
100	50.774	1.673	20	0	0.00
101	50.779	1.606	87	50	0.36
102	50.807	1.690	32	0	0.00
103	50.797	1.688	27	1	0.04
104	50.801	1.690	17	1	0.06
105	50.789	1.690	13	0	0.00

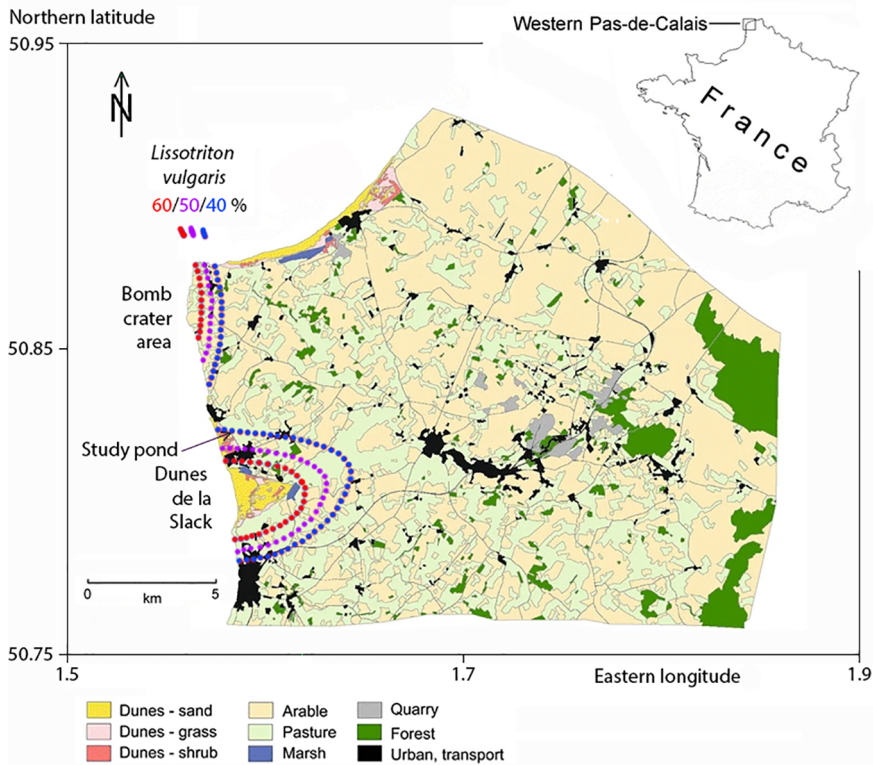


FIGURE 1 Land use map of the study area in the western part of the department Pas de Calais in the northwest of France (see insert), after Curado et al. (2011) and Arntzen et al. (2017). The small-bodied newt species *Lissotriton helveticus* and *L. vulgaris* are frequently syntopic (for data see table 1), but have different strongholds in and outside the 'Dunes de la Slack' and the bomb crater areas, respectively. The partial spatial separation is illustrated by dotted contour lines where *L. vulgaris* is at 60% (red dots), 50% (purple dots) or 40% (blue dots) of the *Lissotriton* total. Note the position of the study pond at the species transition.

SD = 78.8, range 126–367) and eight *L. vulgaris* ($\tilde{N}_{00} = 158.5$, SD = 42.6, range 108–217; the four additional specimens were collected in early spring 1992 at the same locality). The difference between the species in oocyte number is statistically significant (Student *t*-test, $t = 2.74$, $df = 18$, $P < 0.05$).

Population dynamics in the focal pond

Species numbers observed over time are presented in table 2 and population size and capture efficiency estimates are shown in table 3. Total numbers of newts of all three species fluctuated widely with possibly a trend to decline, in line with the pond's

gradually decreasing volume. The estimated capture efficiency ranged from 0.58 in 1988 to 0.91 in 1992. Although the *L. helveticus* population fluctuated over time, there was no long-term change in its overall relative abundance which averaged at about 60% (fig. 2). In contrast, *L. vulgaris* declined while *I. alpestris* increased after 1994. From 1975–1993 *L. vulgaris* was the second most common at around 30%, after which date *I. alpestris* was the more numerous species, also at ca. 30%. Among years with population size estimates, high *L. helveticus* frequencies were observed in the year 1986 at the early spring mortality event and in 1988, 1990, 1992, 1994 and 1995.

TABLE 2 Numbers of adult newts observed in the focal pond near Ambleteuse, Pas de Calais, France

Year	Method	<i>Ichthyosaura alpestris</i>	<i>Lissotriton helveticus</i>	<i>Lissotriton vulgaris</i>
1975	Dipnet	3	31	10
1979	Dipnet	5	47	18
1980	Dipnet	4	68	38
1981	Dipnet	7	118	40
1982	Dipnet	2	15	13
1983 \$	Dipnet	28	363	208
1984	Dipnet	13	172	82
1986 \$	Dipnet	22	226	184
1986 #	Dipnet	23	731	192
1988 \$	Dipnet	29	413	132
1989 \$	Dipnet	100	396	228
1990 \$	Dipnet	24	297	71
1991 \$	Dipnet	71	251	115
1992 \$	Dipnet	19	388	162
1993 \$	Dipnet	44	193	111
1994 \$	Dipnet	26	132	9
1995 \$	Dipnet	91	570	52
2003 \$	Dipnet	98	156	4
2012 \$	Funnel trap	213	426	81
2021	Funnel trap	30	71	12

\$ = for population size estimates see table 3; # = including animals found dead.

Those years are alternated by 1986 after the mass mortality event and 1989, 1991 and 1993, when relatively low *L. helveticus* frequencies were observed.

Discussion

Amphibians are under pressure around the globe from a wide variety of causes of which habitat deterioration is the prime one (Green et al., 2020). In particular pond loss, that terminates the population and weakens the meta-population structure through the increase of dispersal distances, has been implied to negatively affect population survival in theoretical (Halley et al., 1996; Rustigian et al., 2003; Swanack et al., 2009) and empirical studies

(Pope et al., 2000; Joly et al., 2001; Arntzen et al., 2017). It has, however, also been suggested that differential dispersal profiles may rapidly evolve, even over historical times, such as in an invading species (Rollins et al., 2015; Hudson et al., 2016) or in stable versus unstable breeding habitat configurations in landscapes subjected to anthropogenic disturbances (Cote et al., 2017; Cayuela et al., 2020a), to the benefit of species survival.

The inventory of two closely related and morphologically similar species of small-bodied newts, *L. helveticus* and *L. vulgaris*, showed their preponderance in pond-sparse and pond-dense areas, respectively. The *Lissotriton* species in Pas de Calais therewith appear to present a fine working example of the principle of competitive exclusion. While

TABLE 3 Estimates on the total adult newt population size (\hat{N}) composed of *Ichthyosaura alpestris*, *Lissotriton hebeticus* and *L. vulgaris* in the focal pond near Ambleteuse, Pas de Calais, France, by a weighted mean capture-recapture method and a removal method (details see text)

Year	Number of visits	Capture event		Weighted mean		Removal		Different individuals	Capture efficiency		
		First	Last	N̂	SE	N̂	SE				
										95% Confidence interval	
										Lower	Upper
1983	3	06-May	19-May	2828	459.0	840	29.0	789	902	560	0.67
1986	5	28-Mar	13-May	806	93.0	508	27.6	463	572	356	0.70
1986 ^a	6	13-Mar	13-May	1320	93.0	1022	27.6	977	1086	870	0.85
1988	6	18-Mar	22-May	1051	110.1	834	32.5	776	903	482	0.58
1989	2	01-Apr	02-Apr	707	53.7	722	19.6	688	764	530	0.73
1990	2	05-May	06-May	426	45.4	420	15.3	394	454	303	0.72
1991	3	10-May	19-May	493	46.1	404	22.7	455	544	322	0.80
1992	7	21-Mar	10-May	477	33.9	406	12.0	390	438	370	0.91
1993	4	28-Apr	05-May	464	38.9	436	21.6	401	486	319	0.73
1994	4	07-Apr	10-Apr	370	75.6	217	17.3	190	259	142	0.65
1995	4	27-Apr	06-May	950	72.7	667	22.4	631	719	541	0.81
2003	4	13-Apr	26-May	255	47.4	154	9.8	142	181	130	0.84
2012	4	09-Mar	13-Apr	990	75.9	909	37.9	842	991	549	0.60

^aIncluding animals found dead.

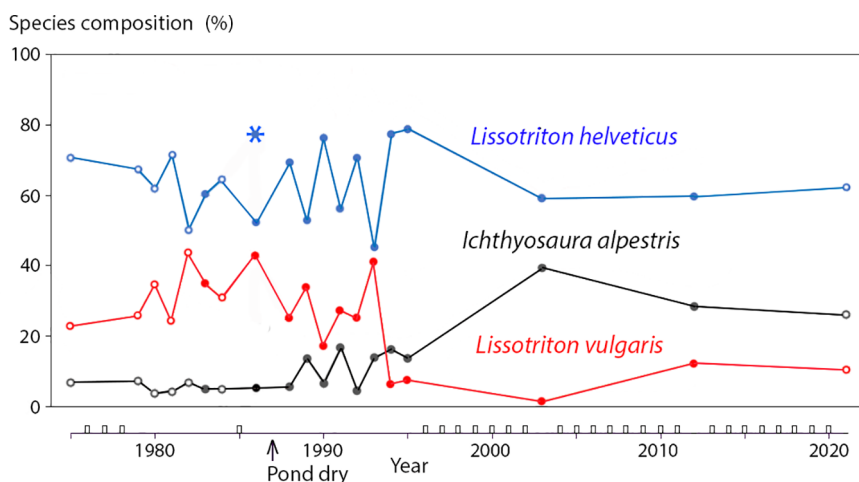


FIGURE 2 Dynamics of the adult newt breeding populations in the study pond, with percentage values over the 1975–2021 period for *Ichthyosaura alpestris* (black), *Lissotriton helveticus* (blue) and *L. vulgaris* (red), with open dots for samples and solid dots for population size estimates (see also tables 2 and 3). Years without observations are marked by open rectangles. The asterisk indicates a hypothetical frequency, on the assumption that the *L. helveticus* cohort that in March 1986 fell prone to a late freezing event (details see text) would have made it to the breeding population.

it might be argued that resources are not in short supply and that *L. helveticus* and *L. vulgaris* are not in competition, a simple thought experiment suggests otherwise. I predict that if *L. vulgaris* was removed from the dunes *L. helveticus* would colonize the vacated ponds. This notion is supported by the wide presence of *L. helveticus* in the coastal dunes of the Vendée, a department located outside but adjacent to the *L. vulgaris* range (Doody, 1991; Groupe herpétologique des Pays de la Loire, 2021). From an evolutionary perspective, a mechanism for limiting competitive exclusion is to adopt alternative life history and dispersal strategies, which are then reinforced through natural selection. This evolutionary process reduces competitive interactions and increases opportunities for colonization in one species and nutrient acquisition in the other, and often operates through catastrophic events (Roxburgh et al., 2004). In view of interspecific competition, we are thus posed with the question if, as theory suggests, *L. helveticus* and *L. vulgaris* differ in life history parameters

such as dispersal strategies and their response to environmental change.

Lissotriton helveticus and *L. vulgaris* show a wide area of range overlap in the west of Europe covering large parts of Scotland, Wales, England, the Netherlands, Belgium, Luxemburg, France and Germany (Sillero et al., 2014). Also at a regional scale, the species mostly show overlap and are regularly found in syntopy (e.g., Zuiderwijk, 1980; Blab & Blab, 1981; Durkin & Cooke, 1984), where they share resources in their aquatic breeding habitat in space, time and food (Griffiths, 1986, 1987). However, disparities exist in terrestrial habitat as well as aquatic habitat preferences (van Gelder, 1972; Cooke & Ferguson, 1975; Cooke & Frazer, 1976; Feldmann, 1981; Geraeds, 2009; Denton, 1991, see also Introduction). In Pas de Calais both species are common and show a marked degree of spatial separation, with *L. vulgaris* prevailing inside, and *L. helveticus* outside the dune and bomb crater areas. The species separation may recently have sharpened, as seen from an analysis of

species-habitat relationships over four decades that showed that *L. vulgaris* became increasingly associated with the dune environment and with well-vegetated ponds such as the bomb craters, whereas *L. helveticus* remained associated with forestation, arable land use and less vegetated ponds (Arntzen et al., 2017). The available knowledge on the species' terrestrial habitat preferences does not readily explain this spatial partitioning. For example, the extend of forestation does not seem to play a role, because locally nothing much changed, as shown by comparing the distribution of woodland on the 18th century maps by the Cassini family (accessible at <https://www.geoportail.gouv.fr/donnees/carte-de-cassini>) with those of the present day (fig. 1; see also Vallauri et al., 2012). Features that both *L. vulgaris* strongholds have in common are a coastal geographical position and a high density of more or less small and often temporary ponds (see also Curado et al., 2011; Arntzen et al., 2017).

A marked spatial separation between the species has also been found in England, possibly related to geology, with soft-water ponds on millstone grit where *L. helveticus* is more common, abruptly transitioning to hard-water ponds on limestone where *L. vulgaris* prevails (Denton, 1991). However, with just presence/absence data available, the sharpness of the species transition is difficult to assess and the question if 'pond density' may play a role in this differential distribution was not tackled. In Pas de Calais hardness of the water was not significantly associated with species composition but given the strength of the association ($0.05 < P < 0.10$) this parameter is a candidate for further investigations, along with salinity that shows a comparable association (supplementary table S1).

Among 91 amphibian species for which maximum observed salinity concentrations were documented (Hopkins & Brodie, 2015),

L. helveticus takes seventh place and *L. vulgaris* takes 13th place. The maximum values are ca. two orders of magnitude higher than what was observed for 28 *Lissotriton* localities in Pas de Calais (supplementary table S1), which would indicate that the local environment poses no restrictions to either species in terms of salinity. An Atlantic climate affecting both species differently is unlikely at the spatial scale concerned so that, in the absence of other clues, pond density is the prime environmental parameter to be considered. It would be instructive to survey other dune areas in Pas de Calais, such as the Dunes d'Amont near Wissant and the Dunes de Hardelot near Hardelot Plage. Another case meriting further investigation is a string of ca. 50 *L. vulgaris* occurrences in the Loire valley, at the very southwestern edge of the species range, amidst an abundance of *L. helveticus* records (Groupe herpétologique des Pays de la Loire, 2021).

The *Lissotriton* species studied are morphologically similar, yet appear to be characterized by different life history parameter values. *Lissotriton vulgaris* thrives and, as seen from their relative numbers, replaces *L. helveticus* in Pas de Calais in two pond-rich areas that are situated in unstable landscapes. The study area was heavily shelled during the Second World War, with no bomb craters visible on aerial photographs of the wider Cap Griz Nez plateau on April 20, 1939 whereas there were thousands on June 12, 1949 (supplementary fig. S3). While most agricultural terrain has since been restored, 12 hectares of pasture remain untreated, with 10–20 craters that are deep enough to keep water up to the summer, at least occasionally. As for the Dunes de la Slack, aerial photography from 1929 onwards reveals a turbulent local history, going from largely barren, due to sand mining and Second World War military activities, to the gradual increase of vegetation. Water

bodies were created for sand extraction, duck hunting, wildlife watering places and, since the turn of the century, for nature conservation. In 1975, 35 amphibian ponds were found in an area of 110 ha. Accordingly, in both areas where *L. vulgaris* dominates, pond density is one or two orders of magnitude higher than in the wider area with a density of 0.01 ponds/ha (Curado et al., 2011; Arntzen et al., 2017) where *L. helveticus* is the more abundant species. Altogether, ca. 73% of amphibian ponds (154 out of 208 in 1975 and 132 out of 186 in 2011) were occupied by one or both *Lissotriton* species (Arntzen et al., 2017). This value is similar to that for *L. helveticus* in the south-east of France, for sections of a study area where pond density is comparably low (≤ 0.02 ponds/ha; Joly et al., 2001). Data from the latter study show that increasing pond densities result in (even) more ponds being occupied, therewith highlighting the role of metapopulation functioning in each of the species that were studied (*L. helveticus*, *I. alpestris* and *T. cristatus*). Population genetic data support the general high connectivity among these newt species' local populations (Jehle et al., 2001; Emaresi et al., 2011; Prunier et al., 2014; Isselin-Nondedeu et al., 2017; Luqman et al., 2018). The present study suggests that high connectivity and dispersal dynamics are features of *L. vulgaris* also, even more so than in its counterpart species and supports the notion (Verrell & Francillon, 1986) that *L. vulgaris* may be an r-selected, colonizing species. Unfortunately, field data on dispersal distances are scarce for amphibians (Smith & Green, 2005; Cayuela et al., 2020b) to which both *Lissotriton* species are no exception (Trochet et al., 2014).

The female fecundity of reproducing *L. helveticus* is about 50% higher than that of syntopic *L. vulgaris*. Data from the literature support the trend for higher oocyte numbers in *L. helveticus* than in *L. vulgaris* (data summarized by Schlüpman & van Gelder, 2004:

812 and Schmidler & Franzen, 2004: 918). Female fecundity is also substantially higher in *L. helveticus* than in its sympatric congener *L. boscai* in the north of the Iberian Peninsula (Brea et al., 2007), suggesting that high fecundity is a feature of *L. helveticus* in particular. One possible corollary is that *L. helveticus*, more frequently than the other species, does not join the breeding population and skips annual breeding opportunities if bodily resources have not been replenished. The observation that *L. helveticus*' contribution to the total newt population shows a spiked pattern, with alternating years of high and low population size following the mortality event in 1986 (figure 2), is in line with this explanation. Clearly, additional research is needed, for example with adults that are individually recognized, either by using pattern-maps or by micro-chip tagging (Arntzen et al., 2004), although it remains to be seen if these techniques are feasible for either species.

Mass mortality events are not rare among vertebrates. Most well-known are evolutionary programmed and disease episodes (Fey et al., 2015; Lamberti et al., 2020) but in amphibians haphazard catastrophic freezing events are also documented (Gill, 1979; Hairston & Hairston, 1987; Schabetsberger & Goldschmid, 1994; Shubin et al., 1995; Cogălniceanu & Hartel, 2005). The loss of ca. two-third of the annual *L. helveticus* breeding population for the study pond in 1986 did not trigger a relative or absolute increase in *L. vulgaris* (fig. 2, table 3). The results are, however, not easy to interpret because the envisaged 'natural field experiment' on the species relative abundance was disturbed straight away by a dry pond with no reproduction in 1987.

The focal pond was chosen for research because of its position in between *L. vulgaris* and *L. helveticus* dominated areas (fig. 1), so that changes in species composition over time might be expected and be tractable. Research

efficacy was high because of large annual total population sizes and reasonably high capture efficiencies (table 3) and although this could not have been foreseen at the start, the pond fortunately persisted till the present day and access remained possible. On the other hand, in some years the research period was fairly long (table 3) so that the assumption of a closed population was challenged. On the long-term, *L. vulgaris* numbers in the study pond have been decreasing and this appears to be associated with local habitat change. The pond has become smaller, more shaded and less vegetated (supplementary figs S1 and S2). This fits the aquatic habitat requirements of *L. helveticus* (Blab & Blab, 1981; de Fonseca & Jocqué, 1982) and that of the third newt species, *I. alpestris* (Feldmann, 1981; Roček et al., 2003; Thiesmeier & Schulte, 2010; van Overstraeten & de Fonseca, 1982) that has taken over the second place. The transition from *L. vulgaris* at 30% (from 1975 to 1993) to *I. alpestris* at 30% (observations in 2003, 2012 and 2021) may represent a 'tipping point' among alternate stable states (Scheffer et al., 1993, Dakos et al., 2019) that are supported by large, open and smaller, shaded pond conditions, respectively. It may though be noted that this concerns a single observation along with a post-hoc explanation. The pond character change and local decline of *L. vulgaris* are paralleled by the area-wide loss of well-vegetated ponds from agricultural land that affects this species more than *L. helveticus* and *I. alpestris* (Curado et al., 2011, Arntzen et al., 2017). Yet, the survey data indicate that *L. vulgaris* may be lingering around at low numbers, providing the species the opportunity to take advantage of changing environmental conditions when these are to arise, such as with the inadvertent pond creation from military activities in the Second World War.

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Supplementary material

Supplementary material is available online at: <https://doi.org/10.6084/m9.figshare.19153097>

References

- Arntzen, J.W. (2002) Testing for equal catchability of *Triturus* newts by dip netting. *Journal of Herpetology* 36, 272–276. [https://doi.org/10.1670/0022-1511\(2002\)036\[0272:TFECOT\]2.0.CO;2](https://doi.org/10.1670/0022-1511(2002)036[0272:TFECOT]2.0.CO;2).
- Arntzen, J.W., Abrahams, C., Meilink, W.M., Iosif, R. & Zuiderwijk, A. (2017) Amphibian decline, pond loss and reduced population connectivity under agricultural intensification over a 38-year period. *Biodiversity and Conservation* 26, 1411–1430. <https://doi.org/10.1007/s10531-017-1307-y>.
- Arntzen, J.W., de Wijer, P., Jehle, R., Smit, E. & Smit, J. (1998) Rare hybridization and introgression in smooth and palmate newts (Salamandridae: *Triturus vulgaris* and *T. helveticus*). *Journal of Zoological Systematics and Evolutionary Research* 36, 111–122. <https://doi.org/10.1111/j.1439-0469.1998.tb00830.x>.
- Arntzen, J.W., Goudie, I.B., Halley, J. & Jehle, R. (2004) Cost comparison of marking techniques in long-term population studies: PIT-tags versus pattern maps. *Amphibia-Reptilia* 25, 305–315.
- Arntzen, J.W. & Zuiderwijk, A. (2020) Sampling efficiency, bias and shyness in funnel trapping aquatic newts. *Amphibia-Reptilia* 41, 413–420. <https://doi.org/10.1163/15685381-bja10004>.
- Begon, M. (1979). *Investigating Animal Abundance*. Edward Arnold. London, United Kingdom.
- Blab, J. & Blab, L. (1981) Quantitative Analysen zur Phänologie, Erfassbarkeit und Populationsdynamik von Molchbeständen des Kottenforstes bei Bonn (Amphibia: Caudata: Salamandridae). *Salamandra* 17, 147–172.
- Boer, P.J. den (1986) The present status of the competitive exclusion principle. *Trends in Ecology and Evolution* 1, 25–28. [https://doi.org/10.1016/0169-5347\(86\)90064-9](https://doi.org/10.1016/0169-5347(86)90064-9).
- Brea, C., Galán, P., Ferreira, R. & Serantes, P. (2007) Datos preliminares sobre la biología reproductora del tritón ibérico (*Lissotriton boscai*) y del tritón palmeado (*Lissotriton helveticus*) en condiciones controladas y naturales. *Munibe* 25, 170–179.
- Cayuela, H., Besnard, A., Cote, J., Laporte, M., Bonnaire, E., Pichenot, J., Schtickzelle, N., Bellec, A., Joly, P. & Léna, J.-P. (2020a) Anthropogenic disturbance drives dispersal syndromes, demography, and gene flow in amphibian populations. *Ecological Monographs* 90, e01406. <https://doi.org/10.1002/ecm.1406>.
- Cayuela, H., Valenzuela-Sánchez, A., Teulier, L., Martínez-Solano, Í., Léna, J.P., Merilä, J., Muths, E., Shine, R., Quay, L., Denoël, M. & Clobert, J. (2020b) Determinants and consequences of dispersal in vertebrates with complex life cycles: a review of pond-breeding amphibians. *The Quarterly Review of Biology* 95, 1–36. <https://doi.org/10.1086/707862>.
- Cogălniceanu, D. & Hartel, T. (2005) Frost induced mass mortality in a high altitude population of *Rana temporaria*. *Froglog* 72, 3–4.
- Cooke, A.S. & Ferguson, P.F. (1975) Is the palmate newt a montane species? *British Journal of Herpetology* 5, 460–463.
- Cooke, A.S. & Frazer, J.F.D. (1976) Characteristics of newt breeding sites. *Journal of Zoology* 178, 223–236. <https://doi.org/10.1111/j.1469-7998.1976.tb06009.x>.
- Cote, J., Bestion, E., Jacob, S., Travis, J., Legrand, D. & Baguette, M. (2017) Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. *Ecography* 40, 56–73. <https://doi.org/10.1111/ecog.02538>.
- Curado, N., Hartel, T. & Arntzen, J.W. (2011) Amphibian pond loss as a function of landscape change—a case study over three decades in an agricultural area of northern France. *Biological Conservation* 144, 1610–1618. <https://doi.org/10.1016/j.biocon.2011.02.011>.

- Dakos, V., Matthews, B., Hendry, A.P., Levine, J., Loeuille, N., Norberg, J., Nosil, P., Scheffer, M. & Meester, L. de (2019) Ecosystem tipping points in an evolving world. *Nature Ecology and Evolution* 3, 355–362. <https://doi.org/10.1038/s41559-019-0797-2>.
- Denton, J.S. (1991) The distribution and breeding site characteristics of newts in Cumbria, England. *Herpetological Journal*, 1, 549–554.
- Doody, J.P. (Editor). (1991). *Sand Dune Inventory of Europe*. Joint Nature Conservation Committee, Peterborough, United Kingdom and The Coastal Union and Leiden, The Netherlands.
- Durkin, J. & Cooke, J. (1984). A study of *T. cristatus* and other amphibians in Northumberland. *The Vasculum* 69: 46–50.
- Emaresi, G., Pellet, J., Dubey, S., Hirzel, A.H. & Fumagalli L. (2011) Landscape genetics of the Alpine newt (*Mesotriton alpestris*) inferred from a strip-based approach. *Conservation Genetics* 12, 41–50. <https://doi.org/10.1007/s10592-009-9985-y>.
- Feldmann, R. (ed.) (1981) Die Amphibien und Reptilien Westfalens. *Abhandlungen aus dem Landesmuseum für Naturkunde zu Münster in Westfalen* 43, 1–161.
- Fey, S.B., Siepielski, A.M., Nusslé, S., Cervantes-Yoshida, K., Hwan, J.L., Huber, E.R., Fey, M.J., Catenazzi, A. & Carlson, S.M. (2015) Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events. *Proceedings of the National Academy of Sciences* 112, 1083–1088. <https://doi.org/10.1073/pnas.1414894112>.
- Fonseca, P. de & Jocqué, R. (1982) The palmate newt *Triturus helveticus helveticus* (Raz.) in Flanders (Belgium). Distribution and habitat preferences. *Biological Conservation* 23, 297–308. [https://doi.org/10.1016/0006-3207\(82\)90086-6](https://doi.org/10.1016/0006-3207(82)90086-6).
- Gelder, J.J. van (1972) Ecological observations on Amphibia in the Netherlands II. *Triturus helveticus* Razoumowski: migration, hibernation and neoteny. *Netherlands Journal of Zoology* 23, 86–108. <https://doi.org/10.1163/002829673X00210>.
- Geraeds, R.P.G. (2009) Vinpootsalamander *Lissotriton helveticus*. Pp. 114–123 in: Creemers RCM, van Delft JJCW (Eds). *De amfibieën en reptielen van Nederland*. Nationaal Natuurhistorisch Museum Naturalis and European Invertebrate Survey. Leiden, The Netherlands.
- Gill, D.E. (1979) Density dependence and homing behavior in adult red-spotted newts *Notophthalmus viridescens* (Rafinesque). *Ecology* 60, 800–813. <https://doi.org/10.2307/1936616>.
- Green, D.M., Lannoo, M.J., Lesbarrères, D. & Muths, E. (2020) Amphibian population declines: 30 years of progress in confronting a complex problem. *Herpetologica* 76, 97–100. <https://doi.org/10.1655/0018-0831-76.2.97>.
- Griffiths, R.A. (1986) Feeding niche overlap and food selection in smooth and palmate newts, *Triturus vulgaris* and *T. helveticus*, at a pond in mid-Wales. *Journal of Animal Ecology* 55, 201–214. <https://doi.org/10.2307/4702>.
- Griffiths, R.A. (1987) Microhabitat and seasonal niche dynamics of smooth and palmate newts, *Triturus vulgaris* and *T. helveticus*, at a pond in mid-Wales. *Journal of Animal Ecology* 56, 441–451. <https://doi.org/10.2307/5059>.
- Groupe herpétologique des Pays de la Loire (2021) Atlas de Amphibiens et Reptiles des Pays de la Loire. Accessible at <https://www.groupeherpetopdl.org/copie-de-cartes-amphibiens-up?lightbox=dataItem-k71xwgmri>.
- Hairston, N.A. & Hairston, N.G. (1987). *Community Ecology and Salamander Guilds*. Cambridge University Press, Cambridge, USA.
- Halley, J.M., Oldham, R.S. & Arntzen, J.W. (1996) Predicting the persistence of amphibian populations with the help of a spatial model. *Journal of Applied Ecology* 33, 455–470. <https://doi.org/10.2307/2404977>.
- Hardin, G. (1960) The competitive exclusion principle. *Science* 131, 1292–1297. <https://doi.org/10.1126/science.131.3409.1292>.
- Hopkins, G.R. & Brodie, E.D. (2015). Occurrence of amphibians in saline habitats: a review

- and evolutionary perspective. *Herpetological Monographs* 29, 1–27. <https://doi.org/10.1655/HERPMONOGRAPHS-D-14-00006>.
- Hudson, C.M., McCurry, M.R., Lundgren, P., McHenry, C.R. & Shine, R. (2016). Constructing an invasion machine: the rapid evolution of a dispersal-enhancing phenotype during the cane toad invasion of Australia. *PloS one*, 11, e0156950. <https://doi.org/10.1371/journal.pone.0156950>.
- IBM SPSS (2021) *IBM SPSS Statistics for Windows, version 28*. IBM Corp., Armonk, New York, USA.
- Isselin-Nondedeu, F., Trochet, A., Joubin, T., Picard, D., Etienne, R., Le Chevalier, H., Legrand, D. & Ribéron A. (2017) Spatial genetic structure of *Lissotriton helveticus* L. following the restoration of a forest ponds network. *Conservation Genetics* 18, 853–866. <https://doi.org/10.1007/s10592-017-0932-z>.
- Jehle, R., Arntzen, J.W., Burke, T., Krupa, A.P. & Hödl, W. (2001) The annual number of breeding adults and the effective population size of syntopic newts (*Triturus cristatus*, *T. marmoratus*). *Molecular Ecology* 10, 839–850. <https://doi.org/10.1046/j.1365-294X.2001.01237.x>.
- Joly, P., Miaud, C., Lehmann, A. & Grolet, O. (2001) Habitat matrix effects on pond occupancy in newts. *Conservation Biology* 15, 239–248. <https://doi.org/10.1111/j.1523-1739.2001.99200.x>.
- Lamberti, G.A., Levesque, N.M., Brueseke, M.A., Chaloner, D.T. & Benbow, M.E. (2020) Animal mass mortalities in aquatic ecosystems: How common and influential? *Frontiers in Ecology and Evolution* 8, 343. <https://doi.org/10.3389/fevo.2020.602225>.
- Lugman, H., Muller, R., Vaupel, A., Brodbeck, S., Bolliger, J. & Gugerli, F. (2018) No distinct barrier effects of highways and a wide river on the genetic structure of the Alpine newt (*Ichthyosaura alpestris*) in densely settled landscapes. *Conservation Genetics* 19, 673–685. <https://doi.org/10.1007/s10592-018-1046-y>.
- Mueller, L. (2019) *Conceptual Breakthroughs in Evolutionary Ecology*. Academic Press. Cambridge, Massachusetts, USA.
- Overstraeten, F. van & Fonseca, P. de (1982) Distribution and habitats of amphibians in the Voerstreek (Provincie of Limburg, Belgium). *Biologisch Jaarboek Dodona* 50, 104–123.
- Pollock, K.H. & Otto, M.C. (1983) Robust estimation of population size in closed animal populations from capture-recapture experiments. *Biometrics* 39, 1035–1049. <https://doi.org/10.2307/2531337>.
- Pope, S.E., Fahrig, L. & Merriam, H.G. (2000) Landscape complementation and metapopulation effects on leopard frog populations. *Ecology* 81, 2498–2508. [https://doi.org/10.1890/0012-9658\(2000\)081\[2498:LCAMEO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[2498:LCAMEO]2.0.CO;2).
- Prunier, J.G., Kaufmann, B., Léna, J.P., Fenet, S., Pompanon, F. & Joly, P. (2014) A 40-year-old divided highway does not prevent gene flow in the alpine newt *Ichthyosaura alpestris*. *Conservation Genetics* 15, 453–468. <https://doi.org/10.1007/s10592-013-0553-0>.
- Rexstad, E. & Burnham, K.P. (1991) *User's Guide for Interactive Program CAPTURE*. Colorado Cooperative Fish & Wildlife Research Unit, Colorado State University, Fort Collins, Colorado, USA.
- Roček, Z., Joly, P. & Grossenbacher, K. (2003) *Triturus alpestris* (Laurenti, 1768) – Bergmolch. Pp. 607–656 in Grossenbacher K, Thiesmeier B (eds.). *Handbuch der Reptilien und Amphibien Europas 4/IIA, Schwanzlurche (Urodela) IIA. Salamandridae ii: Triturus* 1. Aula Verlag, Wiesbaden, Germany.
- Rollins, L.A., Richardson, M.F. & Shine, R. (2015). A genetic perspective on rapid evolution in cane toads (*Rhinella marina*). *Molecular Ecology*, 24, 2264–2276. <https://doi.org/10.1111/mec.13184>.
- Roxburgh, S.H., Shea, K. & Wilson, J.B. (2004) The intermediate disturbance hypothesis: patch dynamics and mechanisms of species

- coexistence. *Ecology* 85, 359–371. <https://doi.org/10.1890/03-0266>.
- Rustigian, H.L., Santelmann, M.V. & Schumaker, N.H. (2003) Assessing the potential impacts of alternative landscape designs on amphibian population dynamics. *Landscape Ecology* 18, 65–81. <https://doi.org/10.1023/A:1022936613275>.
- Schabetsberger, R. & Goldschmid, A. (1994) Age structure and survival rate in alpine newts (*Triturus alpestris*) at high altitude. *Alytes* 12, 41–47. <https://doi.org/10.1111/j.1365-2427.1995.tb00385.x>.
- Scheffer, M., Hosper, S.H., Meijer, M.-L., Moss, B. & Jeppesen, E. (1993) Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution* 8, 275–279. [https://doi.org/10.1016/0169-5347\(93\)90254-M](https://doi.org/10.1016/0169-5347(93)90254-M).
- Schlüpmann, M. & Gelder, J.J. van (2004) *Triturus helveticus* (Razoumowsky, 1789) – Fadenmolch. Pp. 759–846 in Thiesmeier B, Grossenbacher K, (eds.). *Handbuch der Reptilien und Amphibien Europas 4/IIB, Schwanzlurche (Urodela) IIB. Salamandridae iii: Triturus 2, Salamandra. Aula Verlag, Wiesbaden, Germany.*
- Schmidtler, J.F. & Franzen, M. (2004) *Triturus vulgaris* (Linnaeus, 1758) – Teichmolch. Pp. 847–967 in Thiesmeier B, Grossenbacher K, (eds.). *Handbuch der Reptilien und Amphibien Europas 4/IIB, Schwanzlurche (Urodela) IIB. Salamandridae iii: Triturus 2, Salamandra. Aula Verlag, Wiesbaden, Germany.*
- Shubin, N., Wake, D.B. & Crawford, A.J. (1995) Morphological variation in the limbs of *Taricha granulosa* (Caudata: Salamandridae): evolutionary and phylogenetic implications. *Evolution* 49, 874–884. <https://doi.org/10.1111/j.1558-5646.1995.tb02323.x>.
- Sillero, N., Campos, J., Bonardi, A., Corti, C., Creemers, R., Crochet, P.-A., Isailović, J.C., Denoël, M., Ficetola, G.F., Gonçalves, J., Kuzmin, S., Lymberakis, P., Pous, P. de, Rodríguez, A., Sindaco, R., Speybroeck, J., Toxopeus, B., Vieites, D.R. & Vences, M. (2014) Updated distribution and biogeography of amphibians and reptiles of Europe. *Amphibia-Reptilia* 35, 1–31. <https://doi.org/10.1163/15685381-00002935>.
- Smith, M.A. & Green, D.M. (2005) Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? *Ecography*, 28, 110–128. <https://doi.org/10.1111/j.0906-7590.2005.04042.x>.
- Swanack, T.M., Grant, W.E. & Forstner, M.R. (2009) Projecting population trends of endangered amphibian species in the face of uncertainty: a pattern-oriented approach. *Ecological Modelling* 220, 148–159. <https://doi.org/10.1016/j.ecolmodel.2008.09.006>.
- Systat Inc. (2008) MyStat 12. Systat Software Inc., Richmond, California, USA.
- Thiesmeier, B. & Schulte, U. (2010) *Der Bergmolch: im Flachland wie im Hochgebirge zu Hause.* Laurenti-Verlag, Bielefeld, Germany.
- Trochet, A., Moulherat, S., Calvez, O., Stevens, V.M., Clobert, J. & Schmeller, D.S. (2014) A database of life-history traits of European amphibians. *Biodiversity Data Journal* 2, e4123. <https://doi.org/10.3897/BDJ.2.e4123>.
- Vallauri, D., Grel, A., Granier, E. & Dupouey, J.-L. (2012) Les forêts de Cassini. Analyse quantitative et comparaison avec les forêts actuelles. Rapport Technique pp. 65, World Wildlife Fund and INRA, Marseille, France. Available at <https://hal.archives-ouvertes.fr/hal-01267936>.
- Veith, M. & Dorr, L. (1985) Zur Variabilität morphognostischer Artmerkmale in mitteleuropäischen Teich- und Fadenmolch-Populationen, *Triturus vulgaris vulgaris* (Linnaeus, 1758) und *Triturus helveticus helveticus* (Razoumowski, 1789) (Caudata: Salamandridae). *Salamandra* 21, 197–218.
- Verrell, P.A. (1986) Male discrimination of larger, more fecund females in the smooth newt, *Triturus vulgaris*. *Journal of Herpetology* 20, 416–422. <https://doi.org/10.2307/1564504>.

- Verrell, P.A. & Francillon, H. (1986) Body size, age and reproduction in the smooth newt, *Triturus vulgaris*. *Journal of Zoology* 210, 89–100. <https://doi.org/10.1111/j.1469-7998.1986.tb03622.x>.
- Zuiderwijk, A. (1980) Amphibian distribution patterns in western Europe. *Contributions to Zoology* 50, 52–72.