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Spatial heterogeneity in the demography of the critically endangered Montseny brook newt (*Calotriton arnoldi*)

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Abstract. The Montseny brook newt (*Calotriton arnoldi*) is one of the most endangered amphibians in Europe, and most aspects of its biology and population dynamics are little known. We estimated the demographic parameters of the species at two distinct sites encompassing the environmental variability in habitat features by using a capture-recapture Huggins robust design model. Despite the small distribution range occupied by this endemic newt, we found differences in survival, emigration and population size between the two sites. We suggest that these differences may be related to the spatial heterogeneity relative to the hydroperiod, the rocky structure of the streambed, and forest productivity along the streams. However, it is unknown whether the demographic differences may drive different population dynamics and from a conservation point of view, different extinction probabilities.

Key words. Amphibia, Caudata, population size, Spain.

Introduction

During the evolution of the family Salamandridae, a transition from terrestriality to the colonization to lentic aquatic habitats resulted in several species developing a biphasic lifestyle (Veith et al. 2018). Thus, most species of newts spend part of their breeding and feeding periods in ponds and other lentic habitats, even generating particular communities (Maletzky et al. 2004). Demography and population dynamics of lentic newts have received much attention (e.g., Aragon et al. 2000, Jehle & Arntzen 2000, Joly et al. 2001, Jakob et al. 2003, Gamble et al. 2007, Denoel et al. 2018, Cayuela et al. 2020), whereas species occurring in reophilous habitats have remained less studied, probably because they are more difficult to sample (Montori et al. 2008, 2012).

One of the stream-breeding lineages of salamandrids, the genus *Calotriton*, lives in mountain ranges in northeastern Iberia and it was for a long time considered to be monotypic. Comprehensive studies on morphology and genetics eventually led to the description of a new species, the Montseny brook newt (*Calotriton arnoldi* Carranza & Amat 2005), on the southeastern-most limits of the genus' distribution. This newt is a micro-endemic species restricted to the upper Tordera River basin (Biosphere Reserve and Natural Park of Montseny, Catalonia, northeastern Spain), where only seven sites of occurrence have been identified along a total of less of 4.5 km of streams (Amat et al. 2014). The species' range is highly fragmented, which may increase its risk of extinction. More precisely, Montseny brook newts live in two different basins of the second order, which are separated by unsuitable habitat, one to the east of the Tordera River and the other to the west. This fragmention into two distribution areas was dated at 8.000–30.000 years ago (Valbuena-Ureña et al. 2017) and left a genetic and morphological signature, resulting in different colour patterns, body proportions, and genetic isolation (Valbuena-Ureña et al. 2013). Within each evolutionary unit, there is also a critical range fragmentation, leading to complete isolation of the three eastern subpopulations from another one and the others in the western (Amat et al. 2014). Habitat alteration and fragmentation by human activities such as logging, water catchment and forest tracks, combined with the potential impacts of emerging diseases and climate change, are currently threatening the species with extinction. To reverse the status of this Critically Endangered amphibian (Carranza & Martínez-Solano 2009) a EU-Life project is currently ongoing (LIFE15 NAT/ES000757).

Amphibian populations exhibit temporal fluctuations shaped by biotic and abiotic factors, acting either as constrainers or enhancers (Semlitsch et al. 1996, Morrison & Hero 2003). To date, the population ecology of *Calotriton arnoldi* remains poorly studied and the only demographic study conducted until now addressed age structure using skeletochronology and sexual size dimorphism (Amat et al. 2015). To preserve an endangered species such as the Montseny brook newt, it is crucial to estimate their demographic parameters and how they vary with environmental and population dynamic processes. The main goal of our research is to study the demographic parameters of *Calotriton arnoldi* (sex ratio, population size; survival and migration rates), and we discuss the results in the light of the environmental variability across its distribution range.

Material and methods

Population demography was studied in two populations of the Montseny brook newt (*Calotriton arnoldi*) using capture-recapture sampling and modelling. One population was located in the species' eastern portion of the range and was sampled during spring in 2007–2009, covering a stretch of 155 m on the upper reaches of a headwater stream in a beech forest at 1100 m altitude (Fig. 1). The other sampled population belongs to the morphological and genetic lineage living in the western part of the species' range and data were collected in spring (2005), spring and autumn (2006), and autumn (2007) in a stretch of 141 m on the midsection of a headwater stream. Here, the habitat features a tiny riparian forest of common alders (*Alnus glutinosa*) and hazels (*Corylus avellana*) surrounded by oak forest (*Quercus ilex*) at 760 m altitude (Fig. 2). The western population inhabits a Mediterranean habitat at a lower altitude, but the stream runs through a deep gorge facing to the north, which ensures low water temperatures. Conversely, the eastern population occurs at higher altitude in a beech forest, but the gorge faces to the southwest and is exposed to higher solar irradiation that is likely to generate higher water temperatures.

The sampling of Montseny brook newt populations provides numerous pointers that the species has adopted a fossorial lifestyle, and individuals spend most of their time hidden under rocks. Sampling was performed at night when activity is at its highest (as for *Calotriton asper*, Montori 1988): we searched for newts passively (i.e., without removing rocks) and we caught them by hand. Individuals were sexed by assessing the sexual shape dimorphism (Amat el. 2015) and especially the shape of the cloacal region. Females have a tubular and protuberant cloaca that is very distinct from the globular and bulbous cloaca of males, thus allowing ready sexual differentiation. Therefore, specimens without an expression of these traits were considered immature individuals and were not included in our models. Sex ratio was calculated as the proportion of mature males in relation to the total number of adults (Wilson & Hardy 2002).

Newts were marked by injection of a visible implant elastomer (VIE, Northwest Marine Technology, Inc.), using a visual code based on seven points of injection, three in the gular region and four in the abdomen by a combination of colours coded for males and females. Our sampling scheme assumed that populations were closed within each year. This assumption is based on the fact that mortality during the relative short sampling period can be considered negligible, and also because, based on our field experience, *Calotriton* newts are not particularly mobile organisms (Montori 1988, Montori et al. 2008). To confirm this assumption, we ran the closure test (CloseTest pro-

Figure 1. Habitat at the sampled section of the stream inhabited by the eastern population, and typical colour pattern of the eastern newt characterized by yellowish blotches.

gram, Stanley & Burnham 1999), which is a flexible tool for testing the assumption of demographic closure in our analysis of capture-recapture datasets. The tool uses a chi-square test for testing the null hypothesis of a closed-population time model against the alternative open-population Jolly-Seber model. This test is most sensitive to permanent emigration and least sensitive to temporary emigration and is of intermediate sensitivity to permanent or temporary immigration. We used 8- and 9-day sampling secondary occasions to obtain capture probabilities of > 0.20, and to maximize the number of sampling occasions without violating population closure assumptions. We also ran a test that uses a vector with the statistic z-value and p-value for the closure assumption using the CAPTURE program (Otis et al. 1978).

Figure 2. Habitat at the sampled section of the stream inhabited by the western population, and typical colour, and pattern of the western newt characterized by the lack of blotches and the whitish upper labial margin in males.

After assessing the assumption of closed population (see Results), we used a capture-recapture closed population model, the Huggins robust design (Huggins 1989), to estimate demographic population parameters. Modelling was carried out using Mark™ software (White & Burnham 1999). For each sampling session (i, each of the years), the model yields estimates of population size (N_i), apparent survival (ϕ_i), temporary emigration (γ''_i), and temporary immigration (γ'_i), the probability of first capture (p_{ij}), and the probability of recapture (c_{ij}), where j indexes the number of sampling occasions (i.e., days) within a trapping session i (i.e., year). In these models, temporary emigration and immigration refer to individuals that leave or enter the sampled study area, respectively, between sampling occasions. In our case, this was likely occurring at the two extremes of the streams where sampling was performed. Modelling started with the more parameterized model, although the limited number of marked animals precluded us to test for an umbrella model, considering the interaction between factors (time and sex) for all parameters, particularly for the western population (see below). From the starting model, we followed up by reducing the number of factors in survival, then in γ, and finally in capture and recapture parameters. We started with models with γ'' and γ' depending only on sex; we cannot test if γ'' changes with time because i = 3, and these two pairs of parameters $\gamma''_{i-1} = \gamma''_i$ and $\gamma'_{i-1} = \gamma'_i$ are confounded. As a consequence, we tested for Markovian models, because i = 3, and a time model was not feasible for γ'' and γ' (Kendall et al. 1997). Both p_i and c_i were set to change with time and sex although there was a risk of obtaining over-parametrized models. Model selection was performed using the AIC value, and two models were considered a statistic equivalent when the difference in the AIC value was < 2 (Burnham & Anderson 2002).

Results

During the study period, we caught 231 adults (122 males and 109 females) and 6 immature individuals, the latter all in the eastern population (Appendix 1). The number of individuals measured and marked was larger in the eastern population (164 newts, 79 males and 85 females) than in the western population (67 newts, 43 males and 24 females). The estimated sex ratio in the eastern population was 0.52 and 0.48 in the western population. The proportion of males versus females was significantly different from parity only in the western population (Chi-square = 4.891, df = 1, P = 0.026).

The CAPTURE test for closure supported the assumption of a closed population (i.e., no emigration, immigration, births, or deaths during the CMR surveys), and the same support was obtained when using the more robust closure test developed by Stanley & Burnham (1999) (Appendix 2).

For the eastern population, we started with a model focusing on ϕ_i depending on time and sex (Model 1, Ta-

Table 1. Modelling demographic parameters of *Calotriton arnoldi* at the eastern population: The factors considered were sex (s), time (t), session (o); constant parameters are marked "·" and interaction between factors "*". Subscripts in factors denote the occasion i (i.e., the sampling year); only those factors deviating from the previous model are noted in the table. Parameters and statistics: ϕ_i = apparent survival; γ" = temporary emigration; γ' = temporary immigration; p_i = probability of capture; c_i = probability of recapture; ΔAICc = difference of AICc value with the best model; w_i = weight of model i; Np = number of identifiable parameters; Deviation = difference between the log-likelihood of the model and perfect fit. The selected model is in bold.

Model	ϕ_i	γ"	γ'	p_i	c_i	AICc	ΔAICc	w_i	Np	Deviance
1	t*s	s	s	t*s	t*s	1605.720	218.214	0.000	110	1161.534
2				t	t	1437.355	49.850	0.000	59	1209.651
3	s					1432.304	44.799	0.000	57	1211.035
4	·					1429.131	41.625	0.000	56	1211.035
5				o		1402.862	15.356	0.000	32	1253.129
6				t	o	1536.430	148.925	0.000	35	1378.896
7				$t_{1,2}$	t	1424.412	36.906	0.000	51	1221.761
8				t_1		1409.936	22.431	0.000	40	1238.960
9				t_2		1415.597	28.092	0.000	43	1236.279
10				o	t_1	1529.078	141.573	0.000	18	1413.349
11					$t_{1,2}$	1541.980	154.475	0.000	28	1402.354
12				t_1	$t_{1,3}$	1394.595	7.089	0.021	30	1249.956
13				$t_{1=2}$		1397.132	9.626	0.006	31	1249.956
14	s			$t_{1,2}$		1397.889	10.384	0.004	30	1253.251
15	·					1389.859	2.353	0.228	28	1250.233
16		γ"=γ'		t_1		**1387.506**	**0**	**0.740**	**27**	**1250.356**
17				p = c		1515.097	127.591	0.000	5	1427.798

ble 1). This model was largely improved by setting p_i and c_i changing only with time and not with sex (Model 2); this model was further improved when ϕ_i depended only on sex (Model 3); AICc was even lower when ϕ_i was set as constant (Model 4). We tested several models in which p_i and c_i had different combinations of time variations for only some of the sessions k. The best combination was obtained in Model 12, in which $p_{2,3}$ and c_2 were constant (Table 2). We re-introduced the sex in ϕ_i but then AICc increased (Model 13). The "no emigration" model (in which there was no temporal emigration and immigration) did not describe the data properly (Model 14). We also tested a model in which the probability of an individual temporarily emigrating during an interval was the same as the probability of staying away for each sex (i.e., a "random emigration" model): this model was good (Model 15), and it was even improved when sex was not considered in the γ parameters (Model 16). We finally tested if p_i and c_i were equal and compared this model with its equivalent, but with p_i and c_i having the same time-dependent values (Model 3): this model (Model 17) had a higher AIC value and it was not selected. This suggested some type of trap-dependence, owing to $c_i << p_i$ (see Tables 2 and 4) so that this trapping effect was probably due to the manipulation during first capture and subsequent capture shyness. Under the finally selected model (Model 16, Table 1), apparent survival (φ) for the two sexes was estimated at 0.501 (SE: 0.051), and temporal entries and exits at the study site (γ) were estimated at 0.458 (SE: 0.140). Estimates of population sizes showed a trend to decrease over time (Table 2).

In the case of the western population, owing to the low number of animals marked, all parameters in our starting model were set to change only with sex (18 parameters, see Model 1, Table 3). Model selection was very similar to that of the eastern population: the final selected model was the random emigration model with constant γ parameters (Model 11). In this population, apparent survival and temporal movements to leave and to enter the study site were much higher than in the eastern population and estimated at 0.806 (SE: 0.094) and 0.679 (SE: 0.077), respectively (Table 4). Conversely, estimates of population size for the western population were lower than for the eastern population (Table 4). Initial capture probabilities, p_i, changed markedly with sampling occasions and sessions (days and years, respectively) for the eastern population, whereas they were constant for the western population (Tables 2 and 4). Recapture probabilities, c_i, were similar between the two populations and were much lower than initial capture probabilities (Tables 2, 4).

Discussion

Our study provides the first demographic estimates of this poorly known, micro-endemic and Critically Endangered newt (Carranza & Amat 2015). Despite its very small geographic range, its distinct populations experience envi-

Table 2. Estimates of demographic parameters (symbols as in Table 1) and adult population size (N_i) of *Calotriton arnoldi* of the eastern population for the different sessions i and occasions j of the study and each sex. SE: standard error; CI: confidence interval; NE: non-estimable parameter.

Parameter	Sex	Year	Estimate	SE	-95% CI	-95% CI
ϕ_i			0.501	0.051	0.402	0.599
γ			0.458	0.140	0.218	0.719
$p_{2007,1}$		2007	0.029	0.012	0.012	0.066
$p_{2007,2}$		2007	0.131	0.030	0.082	0.202
$p_{2007,3}$		2007	0.139	0.035	0.082	0.225
$p_{2007,4}$		2007	0.161	0.039	0.099	0.253
$p_{2007,5}$		2007	0.193	0.044	0.120	0.295
$p_{2007,6}$		2007	0.299	0.062	0.191	0.434
$p_{2007,7}$		2007	0.255	0.067	0.147	0.406
$p_{2007,8}$		2007	0.611	0.097	0.413	0.778
$p_{2007,9}$		2007	0.689	0.290	0.135	0.969
$p_{2008,1}$		2008	0.084	0.024	0.048	0.146
$p_{2009,1}$		2009	0.248	0.071	0.136	0.413
$c_{2007,1}$		2007	NE	–	–	–
$c_{2007,2}$		2007	0.062	0.059	0.008	0.328
$c_{2007,3}$		2007	NE	–	–	–
$c_{2007,4}$		2007	0.075	0.040	0.025	0.200
$c_{2007,5}$		2007	0.038	0.022	0.011	0.117
$c_{2007,6}$		2007	0.014	0.011	0.003	0.065
$c_{2007,7}$		2007	0.052	0.022	0.022	0.120
$c_{2007,8}$		2007	0.010	0.008	0.002	0.049
$c_{2008,1}$		2008	0.041	0.008	0.028	0.062
$c_{2009,1}$		2009	NE	–	–	–
$c_{2009,2}$		2009	0.047	0.046	0.006	0.270
$c_{2009,3}$		2009	0.030	0.029	0.004	0.181
$c_{2009,4}$		2009	0.052	0.034	0.014	0.176
$c_{2009,5}$		2009	NE	–	–	–
N_i	♂♂	2007	50	2.009	48	59
		2008	47	9.402	37	78
		2009	24	3.829	21	39
	♀♀	2007	53	2.110	51	62
		2008	44	8.881	34	73
		2009	28	4.298	24	44

ronmental spatial heterogeneity (Amat et al. 2014), which may drive the differences we found in their demographic parameters. Remarkably, apparent survival is lower in the eastern population than in the western population, whereas population size follows an opposed pattern. One potential explanation for this is that larger population density increases competition for resources and leads to higher mortality (Harper & Semlitsch 2007). A non-exclusive, alternative explanation may be that permanent emigration in the upper and lower portions of the sampling stretches was different between the two streams, affecting the estimation of local survival. The estimation of demographic parameters in this elusive species is challenging and recapture probabilities were relatively low, which likely affected the uncertainty of demographic parameters. First, newts spend most of their time in the interstitial hypogeum environment of the stream bed. Second, we avoided removing rocks to locate newts to limit the impact of our study, but this likely decreased capture and recapture probabilities. Finally, the physical environment of the two streams was different: the stream bed at the eastern site is covered by rocks and it lacks big and deep ponds, whereas the western population inhabits a succession of very small waterfalls, riffles and well-defined pools. These differences may influence the closure assumptions of the models, which may be different between the two streams.

Despite the potential methodological biases caused by the physical differences between the two streams, environmental spatial heterogeneity may cause real differences between the demographic parameters of the two populations. For instance, the type of forest combined with the inner rocky matrix along the streams may be a relevant driver of that heterogeneity. At the eastern stream, the fully developed deciduous beech forest produces a comparatively larger amount of falling leaves than the oak and tiny riparian forest along the western stream. These falling leaves constitute the main source of allochthonous organic material for the streams that may increase the density of aquatic invertebrates that are preyed upon by newts (Wallace et al. 2015). Prey availability (mostly larval stages of insects and other aquatic invertebrates) in streams running through beech forests could be larger, as it was also recorded for the sister species *Calotriton asper* (Montori 1991, Sánchez-Hernández et al. 2019). The eastern stream also has a greater availability of interstitial microhabitats as refuges, and altogether these differences may result in greater population densities in the eastern population. Mediterranean headwater streams experience abrupt changes in water flow especially in spring when torrential rains can cause the drifting of aquatic salamanders (Romano & Ficetola 2010) but not in *Calotriton* newts (Montori et al. 2008, Montori et al. 2012). It is likely that the characteristics of the inner rocky matrix of streams may affect the ability of newts to cope with this sudden flow increase and impact on their survival. A previous study demonstrated that age structure, longevity and age at sexual maturity were similar between these two populations (Amat et al. 2015). Nevertheless, our results suggest that there are differences in the demography of the two populations.

Montori et al. (2008) indicated that habitat parameters affect the small-scale distribution and abundance of *Calotriton asper* in the streams, and Camarasa et al. (2020) also indicated that environmental factors explain variations in life-history traits. These results agree with our hypothesis according to which differences in habitat would explain the differences in demographic parameters between the two populations of the Montseny brook newt. However, some demographic parameters, like sex-ratio that shows great differences between the two studied populations, seem to be characteristic of the genus *Calotriton*

Table 3. Modelling demographic parameters of *Calotriton arnoldi* of the western population: The factors considered were: sex (s), time (t), session (o); constant parameters are marked "·" and interaction between factors "*". Subscripts in factors denote the occasion i (i.e., the sampling year); only those factors deviating from the previous model are noted in the table. Parameters and statistics: ϕ_i = apparent survival; γ" = temporary emigration; γ' = temporary immigration; p_i = probability of capture; c_i = probability of recapture; ΔAICc = difference of AICc value with the best model; w_i = weight of model i; Np = number of identifiable parameters; Deviation = difference between the log-likelihood of the model observed and perfect fit. The selected model is in bold.

Model	ϕ_i	γ"	γ'	p_i	c_i	AICc	ΔAICc	W_i	Np	Deviance
1	s	s	s	s	s	525.632	28.409	0	18	378.062
2	·					522.549	25.326	0	17	378.062
3		·				519.951	22.728	0.000	16	378.466
4			·			517.762	20.539	0.000	15	379.201
5				o		510.188	12.965	0.001	12	379.962
6					o	505.095	7.872	0.011	9	382.600
7				·		503.380	6.1576	0.025	7	385.736
8					·	499.458	2.235	0.176	5	386.442
9		fixed to 0				503.958	6.735	0.019	5	390.942
10		$\gamma"_s = \gamma'_s$				499.441	2.218	0.177	5	386.424
11		γ" = γ'				**497.223**	**0**	**0.538**	**4**	**386.442**
12		·		$p = c$		504.971	7.748	0.011	3	396.37
13	t*s			·	·	502.258	5.036	0.043	7	384.614

Table 4. Estimates of adult population size (N_i) and other demographic parameters (symbols as in Table 1) in *Calotriton arnoldi* of the western population for the different sessions i of the study and each sex. Estimates were obtained from the selected best capture-recapture model (see Table 3). SE: standard error; CI: confidence interval.

Parameter	Sex	Year	Estimate	SE	-95% CI	-95% CI
ϕ_i			0.806	0.094	0.560	0.931
γ			0.679	0.077	0.513	0.809
p_i			0.200	0.039	0.130	0.284
c_i			0.043	0.009	0.028	0.067
N_i	♂♂	2007	29	3.009	26	40
		2008	24	5.338	18	41
		2009	17	2.656	14	26
	♀♀	2007	17	2.097	16	25
		2008	9	2.756	6	19
		2009	9	1.786	7	16

(Montori & Herrero 2004, Camarasa et al. 2020) and cannot be explained by habitat differences.

Newts inhabiting the eastern stream have a higher occurrence of melanomas (27.7% in the sampled stretch, Martínez-Silvestre et al. 2011), which are absent in the western population. The eastern population is likely more sensitive to the effects of higher temperature due to its exposure and larger habitat alteration by human activities, which may decrease adult survival. Furthermore, the two studied streams markedly differ in their hydroperiod regimes. The eastern stream commonly experiences droughts during summer, which results in the disappearance of most of the surface water, whereas surface water levels in the western stream are more constant and higher throughout the year. Previous studies on a range of different animal species, including amphibians, have revealed that local differences in environmental features may drive differences in ecological and demographic processes (de Neve et al. 2006, Louzao et al. 2008, Korta et al. 2010, Doddington et al. 2013, MacRae & Travis 2014, Senner et al. 2017). On the other hand, the two streams studied here markedly differ in their hydroperiod regimes. With the only exception of unusual rainy summers, the eastern stream experiences droughts during summer, which results in the disappearance of most of the surface water. The Montseny brook newt is an almost fully aquatic species relying on cold and well-oxygenated waters. All future regional climate scenarios project a significant decrease in annual waterflow (from 21% to as much as 67%) and a dramatic increase in the frequency and duration of low-water periods compared to the present reference period (Ledesma et al. 2019). These scenarios, together with other anthropogenic impacts such as pollution and habitat loss, pose a major threat to the species and urge for an evidence-based approach for its conservation. Our study provides the first demographic parameters of the Montseny brook newt, and also shows spatial differences between populations that are subjected to heterogeneous environments. More research is needed to decrease the uncertainty in the estimation of demographic parameters, to assess the influence of environmental factors on vital rates, and to perform a reliable population viability analysis, taking into account the potential impact of the agents of global change on this Critically Endangered micro-endemic species.

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Appendix 1

Number of newts captured and recaptured at least once by population and year.

Population	Year	Captures	Recaptures
Eastern	2007	87	11
	2008	46	14
	2009	34	2
Western	2005	32	9
	2006	24	7
	2007	22	1

Appendix 2

Results of tests for population closure of the two populations of *Calotriton arnoldi*.

	Test for closure	
Population and occasion	CAPTURE (Otis et al. 1978)	Stanley & Burnham 1999
Western population		
2007	z = -0.282, P = 0.389	= 17.689, P = 0.090
2008	z = -0.377, P = 0.353	= 12.498, P = 0.085
2009	z = -0.655, P = 0.256	= 2.804, P = 0.833
Eastern population		
2007	z = -0.235, P = 0.407	= 13.967, P = 0.301
2008	z = -0.561, P = 0.288	= 14.005, P = 0.122
2009	z = -0.399, P = 0.345	= 10.744, P = 0.622