Variation in sexual dimorphism between two populations of the Pyrenean salamander *Euproctus asper* from ecologically different mountain sites

Jordi Serra-Cobo [1], **Franz Uiblein** [2] **and Juan Pablo Martínez-Rica** [1]

[1] **Instituto Pirenaico de Ecología (CSIC), Avda. Montañana, 177. Apdo. 202. E-50080 Zaragoza, Spain**
[2] **Institute of Zoology, University of Salzburg, Hellbrunnerstr. 34, A-5020 Salzburg, Austria.**

ABSTRACT. Morphological variation and ecological characteristics of habitats of two populations of the Pyrenean salamander *Euproctus asper* from the Flumen river, Prepyrenees, and the Salto del Pis torrent, Central Pyrenees, were studied to determine whether intraspecific differences in body form and sexual dimorphism occur and if they can be functionally related to ecological differences between the two study sites. While the Flumen river was found to be characterized by a Mediterrenean-influenced moderate mountain climate and high eutrophication, the Salto del Pis torrent represents a typical alpine habitat with long winters accompanied by snow cover, frequent avalanches, and short, mostly cool summers. Uni- and multivariate comparisons were performed on 12 size-adjusted measures of body form and weight from a total of 85 living specimens, grouped according to sex and geographic origin. Major differences were found mainly in those characters that manifest sexual dimorphism, such as head size, tail length, tail depth, leg length, and body weight. Sexual dimorphism was more strongly expressed in the Central Pyrenean population where females showed longer tails and smaller heads, while males had more robust tails and higher body weights compared with the Flumen population. Based on ecomorphological considerations and previous genetic studies, we argue that geographic divergence in sexual dimorphism of the Pyrenean salamander reflects longterm evolutionary adaptations in response to increased selection pressures favouring high reproductive efficiency and reduced intersexual competition under alpine, high-mountain climate conditions.

KEY WORDS: Urodela, mountain climate, morphometrics, body size, reproduction.

INTRODUCTION

Sexual dimorphism facilitates mate choice based on traits that signal fitness. Sex-specific, conspicuous morphology, colouration, or behaviour may advertise good health, good condition, and reproductive advantage. Sexual dimorphism may also allow reduction of intraspecific competition through resource partitioning mediated by differential ecological, morphological, or behavioural specializations between the sexes. Larger body size in one sex, for instance, may indicate sexual selection for this trait by the other sex or may result from intersexual competition for certain food resources. If two populations live in ecologically different areas, geographic differences in sexual dimorphism may occur due to ecological constraints on sexual selection or competition (Selander, 1966; Dobson & Wigginton, 1996; Frafjord & Stevy, 1998).

Recent investigations of fishes, amphibians, reptiles, and birds have emphasized that between geographically separated populations climatically induced differences in reproductive seasonality (Uiblein *et al.*, 1998), thermal ecology (Navas, 1996), morphology (Brown *et al.*, 1991; Landmann & Winding, 1995), and resource partitioning with other species (Serra Cobo *et al.*, 1998) may occur. Different climatic conditions may also influence the degree of sexual dimorphism in body size, as has been recently shown in North American bobcat and European fox populations (Dobson & Wigginton, 1996; Frafjord & Stevy, 1998). However, sexes often differ not only in body size, but also in other traits that may be influenced by distinct ecological factors including site-related cli-

Corresponding author: Franz Uiblein, e-mail: franz.uiblein@sbg.ac.at

mate conditions. One species of particular interest in this respect is the Pyrenean salamander *Euproctus asper* (Dugés, 1852). This species lives in climatically different areas in the Pyrenees and in several geographically separated localities along the northern and southern margins of the major distribution area in brooks, lakes, springs, and aquatic caves at altitudes between ca. 200 and 3000 m (Martínez-Rica & Clergue-Gazeau, 1977; Clergue-Gazeau & Martínez-Rica, 1978; Serra-Cobo *et al.*, 1998). The Pyrenean salamander usually shows marked sexual dimorphism, with males having larger and more robust bodies with larger heads and cloacal tubes and shorter tails than females. In various earlier studies morphological differences were found between populations of the Pyrenean salamander from climatically different sites in the Pyrenees and isolated areas in the Spanish Prepyrenees (Martínez-Rica, 1980; Gasser & Clergue-Gazeau, 1981). Furthermore, in specimens from the Central Pyrenees the occurrence of melanism was reported (Serra-Cobo, 1989).

Here we investigate two populations of the Pyrenean salamander from two climatically different sites, the Flumen river in the Prepyrenees and the Salto del Pis torrent in the Central Pyrenees (Fig. 1). A short ecological characterization of the two sites is followed by a uni- and multivariate comparison of the two populations separated into four groups according to sex and geographic origin. Furthermore, the presence or absence of melanism was recorded in the two populations.

Geographical variation between populations may concern not only sexually dimorphic features, but also traits that are common to both sexes. The following questions were considered: (1) Do populations of *Euproctus asper* from different geographical sites differ in morphometric characters, and to what extent does this concern sexual dimorphism? (2) Is this morphological variation functionally related to ecological differences between the two sites?

MATERIAL AND METHODS

Study sites

The study area of the Prepyrenean population is situated in the upper Flumen river in the Sierra de Bonés about 60 km south of the central chain of the Pyrenees (42º20'N, 0º26'W) at an altitude of 1250 m. The other study site is located in the Salto del Pis torrent, below a waterfall in the upper river Ara valley near the Ordesa and Monte Perdido National Park (Central Pyrenees, 42º43'N, 0º08'W) at an altitude of 1520 m.

Between March and July in 1995-1997 both localities were visited repeatedly. To compare the ecological conditions between the two sites, measures of temperature, pH, and water velocity were performed on the same visiting days within an interval of a few hours. Water velocity was measured by a current meter that was positioned 5 cm above the bottom at selected places with reliable water flow throughout the study season. Measures of conductivity, dry residuals, and the concentrations of Mg^{++}, Ca^{++}, Na+, K+, Cl-, CO_3H-, and NO_3- were also obtained. The latter analyses were done in the Instituto Pirenaico de Ecología using EDTA titration, flame photometry and colorimetric techniques.

Study of newts and measures obtained

For the morphometric measurements 85 *Euproctus asper* with total lengths between 87.2 and 116.6 mm were captured by hand at the two sites. Forty seven specimens from the Flumen river consisting of 25 males and 22 females, and 38 specimens from the Salto del Pis torrent consisting of 20 males and 18 females were measured immediately after capture, and then released at the collecting sites. This method did not cause any observable harm to the animals. In the Flumen river, all specimens were collected at one date, whereas two visits to the Salto

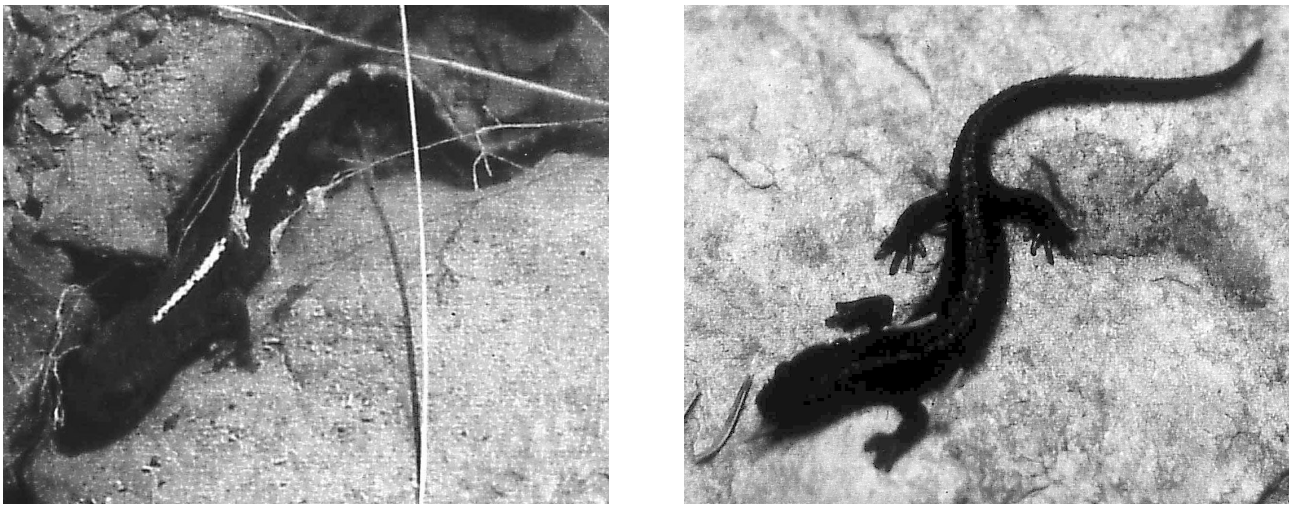

Fig.1. – Black-and-white photographs of two males of the Pyrenean salamander *Euproctus asper* from the Salto del Pis river, Central Pyrenees. The specimen on the left has a grey body with a contrasting yellowish dorsal band. The specimen on the right shows melanism with a entirely black body.

del Pis torrent were necessary. To avoid repeated observations of the same specimens, only the measures obtained from the males collected during the first visit and those from the females collected during the second visit were used for the subsequent comparison.

The following 13 measures were obtained (with abbreviations in brackets and followed by explanations where necessary): total length (TL); tail length (TAL): distance between the hind margin of the cloacal tube and the tip of the tail; maximum tail depth (TD); head length (HL); maximum head width (HW); maximum interorbital distance (IBE): distance between hind corners of the eyes; internasal distance (IN); minimum interorbital distance (IFE): distance between anterior corners of the eyes; eye length (EL); foreleg length (FLL): distance between the forward leg basis and distal extreme of the third finger; finger length (TF): length of third finger of forward leg; cloacal tube length (CL); total weight (W).

All morphometric measures were size-adjusted by performing log-log regressions with TL. Body weight was adjusted by calculation of the cubic roots followed by regression with log TL. All regressions were strongly correlated ($n=85$, $r > 0.28$) and highly significant ($p < 0.01$). The residuals of the regressions were subjected to a one-way ANOVA for determining possible differences among character scores. Tukey test was used to perform multiple comparisons among four groups, Flumen males (Fm), Flumen females (Ff), Salto del Pis males (Pm), and Salto del Pis females (Pm). To determine combined sets of variables with maximal separation among individuals belonging to the different groups, canonical variates analysis (CVA) was carried out. One-way ANOVA followed by Tukey test was used to examine the four groups for possible differences in the character scores produced by CVA.

Additional observations concerned the start of the reproductive period, i.e. the first date when amplexus formation was observed in either population. To determine the occurrence of melanism, the pigmentation of 61 individuals of the Salto del Pis population and of 194 individuals of the Flumen population was recorded. Only those individuals which were completely black were considered as showing melanism.

RESULTS

Ecological characterization of the study sites

The study area of the Flumen river is situated in a pasture zone dominated by *Pinus sylvestris* with some *Crataegus monogyna*. The river is about 0.4-3.0 m wide and 20-65 cm deep and descends moderately (3.5% slope) with a slow current velocity (Table 1). The increased value obtained in July corresponds with the maximum velocity in this river, which usually occurs only immediately after thunderstorms. Water temperature ranged between 8 °C in March and 12 ºC at the begining of July. The water of the Flumen contains a higher concentration of salts than does that of the Salto del Pis (Table 1). The river bed consists of mud with partly anoxic conditions and of gravel and stones, mostly covered by algae. The hard bottom substrate is calcareous with numerous holes due to tuff formation, which serve as refuges for the newts. There is abundant aquatic vegetation, particularly in summer. The climate is typically supramediterranean with short winters between December and March. The precipitation is rather low throughout the year. Together with the Pyrenean salamander occur also the three amphibians *Bufo bufo*, *Rana perezi* and *Alytes obstetricans*. No fishes occur in the study area. Among the aquatic invertebrates, insects (*e.g.*, *Notonecta* sp., *Gerris* sp.) and water snails are abundant. In summer the frequent presence of cattle in this area contributes to the eutrophication of the water.

The Salto del Pis torrent is situated in the beech-fir domain. The bed of the torrent is composed of sediments with larger grain size, mainly stones and small rocks, which originate from avalanches or from the upper parts of this torrent. The hard subtrate is calcareous. The width

TABLE 1

Comparative environmental parameters recorded during four visiting days between March and July in the Flumen river and the Salto del Pis torrent.

Salto del Pis	**March**	**April**	**May**	**July**
Temperature	1ºC	7ºC	8ºC	7ºC
PH	8.08	8.25	8.25	8.13
Current velocity (m/s)	0.8	0.8	0.53	0.7
Conductivity (s/cm)	137	123	124	156
Mg^{++} (mg/l)	3.40	0.49	3.65	1.46
Ca^{++} (mg/l)	22.44	25.65	24.00	28.80
Na^{+} (mg/l)	0.53	0.21	0.40	0.30
K^{+} (mg/l)	0.11	0.06	0.10	0.10
Cl^{-} (mg/l)	3.00	2.50	2.00	2.00
CO_3H^{-} (mg/l)	70.20	70.20	0.80	92.70
NO_3^{-} (mg/l)	0	0	0.8	0
Dry residue (mg/l)	0	152	70	92
Flumen	**March**	**April**	**May**	**July**
Temperature	8ºC	10 ºC	12 ºC	11 ºC
PH	7.86	7.46	7.91	7.79
Current velocity (m/s)	0.22	0.25	0.43	0.92
Conductivity (s/cm)	508	516	527	450
Mg^{++} (mg/l)	2.43	4.86	5.35	4.38
Ca^{++} (mg/l)	94.59	96.19	99.20	100.80
Na^{+} (mg/l)	1.75	1.71	2.10	2.80
K^{+} (mg/l)	0.48	0.46	0.50	0.80
Cl^{-} (mg/l)	4.00	4.00	2.00	5.00
CO_3H^{-} (mg/l)	328.20	322.70	344.70	243.40
NO_3^{-} (mg/l)	0	0	0.4	0
Dry residue (mg/l)	198	326	288	264

is between 1.5-2.6 m and the water depth varies between 20 and 50 cm. Water velocity (Table 1) and the degree of inclination of the river bed (29%) are higher than in the Flumen river. The water temperature is much lower than in the Flumen and remains usually between the freezing point and less than 8°C till June. This is due to snow and ice accumulation caused by avalanches, which descend each year close to the torrent till May. Late snowfalls in the Central Pyrenees until July may cause additional reduction of water temperature during summer. However, the Salto del Pis and the Flumen may both reach similar maximum temperatures of around 20ºC.

The water of Salto del Pis is more oligotrophic and has a slightly higher pH value than the Flumen (Table 1). Furthermore, the aquatic vegetation and the invertebrate fauna occur at much lower abundances. Mainly due to the particular climatic conditions and repeated avalanche activity, which cause high variability in river bed structure, the Salto del Pis represents a much less stable habitat than the Flumen with typical alpine, high-mountain conditions.

Morphometric comparison

The means and standard deviations of the morphometric measurements obtained from each of the four groups are shown in Table 2. One-way ANOVA of log TL revealed significant differences among the four groups ($F_{(3.81)}$ = 7.08, $p < 0.005$) with the females of the Flumen being significantly smaller than the other three groups according to multiple comparisons by Tukey test ($p < 0.05$). No other differences in TL could be found.

TABLE 2

Means and standard deviations of total length (TL; in mm), of 11 morphometric characters (in mm; see Materials and Methods for explanations of abbreviations), and of body weight (W; in g) in four groups of the Pyrenean salamander *Euproctus asper*.

	Flumen males (n=25)	Salto del Pis males (n=20)	Flumen females (n= 22)	Salto del Pis females (n=18)
TL	104.36±5.87	103.63±6.49	98.95±4.83	106.64±4.69
TAL	43.59±3.13	43.16±3.75	44.32±2.81	49.37±2.55
TD	7.53±0.64	8.06±0.73	5.53±0.45	5.62±0.51
HL	13.64±0.70	13.81±0.94	12.30±0.43	12.28±0.44
HW	12.13±0.86	11.70±0.82	10.24±0.45	9.70±0.49
IBE	8.64±0.65	8.89±0.71	7.73±0.37	8.22±0.37
IN	3.59±0.30	3.51±0.26	3.01±0.24	2.95±0.23
IFE	5.81±0.48	6.00±0.51	5.24±0.31	5.10±0.37
EL	3.20±0.26	3.00±0.18	2.84±0.16	3.20±0.21
FLL	18.30±0.90	18.40±1.02	16.08±0.89	16.60±0.54
TF	4.24±0.40	4.08±0.41	3.71±0.44	4.10±0.32
CL	6.68±0.67	6.85±0.70	5.42±0.49	6.55±0.57
W	4.84±1.00	5.89±1.28	3.40±0.47	4.10±0.85

TABLE 3

Means, F-values of one-way ANOVA, and results of multiple comparisons for the transformed values (multiplied by 10^2) of 11 morphometric characters and body weight in four groups of the Pyrenean salamander. Parentheses separate those groups shown to be significantly different by Tukey test (* $p < 0.02$, ** $p < 0.001$).

	Flumen Males (Fm)	Salto del Pis males (Pm)	Flumen females (Ff)	Salto del Pis females (Pf)	F-value	p	Tukey test
TAL	-1.74	-1.88	1.50	2.67	40.81	**	(Fm,Pm)(Ff)(Pf)
TD	5.06	8.25	-6.25	-8.56	115.28	**	(Fm)(Pm)(Ff,Pf)
HL	1.70	2.40	-1.27	-3.46	67.43	**	(Fm,Pm)(Ff)(Pf)
HW	3.97	2.65	-1.71	-6.37	123.11	**	(Fm,Pm)(Ff)(Pf)
IBE	1.04	2.50	-2.01	-1.76	16.92	**	(Fm,Pm)(Ff,Pf)
IN	3.71	2.92	-2.23	-5.67	44.58	**	(Fm,Pm)(Ff)(Pf)
IFE	1.76	3.30	-1.39	-4.43	26.75	**	(Fm,Pm)(Ff,Pf)
EL	1.59	-0.92	-1.67	0.86	7.14	**	(Fm,Pf)(Pm,Ff)(Pm,Pf)
FLL	1.99	2.42	-2.12	-2.87	53.30	**	(Fm,Pm)(Ff,Pf)
TF	1.79	0.43	-2.15	-0.38	3.60	*	(Fm,Pm,Pf)(Pm,Ff,Pf)
CL	1.66	3.16	-4.43	-0.40	15.32	**	(Fm,Pm)(Fm,Pf)(Ff)
W	2.25	14.76	-7.38	-10.52	55.88	**	(Fm)(Pm)(Ff,Pf)

The means of the size-adjusted, transformed values of the morphometric characters and body weight, and the results of one-way ANOVA with subsequent multiple comparisons are shown in Table 3. Accordingly, females differ significantly from males in having longer tails (TAL), and being smaller in TD, HL, HW, IBE, IN, IFE, FLL, and W. Females of the Flumen show significantly lower values in TAL, EL, and CL and higher values in HL, HW, and IN than females of the Salto del Pis. Males of the Flumen show particularly large eyes. Males of the Salto del Pis show thicker tails and a higher weight than all other groups.

Table 4 provides an overview of the results of the three canonical variates generated by the CVA. The first canonical variate (CV1) explains 79.03%, the second (CV2) 12.4%, and the third (CV3) 8.57% of total variance. The individual character scores for CV1 and CV2 are plotted in Fig. 2. The characters showing the highest correlations ($r > 0.4$) with CV1 were HW, TD, HL, FLL and W. One-way ANOVA of the character scores along CV1 and subsequent multiple comparisons revealed major differences between sexes and among the females of either site. W was highly correlated with CV2. Along this axis major differences in character scores were found between the sexes and the males of the two sites. CL showed a high correlation with CV3. The major differences were detected between the sexes and between the females of the two sites.

TABLE 4

Correlations of 11 morphometric characters and body weight with three canonical variates of the CVA based on four groups of the Pyrenean salamander. For each canonical variate the Eigenvalue, the percentage of variance explained, the F-values of ANOVA from comparisons among the character scores of either group, and the results of multiple comparisons are given. Parentheses separate those groups shown to be significantly different by Tukey test (** $p < 0.001$).

	CV1	CV2	CV3
TAL	-0.388	0.086	-0.134
TD	0.629	-0.377	0.394
HL	0.497	-0.217	-0.033
HW	0.677	0.110	-0.195
IBE	0.221	-0.220	0.259
IN	0.410	0.017	0.004
IFE	0.307	-0.202	-0.062
EL	0.032	0.267	0.369
FLL	0.435	-0.146	0.279
TF	0.081	0.081	0.237
CL	0.157	-0.149	0.524
W	0.383	-0.615	0.217
Eigenvalue	9.82	1.54	1.07
% variance	79.03	12.40	8.57
F-value	265.13	41.60	28.77
p	**	**	**
Tukey test	(Fm,Pm)(Ff)(Pf)	(Fm)(Pm)(Ff,PF)	(Fm,Pm)(Pf)(Ff)

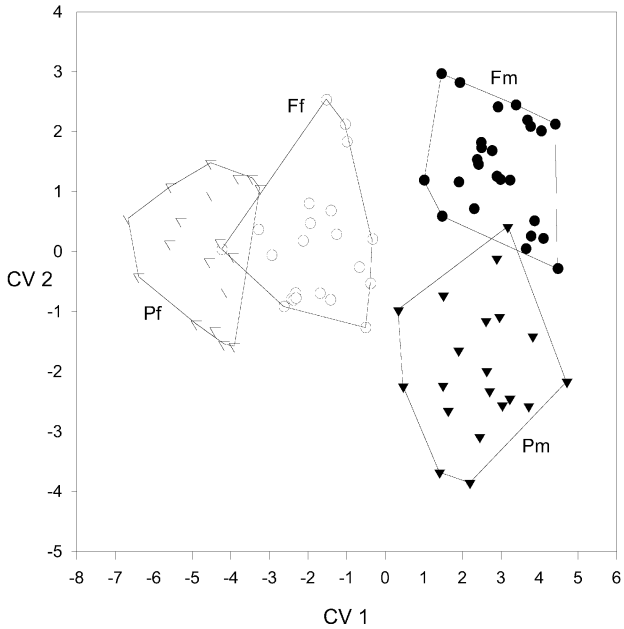

Fig. 2. Scores for the first and second canonical variate (CV1, CV2) generated from 12 morphometric characters of males and females of the Flumen river (Fm, Ff) and males and females of the Salto del Pis torrent (Pm, Pf).

Of all cases entered into the CVA, 95.29% were correctly classified. Only two males of Salto del Pis torrent and two females of Flumen river were classified as belonging to the other site, respectively. Sexes were correctly classified for all cases.

Further observations

In the Flumen, the first occurrence of reproductive behaviour indicated by amplexus formation between males and females was recorded in March. In the Salto del Pis torrent, reproductive activity started much later and at the earliest in the middle of April or in the beginning of May. In the Flumen amplexus formation was observed both in the central stream and the marginal areas while in the Salto del Pis it occurred mainly in areas with reduced water flow. However, in most of these microhabitats current velocity was still higher than in the central stream areas of the Flumen.

Of the 29 males and 32 females of the Salto del Pis examined for the occurrence of melanism, 2 (6.9%) and 6 (18.8%), respectively, showed a completely black colouration. None of the 194 individuals of the Flumen population showed any indication of melanism.

DISCUSSION

The Flumen river and the Salto del Pis torrent are characterized by differences in climatic as well as in other ecological conditions. The morphological differences between the populations of the Pyrenean salamander living in these two habitats are to a considerable extent related to sexual dimorphism and may reflect distinct influences of the conditions prevailing in the respective habitats.

The results of the univariate and multivariate comparisons among the four groups indicate clear site- and sex-related variations. Sexual dimorphism concerns mainly the following characters: females have thinner and longer tails, smaller heads, shorter legs, shorter cloacal tubes, and less weight than males. This dimorphism is not equally expressed at the two study sites. Females of the Salto del Pis show rather thin, long tails and males from this site show a particularly high weight and thick tails. In the Flumen sexual dimorphism was also found in body length and eye size with higher values in males than in females.

The strongly expressed sexual dimorphism in the Pyrenean salamander points to different trends of adaptation in males and females. Males have large, heavy bodies and heads, with long legs and short, robust tails that may assist them in walking on the bottom without being carried away by the water flow and/or in efficiently foraging for large and evasive prey. In a comparison of the feeding behaviour of several populations of the Pyrenean salamander, MONTORI (1988) showed that females frequently feed on smaller-sized prey items than do males. The smaller head size may hence induce females to select smaller prey and allow a reduction in intersexual food competition.

The differences in tail form may have been caused by sexual selection for long thin tails in females and strong robust tails in males. Observations of the reproductive behaviour revealed that after presenting their tails in a straight upward position as a courtship display, males embrace approaching females at their tail thus forming an amplexus with direct transfer of spermatophores from the male to the female cloaca (BARBADILLO ESCRIVA, 1987; LENGVENUS & PARZEFALL, 1992).

In an earlier comparison between the Flumen and Central Pyrenean populations, MARTÍNEZ-RICA (1980) found clear differences in their reproductive periods. Amplexus formation started much earlier in the Prepyrenean population. This finding is consistent with our observations. The need to reproduce successfully within a relatively short time interval may have led to increased sexual selection in the Salto del Pis population with the consequence of a more advanced sexual dimorphism. The strong tail of males enables them to efficiently embrace the females during formation of the amplexus. The long and thin tail of the females may facilitate the embracement by the males. It may also assist in swimming or keeping a firm position in the relatively fast flowing water or provide less drag and resistence during amplexus formation. The larger size in the females and the heavier bodies in the males of the Salto del Pis may be related to the particularly long or robust tails in either sex, respectively. A large body may also entail the additional advantage of improving the energy conservation capabilities, which may be particularly important under the extreme climatic conditions of the Central Pyrenees.

The presence of melanism in the Salto del Pis population concerns both sexes, but only a few individuals. It may be a response to the lower temperatures in this alpine habitat allowing a better thermoregulation through absorption of more radiation leading to an increased body temperature. Melanism has been observed in many mountain-dwelling animals (MARGALEF, 1991). In the Pyrenean salamander it has been found in several populations from the central chain of the Pyrenees, but not in the Prepyrenees (SERRA-COBO, 1989).

The Pyrenean salamander is considered to be a relict species that originated in the early tertiary (HERRE, 1935; STEINER, 1950; GASSER & CLERGUE-GAZEAU, 1981). The ecological characteristics of the two sites reflect mainly climatic differences, which may have exerted different selective pressures on these two apparently isolated populations over long evolutionary time periods. This influence should have lead to genetically manifested, morphological, behavioural, and physiological differentiation. The electrophoretic study of GASSER & CLERGUE-GAZEAU (1981) based on the analysis of seric proteins indicated clear genetic differences between the Pyrenean salamander of the Flumen river and various populations of the Central Pyrenees.

The present study provides to our knowledge the first clear evidence for variation in sexual dimorphism among populations of the Pyrenean salamander from geographically separated, ecologically different sites. One conclusion to be derived from these data is that the extreme climatic conditions prevailing at the Central Pyrenean site may have exerted a high selection pressure on several sexually dimorphic traits with the expected effects of increased reproductive efficiency and reduced intersexual competition.

ACKNOWLEDGEMENTS

The authors thank Carmen Pérez and Dr. Melchor Maestro for assistance in the analyses of water samples. The cooperation with the Parque Natural de la Sierra de Guara and the Dept. of Vida Silvestre de la Diputación General de Aragón throughout this study is gratefully acknowledged. The work was carried out within the framework of the European project VAMPHIRE.

REFERENCES

BARBADILLO ESCRIVA, L.J. (1987). *La Guia de Incafo de los anfibios y reptiles de la peninsula Iberica, Islas Baleares y Canarias*. INCAFO, Madrid.

BROWN, R.P., R.S. THORPE & M. BÁEZ (1991). Parallel within-island microevolution of lizards on neighbouring islands. *Nature,* 352: 60-62.

CLERGUE-GAZEAU, M. & J.P. MARTÍNEZ-RICA (1978). Les différents biotopes de l'urodèle pyrénéen: *Euproctus asper*.

Bulletin Société d'Histoire Naturelle Toulouse, 114: 461-471.

DOBSON, F. & J.D. WIGGINTON (1996). Environmental influences on the sexual dimorphism in body size of western bobcats. *Oecologia,* 108: 610-616.

FRAFJORD, K. & I. STEVY (1998). The red fox in Norway: morphological adaptation or random variation in size? *Z. Säugetierkunde,* 63: 16-25.

GASSER, F. & M. CLERGUE-GAZEAU (1981). Les proteines sériques de l'urodèle *Euproctus asper* (Dugès). Elements de différentiation génétique dans les Prepyrénées espagnols. *Vie et Milieu,* 31: 297-302.

HERRE, W. (1935). Die Schwanzlurche der mitteleocänen (oberlutetischen) Braunkohle des Geiseltales und die Phylogenie der Urodelen unter Einschluss der fossilen Formen. *Zoologica,* 87: 1-85.

LANDMANN, A. & N. WINDING (1995). Adaptive radiation and resource partitioning in Himalayan high-altitude finches. *Zoology,* 99: 8-20.

LENGVENUS, W. & J. PARZEFALL (1992). The role of the visual reaction in the behaviour of an epigean and a cave living population of *Euproctus asper* Duges (Salamandridae, Urodela). *Mém. Biospéol.*, 19: 111-115.

MARGALEF, R. (1991). *Ecología*. Ed. Omega, Barcelona.

MARTÍNEZ-RICA, J.P. (1980). Algunos datos sobre las poblaciones meridionales de tritón pirenaico, *Euproctus asper* Dugès. *Studia Oecologica,* 2: 135-154.

MARTÍNEZ-RICA, J.P. & M. CLERGUE-GAZEAU (1977). Données nouvelles sur la répartition géographique de l'espèce *Euproctus asper* (Dugès). *Bulletin Société d'Histoire Naturelle Toulouse,* 113: 318-330.

MONTORI, A. (1988). *Estudio sobre la biología y ecología del tritón pirenaico Euproctus asper (Dugès, 1852) en la Cerdanya*. PhD thesis, Univ. Barcelona.

NAVAS. C.A. (1996). Implications of microhabitat selection and pattern of activity on the thermal ecology of high elevation neotropical anurans. *Oecologia*, 108: 617-626

SELANDER, R.K. (1966). Sexual dimorphism and differential niche utilization in birds. *Condor*, 68: 113-151.

SERRA-COBO, J. (1989). Presencia de tritón melánico (*Euproctus asper*) en el Parque Nacional de Ordesa y Monte Perdido. *Lucas Mallada,* 1: 203-204

SERRA-COBO, J., G. LACROIX G. & S. WHITE (1998). Comparison between the ecology of the new European frog *Rana pyrenaica* and that of four Pyrenean amphibians. *J. Zool.,* 246: 147-154.

STEINER, H. (1959). Die Differenzierung der paläarktischen Salamandrinen während des Pleistozäns. *Rev. Suisse Zool.,* 57: 590-603.

UIBLEIN, F., F. BORDES, R.CASTILLO & A. RAMOS (1998). Spatial distribution of shelf- and slope-dwelling fishes collected by bottom longline off Lanzarote and Fuerteventura, Canary Islands. *Marine Ecology,* 19: 53-66.

Received: June 9, 1999
Accepted: September 13, 1999