

Sexual dimorphism in a French population of the marbled newt, *Triturus marmoratus* (Urodela: Salamandridae)

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Abstract. Amphibians have developed a large set of life-history strategies and demonstrate an impressive diversity of reproductive patterns compared to other vertebrates. Various selection pressures impact on males and females and see them produce different degrees of sexual dimorphism in order to maximise their reproductive success. In an extended morphometric analysis that included 27 body- and head-related characters, we studied the pattern of sexual dimorphism of a French population of the marbled newt, *Triturus marmoratus*. We analysed the characters by employing GLM methods (ANCOVA) and found 16 of them to be dimorphic between the sexes. In general, females differ in head–body size, such as snout–vent length, but males rather in shape or body proportions (e.g., limb proportions). The various expressions of sexual size dimorphism among large-bodied marbled newts and allies demonstrate that more than one evolutionary model works simultaneously on different traits.

Key words. SSD, fecundity, sexual selection, salamanders, *Triturus*, morphometrics.

Introduction

Sexual dimorphism is a common phenomenon among animals. Opposing selection forces equilibrate differently in the sexes of the same species and are responsible for a variety of phenotypic differences (BLANCKENHORN 2005, FAIRBAIRN 2007). Sexual differences can be permanent or seasonal, whilst seasonal differences are often influenced by hormones and tightly connected to reproduction (SHINE 1990, MALMGREN & THOLLESSON 1999). Some traits can be easily observed, for example body size and shape, as well as colouration (MALMGREN & THOLLESSON 1999). Concerning head–body size, examples of females or males that weigh or grow to sizes several times that of their conspecific mates can be found (e.g., in some fishes, spiders or marine invertebrates; see BLANCKENHORN 2005). Female-biased sexual size dimorphism is common amongst invertebrates and poikilothermic vertebrates, whereas males are larger in most mammals and birds (ANDERSSON 1994, ABOUHEIF & FAIRBAIRN 1997, BLANCKENHORN 2005). Sexual and fecundity selection are the major forces that drive the evolution of sexual dimorphism, but ecological factors, e.g., resource utilization through niche partitioning, can contribute as well (SHINE 1989, MALMGREN & THOLLES-

SON 1999) and cause, for example, differences in head morphology due to different feeding strategies (MALMGREN & THOLLESSON 1999). If males are generally larger, they will have an advantage in male–male combat or resource protection and this in turn increases their mating and thus reproductive success (e.g., KUPFER 2007). Females also profit from a large body size, as a lot of studies have shown that clutch size or the size of eggs and offspring, and consequently their reproductive success, increases with female size in poikilothermic animals (reviewed in BLANCKENHORN 2005). Thus, sexual dimorphism is often seen as a life-history adaptation (e.g., ENDLER 1983, MALMGREN & THOLLESSON 1999) and should be considered in the context of the species' biology, as natural and sexual selection interact and determine the type and the degree of sexual dimorphism (FICETOLA et al. 2013).

Amphibians exhibit a unique diversity of life-history strategies (DUELLMAN & TRUEB 1994, KUPFER 2007). This makes them ideal for studies of sexual size dimorphism (SSD), which is important for understanding the evolution of mating systems. SSD is present in all amphibian orders (KUPFER 2007), and among salamanders, most species exhibit a female-biased size dimorphism, whereas male-biased dimorphism mainly occurs in species with aggressive

Table 1. Description of morphometric body and head characters that were used for the analysis of sexual size dimorphism of the marbled newt *Triturus marmoratus*.

Character abbreviation	Description of measurement
Body-related traits	
OAL	overall length
SVL	snout–vent length from the tip of the snout to the posterior edge of the cloaca
TL	tail length from posterior edge of the cloaca to the tip of the tail
TH	tail height at mid-tail
UAL	upper arm length from the posterior margin of the front leg (axilla) to the angle of the elbow
LAL	lower arm length from the angle of the elbow to the wrist
LAL2	lower arm length measured to the tip of the longest finger
TAL	total arm length from the axilla to the tip of the longest finger
ULL	upper leg length from the posterior margin of the hind leg (groin) to the angle of the knee
LLL	lower leg length from the angle of the knee to the ankle
LLL2	lower leg length measured to the tip of the longest toe
TLL	total leg length from the groin to the tip of the longest toe
CL	cloacal length
CW	cloacal width
BWM	body width at mid-body
CHW	chest width from axilla to axilla
GG	distance from groin to groin
DEX	distance of extremities from axilla to groin
CH	crest height (males only)
Head-related traits	
HL	head length
HW	head width at the angle of the jaw
ED	diameter of the eye
ON	orbitonarial distance from the anterior edge of the eye to the centre of the nostril
IO	interorbital distance from one eye to the other across the centres of the eyes
IN	internarial distance from nostril to nostril
ES	eye–snout distance from the anterior edge of the eye to the tip of the snout
IC	intercanthal distance from one anterior edge of the eye to the other

or territorial habits (SHINE 1979). The large-bodied Eurasian salamandrid genus *Triturus* is known for its high degree of sexual dimorphism (e.g., ANDERSSON 1994, MALMGREN & THOLLESSON 1999), which does not only include general head–body size, but also body shape and secondary sexual characters, such as colouration or the development of dorsal crests (e.g., ANDERSSON 1994, MALMGREN & THOLLESSON 1999, KUPFER 2007).

Here, we explore the degree of sexual size and shape dimorphism in a French population of the large-bodied marbled newt, *Triturus marmoratus* (LATREILLE, 1800). We aim to describe the expression of intersexual differences and discuss the evolution of sexually dimorphic traits in the context of the ecology and reproductive biology of *Triturus marmoratus* and its close relatives.

Material and methods

Study species

Large-bodied marbled newts, *Triturus marmoratus*, are widely distributed in southwestern Europe, especially on

the Iberian peninsula and in large parts of western France (GRIFFITHS 1996, HERRERO et al. 2003a). It has been elevated to species level, because no signs of present or past hybridisation with closely related taxa were found (GARCÍA-PARIS et al. 1993, 2001). Beforehand, it was dealt with as the nominotypical form next to its assumed sister subspecies *T. m. pygmaeus*, which now regarded as *T. pygmaeus* (WOLTERSTORFF, 1905) and occurs in the southwestern Iberian peninsula and grows to a much smaller head–body size than *T. marmoratus* (HERRERO et al. 2003a).

Marbled newts reproduce annually in stagnant or slow-flowing waters or even in temporary pools with no specific association to a special vegetation type (GRIFFITHS 1996, HERRERO et al. 2003a). It is oviparous, and adults leave the water after the end of the reproductive period (HERRERO et al. 2003a). Its sexual dimorphism is quite pronounced, with females often being reported to be the larger sex (e.g., FRANCILLON-VIEILLOT et al. 1990, HERRERO et al. 2003a). Furthermore, males are easily distinguished from females by their developing a dorsal crest and an enlarged tailfin, which regresses at the end of the annual reproductive pe-

Sexual dimorphism in a French population of *Triturus marmoratus*Table 2. Analysis of sexual size dimorphism in *Triturus marmoratus* (n = 35 males, n = 67 females). The means (M), standard deviations (SD), minimum and maximum ranges of 27 characters are listed. Results of t-tests (two-tailed, $\alpha = 0.05$) are shown in the last column.

Character	Males (n = 35)		Females (n = 67)		P
	M±SD	Range	M±SD	Range	
Body					
SVL	68.53±3.36	60.34–75.55	71.9±3.13	64.43–79.36	<0.001
OAL	121.03±6.04	108.46–134.31	130.44±5.75	115.82–141.23	<0.001
TL	52.5±3.55	44.31–61.27	58.54±3.49	48.17–66.4	<0.001
TH	14.8±2.42	11.07–19.83	12.22±1.8	9.3–17.69	<0.001
UAL	10.22±1.05	7.43–13.03	10.03±0.8	7.58–12.07	n.s.
LAL	7.95±0.5	7.06–9.3	7.85±0.65	6.73–9.75	n.s.
LAL2	17.02±1.17	14.47–19.68	16.55±1.0	12.68–18.35	<0.05
TAL	27.24±1.9	21.9–31.91	26.58±1.47	21.73–29.72	n.s.
ULL	9.02±0.73	7.1–10.15	9.37±0.64	7.52–10.72	<0.05
LLL	8.24±0.69	6.98–9.31	8.47±0.71	6.94–9.97	n.s.
LLL2	19.03±0.99	17.06–20.71	17.72±1.0	14.56–19.68	<0.001
TLL	28.05±1.39	25.09–30.7	27.08±1.4	22.92–29.79	<0.01
CW	7.81±0.97	6.34–9.12	4.24±0.34	3.32–5.03	<0.001
CL	9.91±0.87	8.53–11.6	6.45±0.4	5.46–7.48	<0.001
CHW	11.38±1.02	8.6–13.61	11.62±0.8	9.94–13.49	n.s.
BWM	14.3±1.51	10.54–18.85	15.12±1.36	12.64–18.22	<0.01
GG	9.53±0.83	7.24–11.41	9.32±0.54	8.1–10.49	n.s.
DEX	33.35±2.12	28.94–37.29	37.51±2.32	32.35–42.96	<0.001
CRH	3.52±1.05	1.84–6.18	–	–	–
Head					
HW	12.4±0.71	10.71–14.42	12.84±0.71	11.64–14.97	<0.01
HL	13.69±0.67	12.36–14.77	14.11±0.66	12.58–15.76	<0.01
ED	3.8±0.34	3.11–4.56	3.73±0.26	3.26–4.43	n.s.
ON	4.25±0.34	3.45–5.08	4.4±0.33	3.51–5.1	<0.05
IO	8.98±0.56	7.88–10.13	9.19±0.46	8.19–10.13	<0.05
IN	3.0±0.26	2.59–3.54	3.2±0.27	2.71–4.01	<0.001
ES	6.31±0.49	5.18–7.31	6.4±0.44	5.52–7.43	n.s.
IC	7.01±0.42	6.08–7.82	6.95±0.35	6.21–7.71	n.s.

riod, but remains visible as a coloured stripe in terrestrial adult males (GRIFFITHS 1996).

We have studied sexual dimorphism in a large series of museum specimens of *Triturus marmoratus* housed at the Zoologische Staatssammlung München (ZSM, Bavarian state collection, Munich). Generally, measurements of large specimen series housed in natural history collections are key to analysing body trait differences between the sexes.

Morphometrics and analysis

Twenty-seven morphometric characters were selected for analysis of body shape and sexual dimorphism in *T. marmoratus* (see Tab. 1 for character descriptions and abbreviations). All measures were taken to the nearest 0.01 mm using a digital calliper (Rok International Industry, Ltd.).

Altogether, 35 males (ZSM 1831/2006–1836/2006, 1876/2006–1897/2006, 1910/2006–1916/2006) and 67 fe-

males (ZSM 1837/2006–1875/2006, 1898/2006–1909/2006, 1917/2006–1932/2006) from Banyuls-Sur-Mer (Pyrenees Orientales, southern France), which were identified as adults, were used for analysis. Specimens were sexed via externally visible sex-indicative characters. The sexual dimorphism index (SDI) was calculated by dividing the mean SVL of the larger sex by the mean SVL of the smaller sex and subtracting a value of 1 ($[(SVL_{large}/SVL_{small})-1]$), following GIBBONS & LOVICH (1990), to obtain a first conception of sexual size dimorphism (if the male measurement is larger, the result needs to be multiplied with -1). All characters measured were tested for normality using the D'Agostino and Pearson omnibus normality test. Univariate t-tests (two-sided at $\alpha \leq 0.05$) were used to test for dimorphism between sexes. In addition, SSD was assessed by an analysis of covariance (ANCOVA) using SVL as a co-variable to adjust the characters to head-body size. All statistical tests were conducted using Microsoft Excel 2007, GraphPad Prism 5.01 and MedCalc 12.7.1.0 for Windows 7.

Table 3. Analysis of sexual size dimorphism in *Triturus marmoratus* (n = 35 males, n = 67 females). Results of one-factor ANCOVA comparing 26 traits of sexes relatively to snout-vent length (SVL). F-values and significance levels are shown in the second and third columns.

Character adjusted for SVL	F	P
Body		
OAL	34.32	<0.001
TL	34.32	<0.001
TH	57.44	<0.001
UAL	13.13	<0.001
LAL	8.31	<0.01
LAL2	40.74	<0.001
TAL	46.46	<0.001
ULL	0.03	0.867
LLL	0.16	0.688
LLL2	112.91	<0.001
TLL	68.16	<0.001
CW	744.98	<0.001
CL	969.03	<0.001
CHW	1.96	0.164
BWM	0.77	0.382
GG	22.44	<0.001
DEX	52.49	<0.001
Head		
HW	0.63	0.431
HL	0.55	0.460
ED	9.28	<0.01
ON	1.37	0.245
IO	0.79	0.376
IN	2.36	0.127
ES	11.39	<0.001
IC	18.81	<0.001

Results

The sexes of the marbled newt were characterized by a significant difference in head-body size. The size dimorphism index (SDI) after GIBBONS & LOVICH (1990) was 0.049 for SVL, expressing that females were about 5% larger than males in our sample (the SDI for OAL accounted for 0.078 and thus nearly 8%). Parametric testing showed significant intersexual differences for the following traits: SVL, OAL, TL, TH, LAL2, ULL, LLL2, TLL, CW, CL, BWM, DEX, HW, HL, ON, IO, and IN (Tab. 2).

When adjusted to SVL, the ANCOVA supported some previous results, but also rejected some others and even identified some cryptic ones (see Tab. 3). All in all, both analyses demonstrated that most characters were significantly different. The ANCOVA additionally revealed differences in UAL, LAL, TAL, GG, ED, ES, and IC, but refuted sexual differences for ULL, BWM, HW, HL, ON, IO, and IN.

This shows how important a proper adjustment of measurement data is and that above all, larger differences in general head-body size can be overlooked or falsify SSD results if the data is not properly adjusted. A female may, for example, have smaller limbs in relation to general head-body size and a male may have larger ones, but a larger female body size might disguise this aspect.

Female marbled newts had a larger SVL, TL, and thus OAL than conspecific males, and the ratio between head-body and tail length was significantly different in both sexes (tail 43.4% in males and 44.9% in females, $p < 0.001^{***}$; head-body 56.6% in males and 55.1% in females, $p < 0.001^{***}$, see Fig. 1). Additionally, females had a larger DEX of 3.5% (all following percent values were adjusted to SVL). All other significant differences were larger in males, impacting on TH (males are on average 4.6% larger), UAL (0.9%), LAL (0.7%), LAL2 (1.8%), TAL (2.8%), LLL2 (3.2%), TLL (3.2%), CW (5.5%), CL (5.5%), GG (0.9%), ED (0.3%), ES (0.3%) and IC (0.5%). The male average dorsal crest height was 3.52 mm (SD = 1.05 mm) and ranged from 1.84 to 6.18 mm. Dorsal crest height did not correlate with male SVL ($r = 0.21$, $p = \text{n.s.}$).

Discussion

Studies of sexual size dimorphism provide information about the general intersexual divergence of the same species and allow insights into the impact of selective forces on the size of males and females. Here, we demonstrate the importance of using comparative analytical methods in relation to general head-body size (SVL). This approach reduces the risk that differences in shape remain undiscovered, especially if head-body size differences between the sexes are large. The marbled newt, *T. marmoratus*, is characterized by a variety of sexual differences. Female size clearly exceeds that of males, as has been shown in previous studies (e.g., FRANCILLON-VIEILLOT et al. 1990, HERRERO et al. 2003a, JAKOB et al. 2003). In general, females differ in head-body size (e.g., SVL, OAL) and males rather in shape or body proportions (e.g., limbs).

JAKOB et al. (2002) reported a significantly longer lifespan for female marbled newts as well as a delayed onset of sexual maturity (minimum male age at maturity of 2, and 3 years in females) in a population in southwestern France. The growth rate of males is higher (JAKOB et al. 2002), and their early sexual maturation contributes to a smaller adult size, because the increased resource usage for gametogenesis decreases the availability of energy for somatic growth (MARZONA et al. 2004). Delayed sexual maturity and thus a greater head-body size are advantageous for female fecundity. This is also reflected in the manifestation of sexual dimorphism in females, because they were larger in head-body size-related traits only, especially in snout-vent length and distance of extremities. Our findings are in concordance with the fecundity model that predicts that larger females are able to produce more or larger offspring, which in turn directly increases their

reproductive success (FAIRBAIRN 2007). A fecundity-related female-biased size dimorphism is common among amphibians (DUELLMAN & TRUEB 1994) and in the Salamandridae (REINHARD & KUPFER 2013). The distance of extremities is directly correlated to the length of the pleuroperitoneal cavity, which provides space for maturing eggs, and a larger trunk promotes female reproductive success (KALEZIC et al. 1992, MALMGREN & THOLLESSON 1999). Trunk length in turn directly affects SVL. Distance of extremities is an important dimorphic measurement in other newt species, such as *T. cristatus* (MALMGREN & THOLLESSON 1999, KUBIŠOVÁ et al. 2007), *T. dobrogicus* (KUBIŠOVÁ et al. 2007), *Lissotriton vulgaris* (MALMGREN & THOLLESSON 1999), and *L. montandoni* (BABIK & RAFIŃSKI 2004). We postulate that this trait may be found in all species of the European newt complex and also in

other species having a female-biased dimorphism, even though this remains to be proven in future studies (see a summary in Fig. 2).

Although males are characterized by divergent body proportions compared to females, the dorsal crest that develops during the breeding season remains the most remarkable trait. Mate choice studies have indicated that females responded more readily to high-crested males (e.g., for *T. cristatus* MALMGREN & ENGHAG 2008, for *Lissotriton vulgaris* GREEN 1991). Crest height in the marbled newt males is likely to be accentuated by female choice. In crested newts, the crest serves as an indicator of good physical condition and additionally increases the surface area of the male body and as a result improves cutaneous respiration, ultimately supporting endurance during courtship (MALMGREN & THOLLESSON 1999).

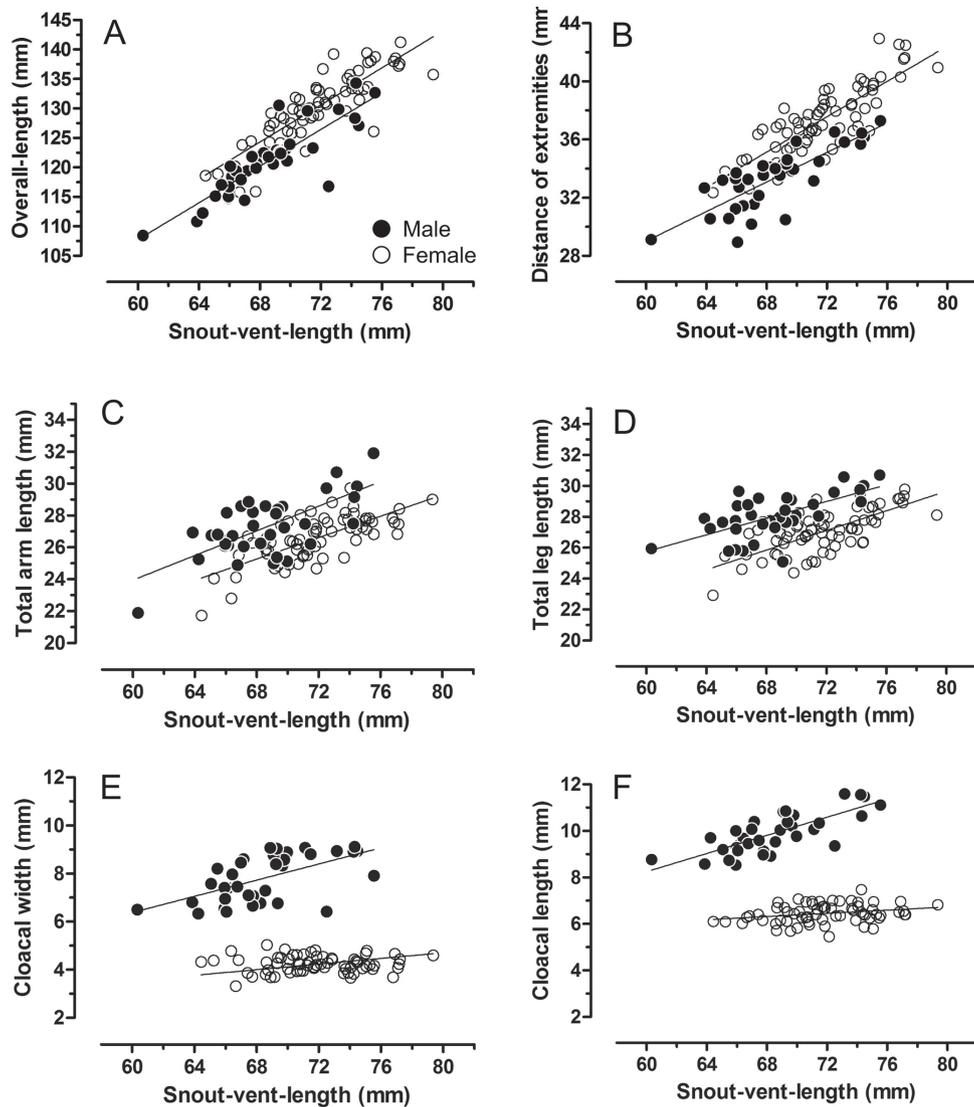


Figure 1. Sexual dimorphism of *Triturus marmoratus*. Some selected characters are shown: A) Overall length OAL – females are larger; B) Distance between extremities DEX – females are larger; C) Total arm length TAL – males are larger; D) Total leg length TLL – males are larger; E) Cloacal width CW – males are larger; F) Cloacal length CL – males are larger.

Another important trait is the significantly larger male tailfin. Males perform tail-lashing during courtship, and fin size likely enhances pheromone transfer. A larger tail creates a stronger water flush, and especially amplifies male behavioural signals such as “whipping” or “whip lashing” (see ARNTZEN & SPARREBOOM 1989 and SPARREBOOM & TEUNIS 1990 for further information on behavioural courtship patterns). Extensive male courtship displays require a firm foothold and enlarged limb parts might aid in stabilizing. Limb dimorphism is also common in other large-bodied newts that display courtship-related behavioural patterns similar to those of *T. cristatus* (MALMGREN & THOLLESSON 1999). Another stabilizing factor during courtship might be influenced by a slightly broader male pelvic girdle. This male anatomical feature might be connected to a larger distance between the groins that causes the femurs to be more widely spaced. However, direct measurements on dry bone material or non-invasive micro-CT scanning could provide further insights into this matter as could state-of-the-art finite element analysis (FEA, see e.g., VEGA & STAYTON 2011, KLEINTEICH et al. 2012).

As is characteristic for most salamanders reproducing by means of internal fertilisation, males of *T. marmoratus* have a more swollen cloaca (HALLIDAY 1990, VERRELL 1989) resulting from its being equipped with a complex set of glands for the release courtship pheromones and sper-

matophore production (SEVER 2003). This trait is likely sexually selected and directly increases the male reproductive success (MALMGREN & THOLLESSON 1999, SEVER 2003). Courtship pheromones play a major role in newt mating (TREER et al. 2013), illustrating the significance of cloacal dimorphism and its direct effect on male reproductive success. Interestingly, visual cues are less important compared to olfactory ones in newts (TREER et al. 2013).

Some head-related characters are sexually dimorphic as well, but only concern shape (sexual shape dimorphism SShD) and not head size. Although the absence of SSD and the presence of SShD is exceptional (SCHWARZKOPF 2005, IVANOVIĆ & KALEZIĆ 2012), it is also known from other newts such as *L. vulgaris* (IVANOVIĆ & KALEZIĆ 2012). According to the ecological model, differences in food resource usage might influence such intersexual shape differences (e.g., SHINE 1989). In fact, LIZANA et al. (1986) found both ontogenetic and intersexual differences in food preferences in a population of marbled newts near Salamanca (HERRERO et al. 2003a). To which extent ecology influences skull shape and geometry needs to be explored further, as well as changes during ontogeny. Geometric morphometrics can be directly studied on dried skull material or, better, using non-invasive μ -CT-scanning of ethanol-preserved specimens (see also STOCK et al. 2003, IVANOVIĆ et al. 2013).

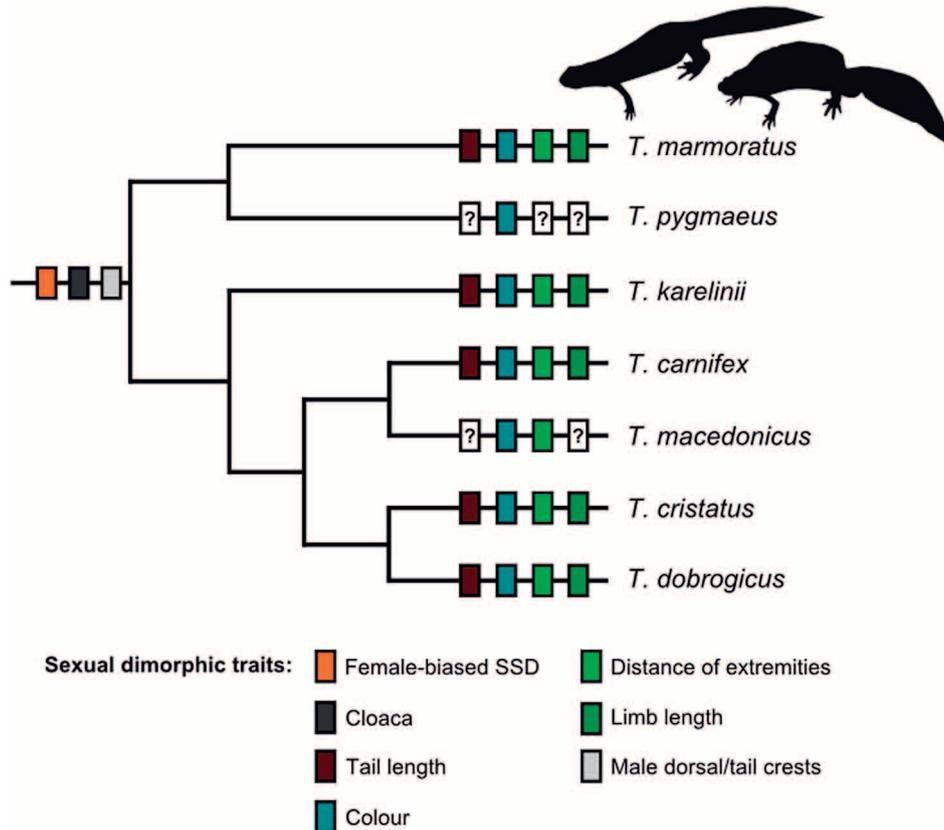


Figure 2. Summary of sexually dimorphic traits within the genus *Triturus*. The phylogeny was modified after WIELSTRA & ARNTZEN (2011). References are listed in the Appendix.

The various expressions of SSD among large-bodied newts demonstrates that more than one evolutionary model works simultaneously on different traits. Different selection pressures interact and directly influence the diversity of manifestations. We postulate that indirect studies of patterns of sexual dimorphism can identify valuable keys to future studies and more direct testing.

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- Appendix**
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