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Variation in the reproductive strategies of *Salamandra salamandra* (Linnaeus, 1758) populations in the province of Gipuzkoa (Basque Country).

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Abstract

Fire salamander [*Salamandra salamandra* (Linnaeus, 1758)] populations show variability in their reproductive strategies across the northern Iberian Peninsula. Females can give birth to aquatic larvae (ovoviviparous mode), to metamorphosed juveniles (viviparous mode) or to both aquatic and metamorphosed juveniles (intermediate mode). The reproductive modes of the populations inhabiting the Basque Country are poorly studied. The objective of this preliminary study was to examine the reproductive strategies of four fire salamander populations, belonging to the subspecies *S.s.fastuosa*, in the province of Gipuzkoa, Basque Country. The main focus was on an urban population inhabiting the park Mount Urgull in San Sebastián. The other three populations were located in forested mountain areas. Eighteen pregnant female salamanders were captured and kept in the laboratory until they gave birth. Females captured in the Urgull population gave birth, either to metamorphosed juveniles, or to metamorphosed juveniles and aquatic larvae. However, due to the lack of water bodies in Urgull, the fire salamanders are mostly viviparous. Two females from the other populations also gave birth to metamor-phosed juveniles and aquatic larvae, which suggests that the populations may have intermediate reproductive mode. The results of this study confirm that there can be intrapopulational variation in the reproductive modes of the *S.s.fastuosa* and that the intermediate (and maybe the viviparous) mode might be more common than previously thought in Gipuzkoa.

• Key words: *Salamandra salamandra fastuosa*, fire salamander, reproductive strategies, viviparity, ovoviviparity.

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RESUMEN

En el norte de la Península Ibérica las poblaciones de salamandra común [*Salamandra salamandra* (Linnaeus, 1758)] muestran variabilidad en sus estrategias reproductivas. Las hembras pueden parir tanto larvas acuáticas (modo ovovíviparo), como juveniles metamorfoseados (modo vivíparo), así como ambos, a la vez larvas y juveniles (modo intermedio). Estas estrategias apenas han sido estudiadas en las poblaciones que habitan el País Vasco. El objetivo de este estudio preliminar era examinar los modos de reproducción utilizados por cuatro poblaciones de salamandra común, pertenecientes a la subespecie *S.s.fastuosa*, en la provincia de Gipuzkoa, País Vasco. El principal foco se puso en la población urbana que habita el monte Urgull, en San Sebastián. Las otras tres poblaciones se localizan en áreas boscosas de montaña. Dieciocho hembras grávidas de salamandra fueron capturadas y mantenidas en el laboratorio hasta que parieron. Las capturadas en la población de Urgull expulsaron sólo juveniles metamorfoseados o tanto juveniles como larvas acuáticas. Sin embargo, debido a la ausencia de masas de agua en Urgull, las salamandras allí serían principalmente vivíparas. Dos hembras de las otras poblaciones también parieron larvas y metamórficos a la vez, lo que sugiere que estas poblaciones tendrían el modo intermedio de reproducción. El resultado de este estudio confirma la existencia de variaciones intrapoblacionales en la estrategia reproductora de *S.s.fastuosa* y apunta a que en Gipuzkoa el modo intermedio de reproducción (y tal vez el vivíparo) sería mucho más común de lo que se pensaba anteriormente.

• PALABRAS CLAVE: *Salamandra salamandra fastuosa*, salamandra común, estrategias reproductoras, viviparismo, ovoviviparismo.

LABURPENA

Iberiar Penintsularen iparraldean bizi diren arrabio arrunten [*Salamandra salamandra* (Linnaeus, 1758)] populazioek ugaltzeko estrategia ezberdinak erabiltzen dituzte. Emeek larba urtarrak erditu ditzakete (modu obobibiparoa) edo metamorfoseaturiko gazteak (modu bibiparoa), baina baita larbak zein jubenilak ere batera (erdibideko modua). Euskal Herriko populazioen ugalketaren inguruan, aldiz, oso informazio eskasa dago. Atariko ikerketa honen helburua Gipuzkoan (Euskal Herria) dauden arrabio arruntaren (*S.s.fastuosa* azpiezpeziekoak) lau populazioren ugaltzeko estrategiak aztertzea zen, Donostiako Urgull mendian bizi den hiriko populazioan arreta berezia jarriz. Gainontzeko hiru populazioak inguruko mendietako basoetan daude. Hemezortzi arrabio eme ernari harrapatu eta laborategian egokitu ziren erditu zuten arte. Urgullen atzemandakoek metamorfoseatu gazteak edo metamorfikoak eta larba urtarrak erditu zituzten soilik. Aitzitik, Urgullen ur-masarik ez dagoenez, gehienak bibiparoak lirateke. Beste tokietako bi emek ere metamorfoseatuak eta larbak batera erditu zituzten. Horrek populazio horietan erdibideko ugalketa-modua, behintzat, ageri dela erakusten du. Ikerketaren emaitzak *S.s.fastuosa* populazioen baitan ugal-estrategia ezberdinak badirela eta Gipuzkoakoetan ugaltzeko erdibideko modua eta, beharbada, bibiparoa, uste baino zabalduago dagoela baieztatzen du.

• GAKO-HITZAK: *Salamandra salamandra fastuosa*, arrabio arrunta, ugaltzeko estrategiak, bibiparismoa, obobibiparismoa.

Introduction

The fire salamander, *Salamandra salamandra* (Linnaeus, 1758) (Amphibia; Caudata), shows a great variation in many aspects of its biology, such as size, colouration as well as in its reproductive strategies (García-París *et al.*, 2004). Ovoviviparity, meaning that females retain the developing embryos in their oviducts and give birth to aquatic larvae, is the most common and ancestral mode of reproduction of the species. In some fire salamander populations, however, females give birth to fully metamorphosed terrestrial juveniles, and the free-living aquatic larval stage is absent. This so-called viviparous reproductive mode (following terminology used in Alcobendas *et al.*, 1996) is characterized by an early hatching of embryos within the maternal oviducts, accelerated developmental rate of embryos and larvae feeding on unfertilized eggs and less-developed siblings within the oviducts of the females (Dopazo & Alberch, 1994; Buckley *et al.,* 2007). Besides these two reproductive modes, there are populations that have intermediate modes: females give birth to larvae at an advanced stage of development or to both aquatic larvae and metamorphosed juveniles (Dopazo & Alberch, 1994; Alcobendas *et al.*, 1996).

Ovoviviparous reproductive mode is found in the entire distribution range of the fire salamander. In contrast, viviparous and intermediate reproductive modes are known to occur only in northern populations across the Iberian Peninsula, almost exclusively in the subspecies *S.s.bernardezi* and *S.s.fastuosa* (García-París *et al.*, 2003), the former having mainly viviparous populations and the latter showing more variation in its reproductive modes having ovoviviparous, viviparous as well as intermediate populations (Joly, 1968; Dopazo & Alberch, 1994). These two subspecies are found in the Cantabrian and Pre-Pyrenean region. In addition to their reproductive mode, they differ from other subspecies by their smaller adult size and colouration pattern characterized by yellow stripes instead of spots and patches (García-París *et al.*, 2004). García-París *et al.* (2003) suggested that viviparity evolved once in an isolated lineage in the Cantabrian Mountains and then spread across populations of these two subspecies. A recent study (Velo-Antón *et al.*, 2007a), however, has shown that two island populations belonging to the subspecies *S.s.gallaica* in Galicia also have a viviparous reproductive mode suggesting that viviparity has evolved at least twice in the species and that the transition from ovoviviparity to viviparity might develop in a relatively short time (Velo-Antón *et al.,* 2012).

The variability of reproductive strategies found in the fire salamander is an infrequent phenomenon among vertebrates, and the factors behind this variation are not fully understood. Giving birth to fully terrestrial offspring allows fire salamanders to cope with environments lacking suitable water bodies. However, populations with viviparous or intermediate reproductive modes are also known to occur in habitats with water bodies apparently suitable for

reproduction (Dopazo & Alberch, 1994; Velo-Antón *et al.*, 2007a; 2012). In these environments, giving birth to fully terrestrial juveniles or to aquatic larvae at an advanced developmental stage may be favourable, for example, due to the unpredictability of the hydroperiod as the offspring are completely independent or less dependent on the water bodies (Velo-Antón *et al.*, 2007a). Furthermore, intermediate reproductive mode is found in contact zones of viviparous and ovoviviparous populations (Galán, 2007), which might be due to a gene flow between populations with distinct reproductive modes (Dopazo *et al.*, 1998).

The Basque Country harbours populations of *S.s.fastuosa*. Reproductive strategies of the salamander populations are poorly studied in this region. Ovoviviparity is thought to be the most common mode because salamander larvae are common in many small streams and ponds (X. Rubio, pers.obs.). An earlier study, however, has demonstrated that there may be intrapopulational variation in the reproductive strategies of *S.s.fastuosa* (Dopazo & Alberch, 1994). This means that in populations where aquatic larvae are commonly observed some females might give birth to metamorphosed juveniles. The intermediate and viviparous reproductive modes may often be overlooked because births of the metamorphosed juveniles are difficult to observe.

In this preliminary study we examined the reproductive strategies of four *S.s.fastuosa* populations in the province of Gipuzkoa, Basque Country. The main focus was on an isolated urban population inhabiting the park Mount Urgull in Donostia-San Sebastián. Due to the lack of surface water bodies suitable for the reproduction the population was expected to be viviparous but this had never been confirmed. In the other three populations, our aim was to examine whether the populations are strictly ovoviviparous or show variation in their reproductive strategies. If different reproductive modes are observed in *S.s.fastuosa* populations over this relatively small geographical area it could offer an interesting scenario to study microevolutionary processes related to the variation in reproductive strategies.

Materials and methods

The study was carried out in four fire salamander populations in the province of Gipuzkoa (Basque Country), in the northern Iberian Peninsula. Mount Urgull is an urban park located by the sea and next to the old town of Donostia-San Sebastián (43°19'15 N, 1°59'92 W; Fig. 1). Originally, it was an island, formed hundreds of thousands of years ago, and during its history it has been periodically connected to the mainland following changes on the sea level. Approximately 5000 years ago Urgull became connected to the continent as a result of accumulation of sediment carried by the Urumea River (Edeso, 2010), after which, there may have been a connection between the fire salamander

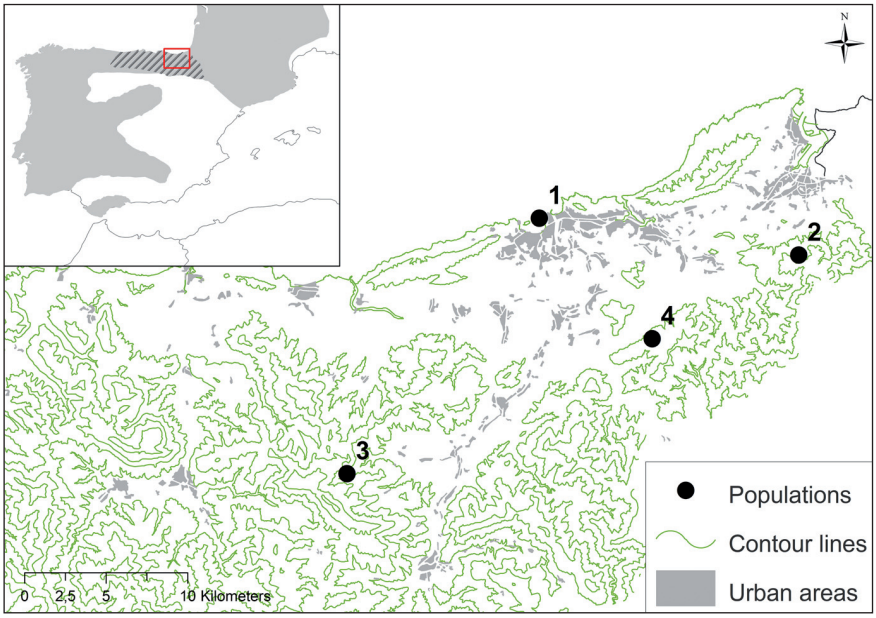

Fig. 1.- The locations of the four populations of the study. 1=Urgull, 2=Aiako Harria, 3=Asteasu, 4=Landarbaso. In the small map, location of the study area (red box) and the distribution ranges of *S.salamandra* (grey) and the subspecies *S.s.fastuosa* (dark grey diagonal stripes) in the Iberian Peninsula are shown

Fig. 1.- Localización de las cuatro poblaciones de estudio. 1=Urgull, 2=Aiako Harria, 3=Asteasu, 4=Landarbaso. En el mapa pequeño, localización del área de estudio (recuadro rojo) y la distribución de *S.salamandra* (gris) y la subespecie *S.s.fastuosa* (bandas diagonales gris oscuro) en la Península Ibérica.

population of Mount Urgull and the mainland populations. The urbanization of the city of San Sebastián in the second half of the 19th century led to the current isolation of the population of Mount Urgull because the city is a barrier impossible for salamanders to pass. Distance to the nearest fire salamander populations inhabiting other urban parks of the city is at least 1.5 km.

The other three populations (Aiako Harria, Landarbaso and Asteasu) were located in forested mountain sites within a 20 km radius from Mount Urgull (Fig. 1) and at altitudes between 200 and 500 metres. In the Aiako Harria population, females lay aquatic larvae into a small pond and streams on granitic bedrock; in the other two populations, females use small streams on limestone bedrock to deliver the larvae.

Captures of salamanders were carried out in Mount Urgull from February to April 2009 and from September to December 2010, and in the other three populations between November 2010 and May 2011, at nights with elevated humidity and mild temperatures. In total 30 (15 from Mount Urgull, 6 from Aiako Harria, 3 from Landarbaso, 6 from Asteasu) females considered being pregnant

based on the size and form of their abdomen were captured and taken to the laboratory where they were photographed, weighed with a digital scale (0.1 g) and their snout-vent length (SVL) was measured to the nearest millimetre. The females were kept in the laboratory in plastic boxes (40 x 35 x 25 cm) containing soil, moss and stones as well as a plastic tray (15 x 15 x 4 cm) filled with water. They were fed with earthworms once a week. The females were released to the site of capture two weeks after they had given birth to the last offspring. The offspring born in the laboratory were weighed, their SVL was measured and they were examined for gill presence in order to know their developmental stage. Offspring were released with their mothers.

RESULTS

Nine females from the Urgull population gave birth in the laboratory (Table 1). Five of them gave birth only to metamorphosed juveniles, while four females had both metamorphic and larvae. There was high variation in the number of offspring per female, the total number of offspring (larvae and juveniles) ranging from 2 to 29 (Table 1). Also, the size of the metamorphosed juveniles varied among females (Table 1; Kruskal-Wallis test: H=39.91, df=8, p<0,001).

Nine females from the three other populations also gave birth in the laboratory (Table 1). Two females from Aiako Harria population gave birth only to aquatic larvae. In contrast, there was some variation in the developmental stages of the offspring belonging to the females of the Landarbaso and Asteasu populations. One female from Landarbaso population gave birth to fully metamorphosed and larval juveniles, another one to aquatic larvae some of which were very large and at a late developmental stage, and a third female had aquatic larvae of relatively equal size. Three females of the Asteasu population gave birth to aquatic larvae, and one female to larvae and metamorphosed juveniles.

The number of offspring per female varied between 16 and 29 in the Asteasu population, between 16 and 32 in the Landarbaso population and between 17 and 46 in the Aiako Harria population (Table 1). The mean SVLs of the aquatic.

Table 1.- Births in the laboratory. The snout-vent length (SVL) of the females, the parturition period indicated as the number of days between the first and last day of observed deposit of offspring, the number of offspring born as metamorphs and larvae, and the SVL and weight of the offspring. U=Urgull, AH=Aiako Harria, As=Asteasu, L=Landarbaso. ►

Tabla 1.- Partos en el laboratorio. La longitud hocico-cloaca (SVL) de las hembras, el periodo de parto indicado como el número de días entre el primer y último día en el que se obsservó deposición de recién nacidos, el número de individuos nacidos como metamóficos y larvas y el SVL y peso de los recien nacidos. U=Urgull, AH=Aiako Harria, As=Asteasu, L=Landarbaso.

Population	Female SVL	Parturition period (days)	nº larvae/ metamorphs	Larvae SVL mean±SD (min-max)	Larvae weight mean±SD (min-max)	Metamorphs SVL mean±SD (min-max)	Metamorphs Weight mean±SD (min-max)
U	99,75	1	0/2			22,62 ± 2,28 (21,00-24,23)	0,40 ± 1,14 (0,3-0,5)
	97,87	1	0/14			23,76 ± 1,42 (19,77-26,15)	0,57 ± 0,08 (0,4-0,7)
	88,66	3	19/5	no data	no data	19,09 ± 0,99 (18,34-20,21)	0,23 ± 0,04 (0,2-0,27)
	77,23	6	4/9	no data	no data	20,58 ± 2,00 (17,66-22,54)	0,29 ± 0,08 (0,2-0,38)
	89,72	1	0/11			22,38 ± 0,50 (19,08-25,12)	
	87,08	1	0/6			24,23 ± 0,92 (22,61-24,84)	0,37 ± 0,03 (0,34-0,42)
	89,21	1	0/6			24,58 ± 1,17 (22,93-26,03)	0,41 ± 0,09 (0,29-0,57)
	105,07	5	3/26	no data	no data	24,77 ± 1,23 (22,33-27,48)	0,46 ± 0,08 (0,35-0,60)
	92	21	7/8	21,00 ± 0,58 (20-22)	0,37 ± 0,06 (0,29-0,47)	22,25 ± 1,49 (20-24)	0,45 ± 0,01 (0,33-0,58)
AH	89	5	17 / 0	21,00 ± 1,25 (18-23)	0,28 ± 0,05 (0,19-0,36)		
	99	7	46/0	19,00 ± 1,00 (16-21)	0,23 ± 0,04 (0,16-0,36)		
AS	116	1	23 / 5	21,76 ± 0,83 (20-23)	0,30 ± 0,03 (0,25-0,36)	21,80 ± 0,45 (21-22)	0,28 ± 0,03 (0,25-0,32)
	96	2	16/0	21,31 ± 0,70 (20-22)	0,38 ± 0,04 (0,29-0,44)		
	97	16	29/0	21,37 ± 1,34 (19-24)	0,37 ± 0,01 (0,25-0,60)		
	104	8	29/0	20,50 ± 0,71 (19-21)	0,39 ± 0,04 (0,33-0,42)		
L	92	5	9/7	21,56 ± 1,23 (20-23)	0,36 ± 0,04 (0,28-0,41)	21,40 ± 1,17 (20-23)	0,35 ± 0,04 (0,30-0,41)
	96	40	32/0	20,00 ± 1,15 (19-22)	no data		
	90	4	18/0	21,00 ± 1,53 (18-24)	0,49 ± 0,16 (0,26-0,72)		

larvae from females of the three populations were quite similar, approximately 20-22 mm, with the exception of the larvae of one female from the Aiako Harria population that gave birth to 46 larvae that were of smaller size on average than the larvae of the rest of the females (Table 1). The observed deliveries lasted less than one week for most of the females, but two females gave birth to a few offspring at a time during a period of 40 and 21 days (Table 1).

Discussion

Females from the Urgull population gave birth either to metamorphosed juveniles or to both metamorphosed juveniles and larvae. This suggests that the population has both viviparous and intermediate reproductive modes. The latter, however, is a maladaptive strategy because aquatic larvae are not likely to survive in Urgull given that there are no water bodies. Parturitions of aquatic larvae might have been premature, caused by the stress the females suffered when being captured and held in captivity. This is likely to be the case for the female that gave birth to 19 aquatic larvae and 5 metamorphs since delivery took place on the night of the capture. Same phenomenon of premature births in captivity has been observed in another study on *S.salamandra* carried out in Galicia (Velo-Antón *et al.*, 2007b). On the other hand, the current isolation of the Urgull population is relatively recent, and earlier the population might have been connected to areas with water bodies suitable for laying larvae. Thus, it is possible that some females from Urgull give birth to aquatic larvae because the population is not yet fully adapted to the lack of water bodies.

There was a great variation in the number of offspring per female in the Urgull population. However, as the observed parturition period of two females lasted from three weeks to over a month, it is possible that some females had already given birth to some offspring before being captured. This could explain part of the observed variation. At any rate, the number of offspring for viviparous females of the Urgull population was observed to range from 2 to 14, which is similar to the number of offspring observed in other viviparous fire salamander populations (Buckley *et al.*, 2007; Velo-Antón *et al.*, 2007a).

Viviparity in the population of Urgull might have evolved as an adaptation to the lack of water bodies suitable for aquatic larvae. In the fire salamander, the transition from ovoviviparity to viviparity may happen fast, especially if there is a strong selection pressure favouring offspring born as metamorphs (Velo-Antón *et al.,* 2012). However, considering that García-París *et al.*, (2003) suggested that viviparity in the *S.s.bernardezi* and *S.s.fastuosa* subspecies has a single origin in the western Cantabrian Mountains and a posterior expansion towards the Pyrenees, it may be more likely that the individuals that colonized Urgull

originated from viviparous or intermediate populations. There is little information about the reproductive modes of the fire salamander populations in the proximity of Urgull; there are only some observations of larvae in small streams on the adjacent Mendizorrotz mountain range (Azpiroz, 2009; X. Rubio pers.obs.). Genetic studies comparing the Urgull population with nearby populations should be carried out in order to understand better the origin of viviparity in the Urgull population.

Our results suggest that the Asteasu and Landarbaso populations have both intermediate and ovoviviparous reproductive strategy, as one female from both populations gave birth to metamorphosed juveniles, and some of the aquatic larvae were born at an advanced developmental stage. In addition, larvae were larger and the number of offspring per female lower than those observed in strictly ovoviviparous populations of the species (*e.g.* Buckley *et al.*, 2007; Galán, 2007). Moreover, there was a considerable variation in the sizes of the offspring belonging to the same clutch which is characteristic to viviparous and intermediate reproductive modes in the fire salamander (Dopazo & Alberch, 1994; Buckley *et al.*, 2007). Buckley *et al.* (2007) suggest that the differences in sizes are caused by intraoviductal competition that promotes acceleration of larval developmental rates as the faster developing larvae have access to more nutrition in the form of unfertilized eggs and smaller siblings and, thus, are more likely to survive than the slower growing larvae. It should be noted, however, that the number of females giving birth in the laboratory was very low for the Asteasu, Landarbaso and Aiako Harria populations, and therefore, more observations are needed to confirm their reproductive strategies.

The results of this study support the findings of an earlier study (Dopazo & Alberch, 1994), which showed intrapopulational variation in the reproductive strategies of the *S.s.fastuosa* populations. Thus, the intermediate mode (and maybe the viviparous mode as well) might be more common than previously thought in the fire salamander populations of Gipuzkoa. Further studies are needed to understand the pattern of variation in the reproductive strategies of the *S.s.fastuosa* populations in this relatively small geographical area and the factors explaining this variation.

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