Natural fluctuations in a stream dwelling newt as a result of extreme rainfall: a 21-year survey of a *Calotriton asper* population

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Amphibians living in streams are often subjected to spates. These waterfloods are the main cause of organism drift and mortality, and these effects can be confounded with population decline. Discrimination between population decline and natural fluctuations in unpredictable habitats requires the study of population dynamics through monitoring and long data series. We conducted a 21-year demographic field survey of a newt (*Calotriton asper*) population in the eastern Pyrenees. Our results indicate that the adult population showed high fluctuations in response to heavy rainfall. Maximal rainfall in 24 h (higher than 50 l / m²) caused population decreases as a result of catastrophic drift. The larval population also decreased after heavy rainfall. The data from this survey show that the population recovered three years after catastrophic drift. Subadult *C. asper* show terrestrial activity and are not affected by waterfloods. Interannual dynamics revealed that the stock of subadults allowed for rapid population recovery after catastrophic drift episodes. Flooding produced higher mortality when it occurred during winter than during the active cycle of newts. This long-term study provides new insights into the survival strategies displayed by newts in response to extreme stream environments.

Key words: *Calotriton*; capture-recapture; natural fluctuations; long-term survey; Salamandridae.

Fluctuaciones naturales en un tritón de arroyo como resultado de la lluvia extrema: seguimiento de una población de *Calotriton asper* durante 21 años. Los anfibios que viven en arroyos están sujetos a menudo al impacto de las crecidas. Estas inundaciones son la causa principal de arrastre y muerte de los organismos, pudiendo confundirse estos efectos con declives poblacionales. Discriminar entre declives y fluctuaciones naturales requiere del estudio de las dinámicas poblacionales mediante la monitorización y las series de datos prolongadas. Realizamos un estudio de campo durante 21 años de una población del tritón pirenaico (*Calotriton asper*) en el Pirineo oriental. Nuestros resultados indican que la población de adultos mostró fluctuaciones marcadas como respuesta a las precipitaciones intensas. La precipitación máxima registrada en un periodo de 24 horas (superior a los 50 l / m²) causó un descenso de la población como consecuencia de una avenida catastrófica. La población de larvas también se redujo tras las lluvias intensas. Los datos del presente estudio muestran que la población se recuperó tres años después de la catástrofe. Los subadultos de *C. asper* presentan actividad terrestre y no se ven afectados por las inundaciones. Las dinámicas interanuales revelaron que la reserva de subadultos permitió la rápida recuperación de la población tras las crecidas catastróficas. Las inundaciones causaron más muertes cuando sucedieron en invierno que cuando lo hicieron durante el periodo de actividad de los tritones. Este estudio a largo plazo ayuda a comprender las estrategias de supervivencia que presentan los tritones en respuesta a ambientes extremos.

Key words: *Calotriton*; captura-recaptura; fluctuaciones naturales; Salamandridae; seguimiento a largo plazo.

Organisms inhabiting running waters are frequently exposed to strong changes in hydrological conditions (RESH *et al.*, 1988), downstream drift being one of the most important factors modifying their population structure (LANCASTER *et al.*, 1990; LANCASTER & HILDREW, 1993) and a major cause of individual mortality (THIESMEIER & SCHUHMACHER, 1990; BARRETT *et al.*, 2010). These catastrophic perturbations are expected to produce high mortality rates in natural populations; however, many species and communities living in these habitats seek shelter in benthic refuges, such as stones, debris dams, woody debris or fissures in the rocky riverbed, and thus typically recover quickly from strong hydraulic discharge (BILBY & LIKENS, 1980; LANCASTER *et al.*, 1990; LANCASTER & HILDREW, 1993). It is expected that organisms from habitats exposed to strong temporal alterations will show high population growth rates and are thus resilient in those constantly altered environments (MAY *et al.*, 1974). The relationship between population growth rate and size is crucial to an understanding of population dynamics and the speed at which populations return to equilibrium (near population carrying capacity) after displacement by an external perturbation (MAY *et al.*, 1974; SALVIDIO, 2011).

Amphibians living in running waters exposed to strong changes in hydrological conditions are good candidates to examine temporal population trends and how they recover after perturbations. In fact, amphibians exhibit strong year-to-year population fluctuations (PECHMANN *et al.*, 1991). Given the current trend in population decline and species extinction worldwide (BLAUSTEIN *et al.*, 1994; HOULAHAN *et al.*, 2000; STUART *et al.*, 2004; BEEBEE & GRIFFITHS, 2005), it is sometimes difficult to distinguish population decline from natural fluctuations. Thus deeper knowledge of amphibian demography in natural habitats over time and the analysis of demographic time-series data may allow for detecting true population trends (BLAUSTEIN *et al.*, 1994; REED & BLAUSTEIN, 1995) and ultimate factors that determine amphibian population dynamics (MEYER *et al.*, 1998). Furthermore, BIEK *et al.* (2002) consider that inventory and monitoring efforts should be complemented by demographic studies in order to apply quantitative analyses to a wide range of species and life-history groups. Accordingly, long-term demographic monitoring is required to analyze temporal fluctuations and how populations recover after natural perturbations.

We have examined temporal variation in population trends in the Pyrenean newt *Calotriton asper*, a species highly adapted to running-water habitats. It presents a flattened body, rough skin, lung reduction and horny nails. This newt inhabits clear oxygen-rich mountain streams throughout the Pyrenean Range (MONTORI & HERRERO, 2004), where spates and hydrological fluctuations are common. It is also found in mountain lakes and subterranean water bodies. The habitats occupied by *C. asper* make it vulnerable to water perturbations.

Newt population size was estimated in a Pyrenean stream during a 21-year fieldwork study (from 1982 to 2002). In November 1982, an unusually high rainfall affected the stream and decreased the newt population as a result of drift caused by the spate (MONTORI, 1988; MONTORI *et al.*, 2008). We collected

demographic data over time to determine the natural dynamics of the population, obtain information on the speed at which the population returns to equilibrium after perturbations, and establish the environmental variables that govern the growth and demographic stochasticity of *C. asper* populations. In summary, this long-term study is aimed to examine how climatic events modify population size and to identify newt recovery strategies in response to catastrophic events.

MATERIALS AND METHODS

Study area

The study was carried out since August 1982 till September 2002 in the Pi brook, a stream located in the Cadí range in the Spanish Pre-Pyrenean Mountain Range (Fig. 1). This is one of a series of chains in the Spanish Pre-Pyrenean Mountains that run mostly in parallel to the main Pyrenean axis (Fig. 1). Located in the "Parc Natural del Cadí-Moixeró", the Pi brook (42° 19' 43.17" N; 1° 45' 18.68" E) descends through the Pi Valley from 1700 to 1100 m above sea level,

and then reaches the Segre River. The stream has riffles, waterfalls, pools and canyons, and receives little direct sunlight during the day because of its northern orientation and vertical surrounding hillsides. The average stream depth and width are 30 cm and 2.5 m, respectively. The water temperature varies from 0.2°C in January to 15.4°C in July. Newts occupy a 4-km stretch of the stream at an altitude between 1150 and 1600 m (MONTORI, 1988). This torrent is considered a characteristic habitat of the Pyrenean newt (CLERGUE-GAZEAU & MARTINEZ-RICA, 1978; MONTORI, 1988).

Newt sampling

Newt sampling was conducted during a 21-year field work (1982-2002, see MONTORI, 1988). Newts were collected by visual observation of active individuals in open water and also by turning rocks.

During the first year (August 1982-August 1983), we estimated population size in a 1500-m stretch of stream using capture-mark-recapture techniques. We caught newts along the stretch on a monthly basis over that year.
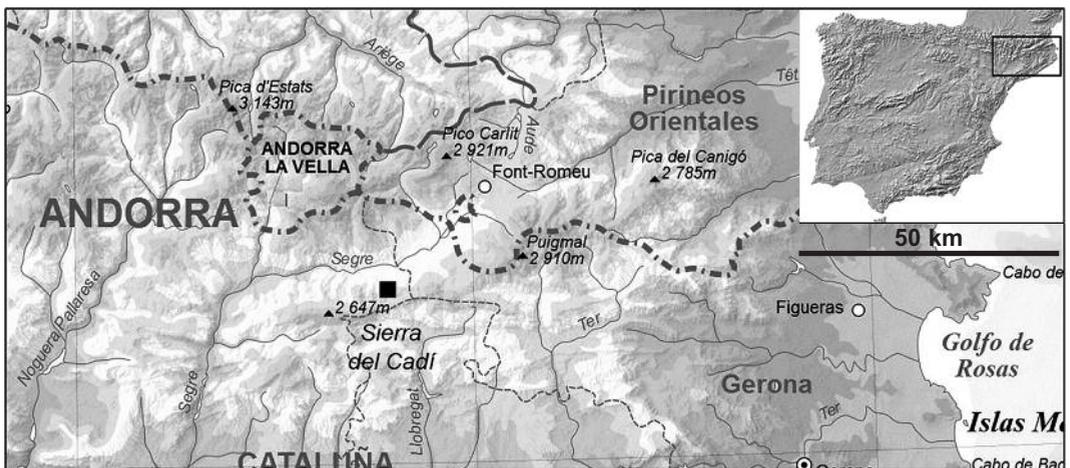

Figure 1: Localization of study stream (Black square).

This intensive method was used to accurately measure population size of *C. asper* in the study area. To maximize marking efficiency, an intensive initial capture was conducted in August 1982. Each newt was marked by toe clipping. No more than one toe per limb (mostly two or three in total) was clipped. Toe-clipping is a standard technique used in amphibian field research. Several studies have found no negative effects of this method (FUNK *et al.*, 2005) and alternative techniques may affect individual survival (e.g. SCHLAEPFER, 1998). MCCARTHY & PARRIS (2004) demonstrated that individual return rates in several frog species were affected only when more than three toes were clipped. Hence, removing two or three toes does not affect newt viability (MONTORI, 1988; MONTORI *et al.*, 2008). After marking the animals, we released them to the same capture or recapture zone. During that period we used beryllium nitrate 0.05 N in order to inhibit toe regeneration (MONTORI, 1988). However, we detected the first regeneration episode in the second study year. For this reason, we stopped the capture-mark-recapture method in 1983 and used transect censuses to estimate annual variation in newt population size thereafter to the end of the study in 2002.

From 1983 to 2002 we surveyed a 150-m stretch within the former 1500-m stretch in order to examine temporal variation in population size over 21 years of fieldwork sampling. This 150-m stretch was subdivided in three 50-m segments in order to obtain three different population size estimations for the 1500-m stream, allowing this procedure to calculate the standard error of mean. These estimations were calculated by comparing the observed abundance of newts in September 1982 with values obtained for each 50-m segment sampled from 1983 to 2002. These three 50-m stretches were chosen on the basis of three conditions: 1) the presence of running water throughout the year, 2) high density of newts, and 3) high density of newts in adjacent segments. To compare inter-annual fluctuations, capture effort was constant along years (i.e. two researchers, same start and end time and zone, and similar hydrological and weather conditions). When meteorological or hydrological conditions changed during the sampling, this survey was excluded and sampling was repeated in the following days.

Estimation of annual population size and statistical analyses

After the first year of capture-mark-recapture fieldwork in August 1982-August 1983, we applied two statistical methods to estimate population size: 1) after the first and second capture-recapture visits in August and September 1982, population size and 95% confidence interval were estimated by Chapman's modification of the Lincoln-Petersen method (CHAPMAN, 1951) for closed populations. Given the low mobility of the species (MONTORI *et al.*, 2008) and the short period between the first and second visits (14 days) we assumed that newt population was closed; 2) for the rest of the year up to August 1983 we used the Jolly-Seber method (JOLLY, 1965; SEBER, 1965) to estimate monthly variation of the number of newts.

The inter-annual population growth rate (R) was defined as $R = \log_e (N_t) - \log_e (N_{t-1})$, where N_t is the number of individuals at time t (BERRYMAN, 1999; SIBLY & HONE, 2002). This demographic parameter provides insight

into whether the population remains constant near its carrying capacity (R = 0), increases (R > 0) or decreases (R < 0) in abundance over time (SIBLY & HONE, 2002).

From September 1983 to September 2002, adult newts and larvae were counted during each annual sampling. Inter-annual balance (BPOP) was estimated as the number of adults in year *i* minus the number of adults in year *i* - 1. Mortality was considered higher than recruitment when BPOP < 0 (population decreases). This assumption assumes that recruitment was offset by natural and waterflow-related mortality, although it is not possible to discern between the proportion of mortality caused by each factor.

A stepwise multiple regression was used to model which climate variables were the best predictors of the number of adult newts and larvae found per year, as well as the inter-annual balance of adult population. For these analyses, the numbers of adults and larvae were log-transformed to linearize regressions.

The following meteorological variables were recorded as they were expected to affect stream hydrology and consequently to influence inter-annual *C. asper* population size variation from 1982 to 2002: annual rainfall, daily thermal oscillation, annual snow, number of days with temperature higher than 30ºC, number of days with temperature lower than -10ºC, number of rainy days, maximal rainfall in 24 h, maximal temperature, minimal temperature, and average temperature. For a census of year *i*, abiotic variables considered for the analysis were those recorded in the previous year (*i* - 1). High scores of the "maximal rainfall in 24 h" variable were used as indicator of unusual or extreme rainfall and waterflow occurrence.

Autocorrelation function (ACF) was used to evaluate periodicity and a partial rate correlation function (ACFP) to detect the feedback dimension in the time series of number of adult newts from 1982 to 2002, number of larvae and inter-annual balance.

An analysis of the variance (ANOVA) was used to compare the mortality of newts related to biological period in which extreme rainfalls occurred (wintering or activity period) using size population balance as a mortality estimator. Wintering in newts occurred approximately between October 15th and March 15th. Analyses were performed with the Statistica software package (StatSoft, Tulsa, Oklahoma, USA).

RESULTS

First-year sampling (August 1982-August 1983)

During the first study period, 1476 adults were captured, marked and released at the place of capture, and 251 newts were recaptured (including multiple recaptures of the same individual). In the study stretch (1.5 km), for the first capture-recapture period (August 1982-September 1982) the estimated population size (mean ± SE) was 4998 ± 948 newts as estimated by the Jolly-Seber method, and 3673 newts (95% confidence interval 3166-4336) as estimated by the Chapman's method (Table 1). Although there was a wide divergence between the two methods, both gave a good indication of the abundance of newts in the stretch sampled.

The unusual rainfall episode in November 1982 (nearly 155 l / m² in one day) produced a severe flood, and the structure of the stream changed drastically, with a dramatic decrease in newt population (Fig. 2). The estimated survival from September 1982 to April 1983 was 0.263.

Table 1: Population size estimations by means of Jolly-Seber and Chapman's modification of the Lincoln-Petersen method in the 1.5 km of brook. n_i: number of newts captured at time i. r_i: number of newly marked newts released at time i. m_i: number of newts recaptured at time i. y_i: number of newts marked at time i and recaptured at time i + 1. N_i: estimated adult population size. Φ_i: survival rate from time i - 1 to time i. B_t: net number of individuals entering the population between samplings. SE: standard error. CI: confidence interval. NC: not calculable because of data structure.

Date	n_i	r_i	Aug 82	Sep 82	Apr 83	May 83	Jun 83	Jul 83	m_i	y_i	Mean	SE	95% CI	Mean	SE	B_t
					Date of last capture							N_i			Φ_i	
Aug 82	724	724								183						
Sep 82	546	438	108						108	41	4998	948		0.263	0.069	389
Apr 83	75	59	11	5					16	12	1561	472		0.754	0.206	-146
May 83	88	62	17	5	4				26	9	975	237		1	-	18
Jun 83	80	51	18	7	2	2			29	7	905	249		0.923	0.301	329
Jul 83	95	67	15	6	3	3	1		28	14	1091	310		NC	-	NC
Aug 83	119	75	13	10	6	4	7	4	44		2317	1327		0.004	0.037	-88
Chapman's modification of the Lincoln-Petersen method											3673		3166-4336			

(left margin label: Jolly-Seber estimation)

After the flood, the number of newts decreased and successive monthly surveys (between March and August) did not show a quick population recovery to the number of newts caught in September 1982 (Table 1), even though the capture effort was constant throughout the study period. From July to August 1983, the number of individuals increased as a result of the incorporation of terrestrial subadults into the torrent upon reaching sexual maturity (immature newts of this species have a terrestrial period until sexual maturity, Fig. 3).
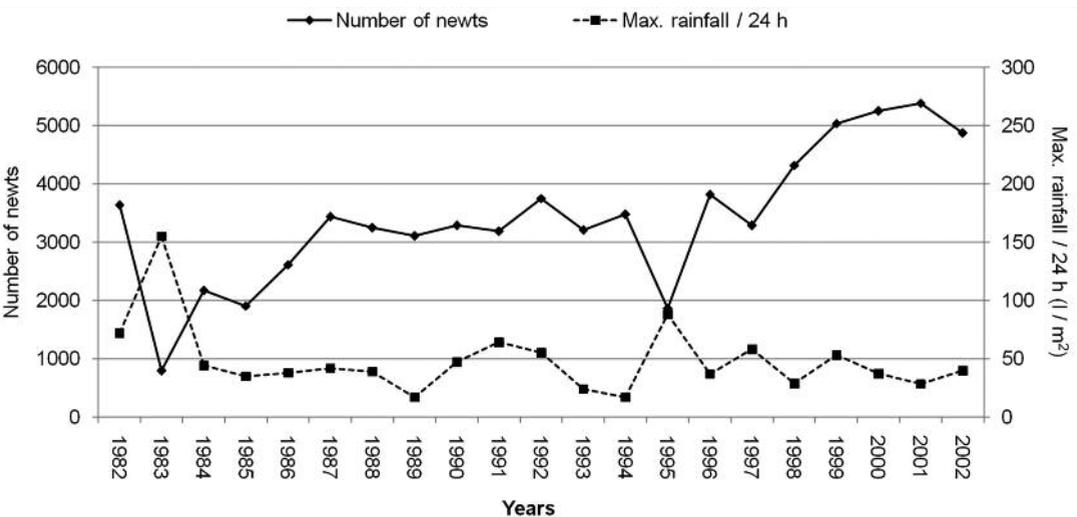
Figure 2: Population size of *Calotriton asper* at the Pi stream (solid line, rhombuses) estimated by transects from 1982 to 2002 and maximal rainfall in 24 h (broken line, squares) occurred before the censuses. R = - 0.539, *P* < 0.01171, overall standard error of the estimation: 1006.5.
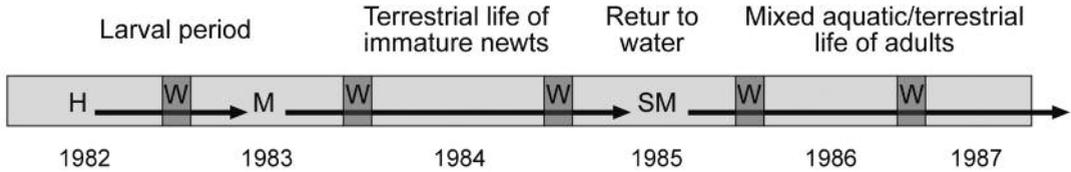
Figure 3: Biological cycle of *Calotriton asper* at the Pi stream in their first five years of life. H: hatching. W: wintering. M: metamorphosis. SM: sexual maturity.

1982-2002 sampling

The annual surveys from 1982 to 2002 also showed a significant decrease in the number of individuals after the sampling in 1982 as a result of the spate that happened in November 1982 (Table 2). In 1984, the number of newts increased as recently matured newts returned to the aquatic environment (Fig. 3). As in 1982, another episode of extreme rainfall followed by high newt mortality occurred in 1994. After both perturbations, the newt population showed rapid recovery: three years after the 1982 and 1994 floods (Fig. 2). The mean estimated

Table 2: Data used in the study. %M: percentage of males. LV: number of larvae. NPOP: estimated population size. SE: standard error. BPOP: balance of population size between years. RMAX24: maximal rainfall in 24 h (l / m²). DTO: daily thermal oscillation (ºC). GS: snow grams. NDT+30: number of days with temperatures above 30ºC. NDT-10: number of days with temperatures below -10ºC. NRD: number of days with rain. RTOT: total annual rainfall (l / m²). TMAX: maximal year temperature (ºC). TMIN: minimal year temperature (ºC). TAVG: annual average temperature (ºC).

Year	%M	LV	NPOP[a]	SE	BPOP	RMAX24	DTO	GS	NDT+30	NDT-10	NRD	RTOT	TMAX	TMIN	TAVG
1982	43.8	1	3673			72.0	11	251	4	0	140	1203	32	-12	8.1
1983	44.0	4	793	125	-2844	155.0	15	98	2	5	109	766	31	-19	9.2
1984	50.8	3	2172	341	1379	44.0	9	117	0	0	131	935	29	-14	7.4
1985	45.0	15	1905	207	-266	35.0	15	102	0	4	122	766	29	-20	8.5
1986	38.5	26	2611	210	706	38.0	12	154	2	1	139	781	31	-16	8.4
1987	46.9	36	3437	136	826	42.0	14	125	2	4	148	1100	32	-15	8.6
1988	55.1	11	3244	129	-193	39.0	10	119	0	4	146	789	29	-17	8.5
1989	60.6	19	3104	53	-140	17.0	6	106	0	0	132	877	30	-12	9.1
1990	51.5	24	3284	142	180	47.0	9	137	0	0	150	1089	29	-15	8.8
1991	66.4	4	3184	74	-100	64.0	10	136	0	0	131	770	30	-16	8.2
1992	51.3	18	3750	280	566	55.0	5	176	0	0	151	1308	28	-11	8.2
1993	51.0	46	3204	263	-546	24.0	11	106	1	0	128	774	31	-11	8.0
1994	49.7	55	3474	422	270	17.0	18	177	1	0	140	1012	39	-14	9.5
1995	57.3	1	1866	172	-1608	88.0	12	105	1	1	147	951	31	-12	8.5
1996	56.7	7	3811	684	1945	37.0	12	192	0	2	164	1373	30	-14	7.6
1997	51.4	20	3283	215	-528	58.0	8	131	0	0	147	1039	29	-13	9.3
1998	49.7	45	4317	278	1034	28.8	10	105	0	0	127	778	30	-12	8.8
1999	52.5	44	5036	537	719	53.0	11	125	0	6	143	1105	29	-16	8.4
2000	54.4	60	5250	324	214	37.2	8	62	0	0	140	947	29	-14	8.9
2001	51.5	54	5385	779	135	28.4	10	70	4	5	122	840	32	-10	8.9
2002	51.5	10	4868	829	-517	39.8	9	58	1	0	152	822	30	-6	8.4

[a] Estimation of 1982 made by the Chapman's method (see Table 1). Estimations from 1983 to 2002 made by contrast with the 1982 value.

inter-annual population growth rate (R) calculated after the 21-year surveys was close to zero (0.0063), thereby indicating that the newt population remained near its carrying capacity.

The ACF used to evaluate periodicity and the ACFP did not detect significant periodicity in annual population estimated from the 1982 to 1992 series.

Abiotic factors determining population size

The explained variances of the stepwise multiple regression analyses were higher than 60% and showed that the variable "maximal rainfall in 24 h" was negatively correlated with the three dependent variables: number of adults, number of larvae and inter-annual population balance (Table 3). Besides, a set of climatic variables were included in the final stepwise models as predictors of the three population parameters (see Table 3 for variables included in the final steptwise models). The intercept of the regression between the population balance and the maximal annual rainfall in 24 h was close to 50 l / m^2 in such period (Fig. 4). We consider that rainfall over this amount may produce a negative population balance. Mortality was higher when extreme rainfall (higher than 50 l/ m^2) occurred during the wintering period than when it happened during newt activity period (ANOVA: $F_{1,18} = 11.801$; $P = 0.0029$) (Fig. 5).

Table 3: Multiple regression summary for three dependent variables (Log of number of adults, Log of number of larvae, inter-annual population balance). Bold values are significant. All variables contributing to increase the R^2 of the model are displayed, regardless of their statistical significance. Variable names are summarized in Table 2.
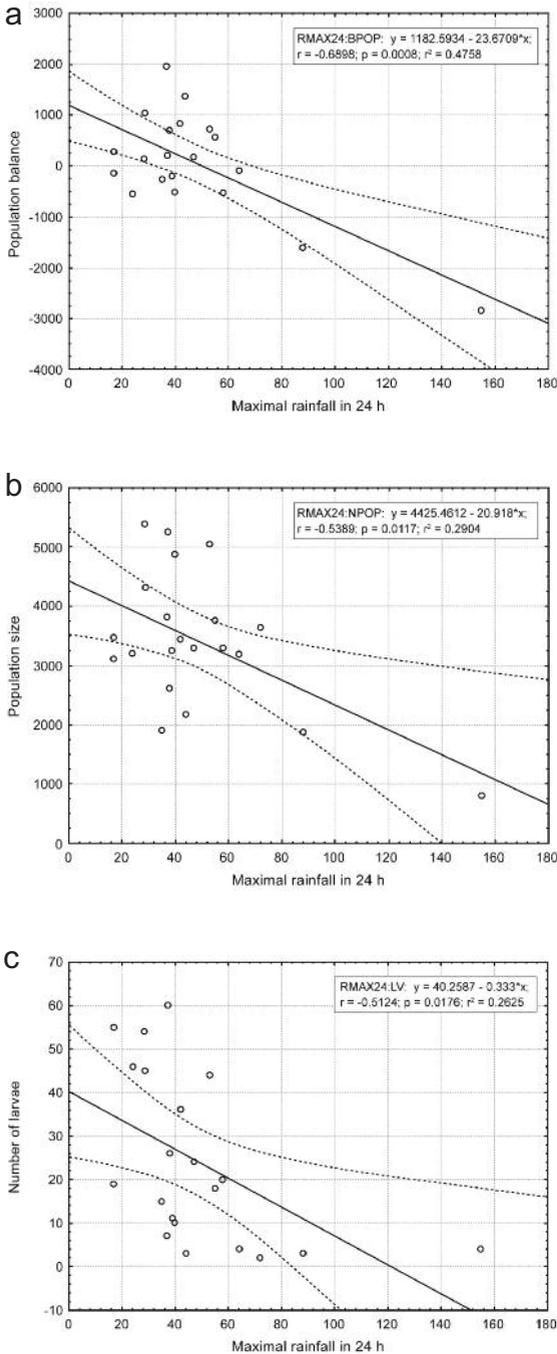
|	Adults					Larvae					Population balance				
	Variable	Beta (SE)	B (SE)	t^a	P	Variable	Beta (SE)	B (SE)	t^a	P	Variable	Beta (SE)	B (SE)	t^a	P
Selected variables	Intercept		3.85 (0.20)	19.16	<0.001	Intercept		-2.08 (1.07)	-1.95	0.068	Intercept		3556.01 (2300.79)	1.55	0.138
	RMAX24	-0.62 (0.14)	0.00 (0.00)	-4.30	**0.001**	**RMAX24**	-0.70 (0.14)	-0.01 (0.00)	-4.87	**<0.001**	**RMAX24**	-0.70 (0.13)	-23.85 (4.34)	-5.50	**<0.001**
	TMIN	0.35 (0.17)	0.02 (0.01)	2.08	0.059	**TAVG**	0.49 (0.14)	0.44 (0.13)	3.48	**0.003**	**RTOT**	0.39 (0.12)	2.20 (0.69)	3.20	**0.006**
	RTOT	0.23 (0.14)	0.00 (0.00)	1.70	0.112	NDT-10	0.25 (0.14)	0.06 (0.03)	1.75	0.10	**TAVG**	-0.32 (0.12)	-623.25 (235.59)	-2.65	**0.018**
	NDT-10	0.25 (0.16)	0.02 (0.01)	1.55	0.140						TMIN	-0.20 (0.13)	-64.74 (41.03)	-1.58	0.143
	DTO	0.25 (0.27)	0.05 (0.05)	0.91	0.394										
Model adjustment	R	0.8537				R	0.8190				R	0.8902			
	R^2	0.7287				R^2	0.6708				R^2	0.7924			
	Adjusted R^2	0.6383				Adjusted R^2	0.6127				Adjusted R^2	0.7370			
	Std. Error	0.11340				Std. Error	0.29545				Std. Error	0.53295			
	F	8.059				F	11.545				F	14.314			
	d.f.	5.15				d.f.	3.17				d.f.	4.15			
	P	0.00073				*P*	0.00023				*P*	0.00005			

^{a}d.f. = 10

DISCUSSION

The two methods to estimate population size during the first sampling year showed considerable divergence in newt population in September 1982 (4997 and 3673 from Jolly-Seber and Chapman methods, respectively). However, both estimators coincided in indicating the high abundance of newts in the 1.5-km stretch of brook.

Our results indicate that maximal rainfall in 24 h (over 50 l / m²) is the main factor influencing newt dynamics. Despite this high newt density, periodic floods in the stream due to extreme rainfall produced marked inter-annual fluctuations in population size. The rapid population recovery detected after floods suggests that this species is highly adapted to survive in running-water habitats affected by periodic and severe floods. Demographic effects of extreme rainfall episodes producing catastrophic drift and high population decline, mainly of larvae, has

Figure 4: Linear regression adjust (± 95% confidence interval) of maximal rainfall in 24 h with (a) inter-annual population balance, (b) estimated population size, and (c) number of larvae. See table 2 for abbreviators.
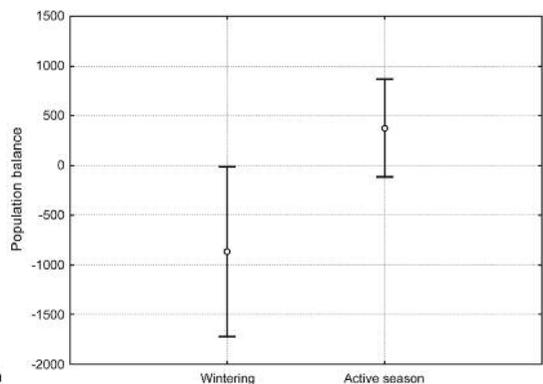
Figure 5: Inter-annual population balance when rainfall occurs during wintering or during the active cycle. Boxes indicate standard error and bars indicate standard deviation of the mean.

been observed previously (MÜLLER, 1954; PETRANKA & SIH, 1986; BARRET et al., 2010). For example, PETRANKA & SIH (1986) analysed the survival rate of *Ambystoma texanum* larvae in relation to various biotic and abiotic factors and reported that up to 90% of young larvae do not survive to periods of high waterflow.

We detected a negative relation between abundance of *C. asper* larvae in the Pi Valley and maximal rainfall in 24 h. These waterflows cause high larval mortality, thereby reducing population recruitment as they determined the number of adult newts present in the stream in subsequent years. Similar findings have been reported by BARRETT et al. (2010) who concluded that the frequency and magnitude of waterflows, which then lead to decreased larval density, were the best descriptors to explain stream salamander decline in urban areas. Moreover, experimental data support that spate frequency (which was highly correlated with spate magnitude) was the best predictor of salamander density across an urban-rural stream gradient (BARRETT, 2009; BARRETT et al., 2010). These examples suggest that salamanders cannot maintain their position in the stream during high flows and that recolonization after subsidence of intensive flows is low. In addition, THIESMEIER (1992) demonstrated that stream dwelling species like *C. asper* or the fire salamander *Salamandra salamandra* drifted less than pond species (e.g. *Triturus* spp).

THIESMEIER & SCHUHMACHER (1990) observed a catastrophic drift of larval *S. salamandra*. Drift of the youngest larvae was determined by the behaviour of spawning females and by stream conditions, whereas the largest larvae

drift occured when their retreats became too small to provide an adequate food supply. However, the *C. asper* population is not food-limited in the Pi Valley stream (MONTORI, 1991, 1992). BAUMGARTNER et al., (1999) used field data to argue that larval *S. salamandra* preferred lower current speeds within a given stream, as they found fewer specimens in streams with higher mean stream discharge.

Other authors have documented species that are susceptible to spates; however, those studies were performed largely in the context of hydrological changes that occur with increasing stream order (DUDGEON, 1993; BAUMGARTNER et al., 1999; LEIPELT, 2005). For example, LEIPELT (2005) used artificial streams to evaluate the response of four species of Odonata to a high-flow stream environment. In that study, the two species most susceptible to drift were found in lower order streams that were less prone to spates. This author interpreted these findings as evidence that hydrological factors shape species distribution and survivorship. Collectively, these studies support the notion that spate frequency and / or magnitude influence the abundance and distribution of stream organisms. Extreme rainfall produces changes in the bed structure and in the bank morphology of streams. However, in a previous study (MONTORI et al., 2008) we demonstrated that the distribution pattern of newts along the stream was not influenced by these structural changes associated with spates.

Thus the question remains as to how *C. asper* maintains or recovers population levels in habitats frequently affected by severe waterfloods. During the 1982-2002 sampling, we recorded two episodes of extreme rainfall, in

1982 and 1994. After these episodes, increased waterflow produced high mortality; however, the population recovered rapidly, despite being a species with a small clutch size if compared to other European newt species (CLERGUE-GAZEAU, 1971; MONTORI, 1988, 1992; MONTORI & HERRERO, 2004). In fact, population quickly recovered values similar to those observed before the flood. This observation is attributed to the fact that subadults are almost exclusively terrestrial until sexual maturity (MONTORI & HERRERO, 2004). Hence, subadult *C. asper* would act as a population stock to facilitate population recovery in a few years after waterfloods. As spates are common in stream environments, this recovery strategy would allow this species to overcome these catastrophic episodes. The findings of our 1982-2002 sampling are consistent with this explanation: the number of newts severely decreased the first year after each catastrophic drift, whereas in the second year the return of sexually mature subadults produced a parallel increase in the population. The decrease in numbers observed in the third year after the flood can be explained by the absence of recruitment as those larvae that should have reached sexual maturity died during the drift caused by the spate. This pattern was observed in the two occasions when extreme rainfall was registered. The hypothesis of a population recover by means of upstream dispersal can be rejected from the results of a previous study demonstrating that no upstream or downstream movements occur in this population (MONTORI *et al.*, 2008).

These data verify for the first time the relevance of the terrestrial life period of newts for the recovery of populations in unpredictable aquatic environments frequently affected by extreme rainfall. In this regard, it is particularly important to determine whether the increases in extreme rainfall caused by climatic change predicted by some authors (BATES *et al.*, 2008) would produce higher vulnerability and risk of extinction for *C. asper* stream populations. Interestingly, mortality was higher when extreme rainfall occurred during the overwinter period than during the activity period. This result indicates that during the active cycle, *C. asper* has developed behavioural strategies to avoid waterflow drift. In fact, MONTORI (2008) reported that Pyrenean newts predict waterflows, although the exact mechanism by which they do this is unknown. According to the field observations made by CLERGUE-GAZEAU & MARTÍNEZ-RICA (1978), in running waters, when a spate starts, newts leave refuges and move to banks where water velocity is lower. In periods of high waterflow, there are observations of newts leaving the water (MONTORI, 2008). These behavioural strategies are not displayed in winter as newts are buried in stream banks.

In conclusion, our findings further demonstrate the adaptability of Pyrenean newts to extreme environments, such as mountain streams where climatic conditions plus periodic waterflows may preclude the dynamic of amphibian species and the presence of richer amphibian communities.

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