THE VENTRAL CRANIAL SIZE AND SHAPE VARIATION BETWEEN MALES AND FEMALES OF EUROPEAN BROWN FROGS: *RANA DALMATINA*, *R. GRAECA* AND *R. TEMPORARIA* (ANURA, AMPHIBIA)

JELENA KRSTIČIĆ RAČKOVIĆ^{1*}, NATAŠA TOMAŠEVIĆ KOLAROV², TANJA VUKOV²

¹Faculty of Science and Mathematics, University of Priština, Kosovska Mitrovica, Serbia

²Institute for Biological Research „Siniša Stanković“, University of Belgrade, Serbia

ABSTRACT

Sexual size and shape dimorphism is a very common phenomenon widely studied in the field of evolutionary biology. The differences between sexes are related to their life strategies and driven by the two evolutionary processes, sexual and natural selection. In amphibians, females are larger sex due to high correlation with fecundity, while dimorphism in body shape is often related to intrasexual competition for opposite sex during the breeding season. The main aim of this study is to describe patterns of ventral cranial size and shape variation between males and females of three species of European brown frogs, *Rana dalmatina*, *R. graeca*, *R. temporaria*, from the Balkan Peninsula. Our results showed that species *R. dalmatina* and *R. graeca* are sexually dimorphic for the ventral cranial size while species *R. graeca* and *R. temporaria* for the ventral cranial shape. Sexual dimorphism in cranial size is most probably an indirect consequence of natural selection favoring larger body for higher fecundity in explosive breeders like brown frogs. Cranial shape variation is under a strong influence of size variation but without allometric scaling between sexes. Sexual shape differences of analyzed brown frog species were most pronounced in the level of connection between cranium and jaw which indicate that differential diet of males and females can be a factor affecting observed sexual dimorphism patterns. More detailed studies of males and females microhabitats are necessary to conclude if differences in intersexual ecology affect intersexual size and shape differences in the cranium.

Keywords: Cranium, Sexual dimorphism, Geometric morphometrics.

INTRODUCTION

Size and shape variations are the principal sources of biological diversity (Hallgrímsson & Hall, 2005) and their origin and maintenance are in the focus of many biological disciplines. Sexual size and shape dimorphism, the morphological difference between sexually mature males and females, is a very common phenomenon widely studied in the field of evolutionary biology (Fairbairn, 2013). The differences between sexes are related to their life strategies and driven by the two evolutionary processes, sexual and natural selection (Shine, 1989; Monnet & Cherry, 2002).

Sexual dimorphism in size (*sexual size dimorphism*, SSD) is the most prominent and most obvious aspect of sexual dimorphism (Shine, 1989; Fairbairn, 1997; Fairbairn et al., 2007). SSD is the topic of a large number of studies for a long time (e.g. Snyder et al., 1976; Shine, 1979; Price, 1984; Cox & Calsbeek, 2010; McPherson & Chenoweth, 2012; Plavcan, 2012; Friedman & Remeš, 2016; Cooper, 2018; Ng et al., 2019), while sexual shape dimorphism (*sexual shape dimorphism*, SShD) is more extensively explored in the last two decades (e.g. Herrel et al., 1999; Bonduriansky, 2006; Berns, 2013; Vladić et al., 2019).

Amphibians are an appropriate group for the sexual dimorphism studies as the difference between males and females is evident for number of morphological features such as body size and shape and body coloration (Monnet & Cherry, 2002; Hoffman & Blouin, 2000; Bell & Zamudio, 2012; Zhang & Lu, 2013; Petrović et al., 2017; Vukov et al., 2018). For example, females are larger sex in 90% of anuran species as the larger body is correlated with higher fecundity (Shine, 1979). Dimorphism in body shape is often related to intrasexual competition through contests for dominance or attracting the opposite sex during the breeding season (Shine, 1979).

Even though the sexual dimorphism of the skull is widely studied in animal groups such as mammals (Gittleman & Valkenburgh, 1997; Morris & Carrier, 2016; Porobić et al., 2016) and lizards (Kuo et al., 2009; Ljubišavljević et al., 2010; Borczyk et al., 2014), it is understudied in amphibians (Ivanović et al., 2007; Ivanović et al., 2008; Ivanović & Kalezić, 2012), especially in anurans (but see Vukov et al., 2018; Krstićić Račković et al., 2019). Therefore, the aim of this study is to describe patterns of ventral cranial size and shape variation between males and females of three species of European brown frogs: *Rana temporaria*, *R. dalmatina* that are widely distributed throughout Europe (Sillero et al., 2014), and *R. graeca*, species endemic in the Balkan Peninsula (Džukić & Kalezić, 2004).

* Corresponding author: jelena.krsticic@pr.ac.rs

MATERIAL AND METHODS

In this study, we included 112 adult skulls (*R. dalmatina*: 20 males, 19 females; *R. graeca*: 19 males, 17 females; *R. temporaria*: 27 males, 10 females) obtained from the Batrachological Collections of the Institute for Biological Research “Siniša Stanković,” Belgrade (Džukić et al., 2015). The sample size in this geometric morphometric study was large enough for the appropriate estimation of different parameters (Cardini & Elton, 2007).

Skulls were taken from adult specimens (determined by gonad examination) and they were cleared with trypsin and potassium hydroxide (KOH), stained with Alizarin Red S to distinguish cranial elements and their articulations better and then preserved in glycerol. Images of the ventral cranium were obtained with a Sony DSC-F828 digital camera (resolution 8.0 MP; Sony Corp., Tokyo, Japan). Eighteen specific two-dimensional landmarks for the ventral cranium were digitized using TpsDig2 software (Rohlf, 2008). The chosen configuration of landmarks provides an adequate summary of specific aspects of the ventral cranium morphology. The specific positions of the chosen landmarks are shown in Figure 1.

Figure 1. Location of the selected landmarks on the ventral cranium of a brown frog (*R. temporaria*). 1,2 Tip of lateral pterygoid process (towards the quadrate); 3,4 Most lateral point of quadrate; 5,6 Suture between parietal and prootic; 7,8 Lateralmost point of sphenethmoid (anterior); 9, 10 Lateralmost point of palatine (towards the maxilla); 11,12 Contact point between maxilla and anterior pterygoid process; 13 Anteriormost point of sphenethmoid; 14, 15 Anteriormost point of maxilla; 16, 17 Anteriormost point of premaxilla; 18 Posteriormost point of parasphenoid.

We applied Generalized Procrustes analysis (GPA) (Dryden & Mardia, 1998) to analyse interspecific, sexual, and body size-related variation in the ventral cranium of brown frogs. A GPA was used to obtain a matrix of shape co-ordinates from which differences due to the position, scale, and orientation were removed (Dryden & Mardia, 1998). Variation in ventral cranial

size (centroid size - CS) was evaluated by ANOVA with sex as factors. Determining the level of sexual dimorphism in size, the standard index is calculated by CS values: $I_{SSD} = \text{size of the larger sex (females)} / \text{size of the smaller sex (males)}$. The differences in shape between sexes are described as Procrustes distances. Procrustes distance, a linear measure of shape differences between landmark configurations, was used as an index of sexual dimorphism in shape (I_{SShD}).

To access the optimal estimate of the impact of allometry on shape changes, we employed two-way permutational MANCOVA with species and sex as factors and CS as covariable. Factor $\times$ CS interaction would indicate that size-dependent shape changes differ between the species or sexes. The percentage of predicted allometry with the statistical significance of the allometric regressions was tested with permutation tests against the null hypothesis of allometry independence. Residuals from the multivariate regression of shape variables on CS were used to visualize non-allometric shape changes in the ventral cranium between sexes by discriminant analysis, and to calculate size corrected index of sexual dimorphism in shape ($I_{SShDcorr.}$).

Analyses were performed in MorphoJ (Klingenberg, 2011), Statistica (StatSoft Inc., 2011), and in R 3.2.0 (R Core Team, 2015).

RESULTS

Cranial size differs significantly between sexes for *R. dalmatina* and *R. graeca* with larger cranium in females, but not for *R. temporaria* (Table 1). Females had larger body size in our sample (*R. dalmatina*: females L = 63.9 mm, males L = 57.2 mm; *R. graeca*: females L = 68.1 mm, males L = 61.9 mm; *R. temporaria*: females L = 85.1 mm, males L = 75.7). The calculated SSD indexes (Table 1) and mean CS values for *R. dalmatina* and *R. graeca* showed that females had 12% larger cranium than males.

Table 1. Means and standard deviations (SD) of cranial size (CS) for males (m) and females (f), and index of sexual size dimorphism (I_{SSD}). Statistically significant values in bold.

species		CS means	CS SD	I_{SSD}	P
<i>R. dalmatina</i>	m	33.47	2.73	1.13	0.003
	f	37.72	5.06		
<i>R. graeca</i>	m	45.71	3.95	1.13	0.010
	f	48.06	5.33		
<i>R. temporaria</i>	m	39.07	4.54	1.05	0.156
	f	44.01	5.48		

Regression analyses showed that the ventral cranium of males and females for all three analysed brown frog species share the same allometric trajectory ($F = 0.6744$, $P = 0.6438$), with 16.91% of shape variation explained by the size variation (P

< 0.0001). Sexual shape differences were significant for *R. graeca* and *R. temporaria*, and not significant for *R. dalmatina*, before and after removing the allometric component of the ventral cranium variation (Table 2). The calculated SShD indexes were similar for *R. graeca* and *R. temporaria* (Table 2).

Table 2. Indices of sexual size dimorphism before (I_{SShD}) and after removing allometric component of variation ($I_{SShDcorr.}$). Statistically significant values in bold.

species	I_{SShD}	P	$I_{SShDcorr.}$	P
<i>R. dalmatina</i>	0.02	0.060	0.01	0.292
<i>R. graeca</i>	0.03	0.001	0.02	0.048
<i>R. temporaria</i>	0.03	0.001	0.03	0.001

Patterns of the intersexual shape variation were the same before and after removing the allometric component. Females of the *R. graeca* had wider skull than males in the posterior part of the cranium (landmarks 1, 2, 3, 4) but shorter snout (landmarks 14, 15, 16, 17), with anteriorly displaced contact between pterygoid and maxilla (landmarks 11, 12) (Figure 2A). In the *R. temporaria* females compared to males the tips of lateral pterygoid process and quadrate bones were displaced posteriorly (landmarks 1, 2, 3, 4), contacts between the palatine and maxilla and pterygoid and maxilla anteriorly (landmarks 9, 10, 11, 12), and snout was slightly longer (landmarks 16, 17) (Figure 2B).

Figure 2. Shape changes associated with non-allometric SShD between sexes in *R. graeca* (A) and *R. temporaria* (B) (from males to females).

DISCUSSION

Three species of the European brown frogs are sexually dimorphic for the ventral cranial size in *R. dalmatina* and *R. graeca* and for the ventral cranial shape in *R. graeca* and *R. temporaria*. Cranial shape variation is under a strong influence of size variation but without allometric scaling between sexes. The most pronounced shape dissimilarities between sexes are found in the posterior part of the ventral cranium.

Two evolutionary processes, sexual and natural selection, have the highest impact on the morphological variability of males and females (Shine, 1989; Andersson, 1994; Fairbairn, 1997; Hendry et al., 2014). Therefore, the difference between sexes is a consequence of differential interaction of each sex with environment and interaction between sexes (Herrel et al., 2001; Sacchi et al., 2009; Peiman & Robinson, 2010; Lailvaux et al., 2012). In the context of sexual selection, sexually dimorphic size and shape of the cranium could evolve through intrasexual competition where cranial traits provide advantages in breeding opportunities to some individuals through contests of dominance or attracting the opposite sex. For example, maximum bite force linked to features of cranial-jaw complex contributes to successful breeding in reptiles (Lappin & Husak, 2005; McBrayer & Anderson, 2007). In addition, sexually dimorphic size and shape of the cranium could arise through natural selection and intersexual niche divergence in order to reduce intersexual competition for resources and habitat use. Indeed, many studies showed that skull dimorphism is mainly restricted to differences in the size and shape of the parts that can affect bite force and prey size (Vincent, et al., 2004; Herrel et al., 2007; Kaliontzopoulou et al., 2007; Ljubisavljević et al., 2010).

Our results showed that females had larger ventral cranium and bodies than males, therefore sexual dimorphism in cranial size is most probably an indirect consequence of natural selection favoring larger body for higher fecundity in explosive breeders like brown frogs (Woolbright, 1983). In addition, brown frogs do not display male to male combats or territorial contests, or intersexual interactions like copulatory bites, so sexual dimorphism in cranial size is probably not a consequence of sexual selection. Sexual shape differences of analyzed brown frog species were most pronounced in the level of connection between cranium and jaw which indicate that differential diet of males and females can be a factor affecting observed sexual dimorphism patterns. However, studies about the diet of brown frogs males and females are almost not existing (Cicort-Lucaciu et al., 2011) so the direct link between observed intersexual cranial shape variation and diet variation cannot be established. Study of the dorsal cranium variation in the European brown species showed that ecologically similar species (in habitat characteristics and type of locomotion) shared the cranial morphology (Krstičić Račković et al., 2019). However, more detailed studies of males and females microhabitats are necessary

to conclude if differences in intersexual ecology affect intersexual size and shape differences in the cranium.

Observed patterns of sexual dimorphism in cranial size and shape of three brown frog species indicate that further studies are necessary in order to find causes and consequences of intersexual variation of the cranium.

ACKNOWLEDGMENTS

The research was funded by the Ministry of Education, Sciences and Technological Development (grant No. 173043) of the Republic of Serbia.

REFERENCES

- Andersson, M. B. 1994. Sexual selection. Princeton, New Jersey: Princeton University Press.
- Bell, R. C., & Zamudio, K. R. 2012. Sexual dichromatism in frogs: natural selection, sexual selection and unexpected diversity. *Proceedings of the Royal Society B: Biological Sciences*, 279, pp. 4687-4693. doi: 10.1098/rspb.2012.1609
- Berns, C. M. 2013. The evolution of sexual dimorphism: understanding mechanisms of sexual shape differences, *Sexual Dimorphism*, IntechOpen doi:10.5772/55154
- Bonduriansky, R. 2006. Convergent evolution of sexual shape dimorphism in Diptera. *Journal of Morphology*, 267(5), pp. 602-611. doi:10.1002/jmor.10426
- Borczyk, B., Kuszniarz, J., Paško, L., & Turniak, E. 2014. Scaling of the sexual size and shape skull dimorphism in the sand lizard (*Lacerta agilis* L.). *Vertebrate Zoology*, 64(2), pp. 221-227.
- Cardini, A., & Elton, S. 2007. Sample size and sampling error in geometric morphometric studies of size and shape. *Zoomorphology*, 126(2), pp. 121-134. doi:10.1007/s00435-007-0036-2
- Cicort-Lucaciu, A. S., Sas, I., Roxin, M., Badar, L., & Goilean, C. 2011. The feeding study of a *Rana dalmatina* population from Carei Plain, South Western Horticulture. *Biology and Environment*, 2(1), pp. 35-46.
- Cooper, M. I. 2018. Sexual size dimorphism and the rejection of Rensch's rule in Diplopoda (Arthropoda). *Journal of Entomology and Zoology Studies*, 6(1v), pp. 1582-1587. doi:10.22271/j.ento.2018.v6.i1v.07
- Cox, R. M., & Calsbeek, R. 2010. Sex-specific selection and intraspecific variation in sexual size dimorphism. *Evolution: International Journal of Organic Evolution*, 64(3), pp. 798-809. doi: 10.1111/j.1558-5646.2009.00851.x
- Dryden, I. L., & Mardia, K.V. 1998. Statistical analysis of shape. New York: John Wiley and Sons.
- Džukić, G., & Kalezić, M. L. 2004. The biodiversity of amphibians and reptiles in the Balkan Peninsula. In H.I. Griffiths, B. Kryštufek, & J.M. Reed Eds., *Balkan biodiversity: Pattern and process in the European hotspot*. Dordrecht: Springer Nature. pp. 167-192; doi: 10.1007/978-1-4020-2854-0_10
- Džukić, G., Cvijanović, M., Urošević, A., Vukov, T. D., Tomašević Kolarov, N., Slijepčević, M., Ivanović, A., & Kalezić, M. L. 2015. The batrachological collections of the Institute for biological research "Siniša Stanković", University of Belgrade. *Bulletin of the Natural History Museum in Belgrade*, 8, pp. 118-167. doi:10.5937/bnhmb1508118D
- Fairbairn, D. J. 1997. Allometry for sexual size dimorphism: Pattern and Process in the Coevolution of Body Size in Males and Females. *Annual Review of Ecology and Systematics*, 28(1), pp. 659-687. doi:10.1146/annurev.ecolsys.28.1.659
- Fairbairn, D. J. 2013. *Odd Couples: Extraordinary differences between the sexes in the animal kingdom*. Princeton: Walter de Gruyter GmbH. doi:10.1515/9781400847600
- Fairbairn, D. J., Blanckenhorn, W.U., Székely, T., & Eds., 2007. *Sex, size and gender roles: Evolutionary studies of sexual size dimorphism*. Oxford: Oxford University Press. doi: 10.1093/acprof:oso/9780199208784.001.0001
- Friedman, N. R., & Remeš, V. 2016. Global geographic patterns of sexual size dimorphism in birds, port for a latitudinal trend. *Ecography*, 39(1), pp. 17-25. doi: 10.1111/ecog.01531
- Gittleman, J. L., & Van, V. B. 1997. Sexual dimorphism in the canines and skulls of carnivores: effects of size, phylogeny, and behavioural ecology. *Journal of Zoology*, 242(1), pp. 97-117. doi: 10.1111/j.1469-7998.1997.tb02932.x
- Hallgrímsson, B., & Hall, B. K. 2005. Variation and variability: Central concepts in biology. In B. Hallgrímsson & B. K. Hall Eds., *Variation*. Burlington, MA, USA: Elsevier. pp. 1-7; doi: 10.1016/B978-012088777-4/50003-X
- Hendry, C. R., Guhier, T. J., & Pyron, R. A. 2014. Ecological divergence and sexual selection drive sexual size dimorphism in new world pitvipers (Serpentes: Viperidae). *Journal of evolutionary biology*, 27(4), pp. 760-771. doi: 10.1111/jeb.12349
- Herrel, A., Damme, R. V., Vanhooydonck, B., & Vree, F. D. 2001. The implications of bite performance for diet in two species of lacertid lizards. *Canadian Journal of Zoology*, 79, pp. 662-670. doi: 10.1139/z01-031
- Herrel, A., Mcbrayer, L., & Larson, P. 2007. Functional basis for sexual differences in bite force in the lizard *Anolis carolinensis*. *Biological Journal of the Linnean Society*, 91, pp. 111-119. doi: 10.1111/j.1095-8312.2007.00772.x
- Herrel, A., Spithoven, L., van Damme, R., & Vree, F. D. 1999. Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. *Functional Ecology*, 13(3), pp. 289-297. doi: 10.1046/j.1365-2435.1999.00305.x
- Hoffman, E. A., & Blouin, M. S. 2000. A review of colour and pattern polymorphisms in anurans. *Biological Journal of the Linnean Society*, 70(4), pp. 633-665. doi: 10.1111/j.1095-8312.2000.tb00221.x
- Ivanović, A., & Kalezić, M. L. 2012. Sexual dimorphism in the skull geometry of newt species of *Ichthyosaura*, *Triturus* and *Lissotriton* (Salamandridae, Caudata Amphibia). *Zoomorphology*, 131(1), pp. 69-78. doi: 10.1007/s00435-011-0143-y
- Ivanović, A., Sotiropoulos, K., Furtula, M., Džukić, G., & Kalezić, M. L. 2008. Sexual size and shape evolution in European newts (Amphibia: Caudata: Salamandridae) on the Balkan Peninsula. *Journal of Zoological Systematics and*

- Evolutionary Research, 46(4), pp. 381-387. doi: 10.1111/j.1439-0469.2008.00479.x
- Ivanović, A., Vukov, T. D., Džukić, G., Tomašević, N., & Kalezić, M. L. 2007. Ontogeny of skull size and shape changes within a framework of biphasic lifestyle: a case study in six *Triturus* species (Amphibia, Salamandridae). *Zoomorphology*, 126(3), pp. 173-183. doi: 10.1007/s00435-007-0037-1
- Kalioztopoulou, A., Carretero, M. A., & Llorente, G. A. 2007. Multivariate and geometric morphometrics in the analysis of sexual dimorphism variation in *Podarcis* lizards. *Journal of Morphology*, 268, pp. 152-165. doi: 10.1002/jmor.10494
- Klingenberg, C. P. 2010. MorphoJ: an integrated software package for geometric morphometrics. *Molecular Ecology Resources*, 11(2), pp. 353-357. doi:10.1111/j.1755-0998.2010.02924.x
- Krstičić, R. J., Tomašević, K. N. T., Labus, N., & Vukov, T. 2019. Interspecific size-and sex-related variation in the cranium of European brown frogs (Genus *Rana*). *Zoomorphology*, 138(2), pp. 277-286. doi: 10.1007/s00435-019-00441-9
- Kuo, C. Y., Lin, Y. T., & Lin, Y. S. 2009. Sexual size and shape dimorphism in an Agamid lizard, *Japalura swinhonis* (Squamata: Lacertilia: Agamidae). *Zoological Studies*, 48(3), pp. 351-361.
- Lailvaux, S. P., Huyghe, K., & Van, D. R. 2012. 'Why can't we all just get along?', Interspecific aggression in resident and non-resident *Podarcis melisellensis* lizards'. *Journal of Zoology*, 288(3), pp. 207-213. doi: 10.1111/j.1469-7998.2012.00943.x
- Lappin, A. K., & Husak, J. F. 2005. Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *The American Naturalist*, 166(3), pp. 426-436. doi: 10.1086/432564
- Ljubisavljević, K., Urošević, A., Aleksić, I., & Ivanović, A. 2010. Sexual dimorphism of skull shape in a lacertid lizard species (*Podarcis* spp. *Dalmatolacerta* sp. *Dinarolacerta* sp.) revealed by geometric morphometrics. *Zoology*, 113(3), pp. 168-174. doi: 10.1016/j.zool.2009.09.003
- Mcbrayer, L. D., & Anderson, R. A. 2007. Sexual size dimorphisms and bite force in the northern alligator lizard, *Elgaria coerulea*. *Journal of Herpetology*, 41(4), pp. 554-560. doi: 10.1670/07-045.1
- Mcpherson, F. J., & Chenoweth, P. J. 2012. Mammalian sexual dimorphism. *Animal reproduction science*, 131(3-4), pp. 109-122. doi: 10.1016/j.anireprosci.2012.02.007
- Monnet, J. M., & Cherry, M. I. 2002. 'Sexual size dimorphism in anurans', *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 269(1507), pp. 2301-2307. doi: 10.1098/rspb.2002.2170
- Morris, J. S., & Carrier, D. R. 2016. Sexual selection on skeletal shape in Carnivora. *Evolution*, 70(4), pp. 767-780. doi: 10.1111/evo.12904
- Ng, T. P., Rolán-Alvarez, E., Dahlén, S. S., Davies, M. S., Estévez, D., Stafford, R., & Williams, G. A. 2019. The causal relationship between sexual selection and sexual size dimorphism in marine gastropods. *Animal Behaviour*, 148, pp. 53-62. doi: 10.1016/j.anbehav.2018.12.005
- Peiman, K., & Robinson, B. 2010. Ecology and evolution of resource-related heterospecific aggression. *The Quarterly Review of Biology*, 85(2), pp. 133-158. doi: 10.1086/652374
- Petrović, T. G., Vukov, T. D., & Kolarov, N. T. 2017. Sexual dimorphism in size and shape of traits related to locomotion in nine anuran species from Serbia and Montenegro. *Folia Zoologica*, 66(1), pp. 11-22. doi: 10.25225/fozo.v66.i1.a4.2017
- Plavcan, J. M. 2012. Sexual Size Dimorphism, Canine Dimorphism, and Male-Male Competition in Primates. *Human Nature*, 23(1), pp. 45-67. doi:10.1007/s12110-012-9130-3
- Porobić, J., Ćirović, D., & Jojić, V. 2016. Cranial variability of the Serbian golden jackal: Geographic variation, sexual dimorphism and allometry. *Zoologischer Anzeiger-A Journal of Comparative Zoology*, 261, pp. 38-47. doi: 10.1016/j.jcz.2016.03.004
- Price, T. D. 1984. The Evolution of Sexual Size Dimorphism in Darwin's Finches. *The American Naturalist*, 123(4), pp. 500-518. doi:10.1086/284219
- R Core Team 2015. R: a language and environment for statistical computing, Version 3.2.0, R Foundation for Statistical Computing, Vienna, <http://cran.R-project.org>
- Rohlf, F. J. 2008. TpsDig. In *Ecology and Evolution*. SUNY at Stony Brook. Version 2.12.
- Sacchi, R., Pupin, F., Gentilli, A., Rubolini, D., Scali, S., Fasola, M., & Galeotti, P. 2009. Male-male combats in a polymorphic lizard: Residency and size, but not color, affect fighting rules and contest outcome, *Aggressive Behavior*. Official Journal of the International Society for Research on Aggression, 35(3), pp. 274-283. doi: 10.1002/ab.20305
- Shine, R. 1979. Sexual Selection and Sexual Dimorphism in the Amphibia. *Copeia*, 1979(2), p. 297. doi:10.2307/1443418
- Shine, R. 1989. Ecological Causes for the Evolution of Sexual Dimorphism: A Review of the Evidence. *The Quarterly Review of Biology*, 64(4), pp. 419-461. doi:10.1086/416458
- Sillero, N., Campos, J., Bonardi, A., Corti, C., Creemers, R., Crochet, P. A., Crnobrnja Isailović, J., Denoël, M., Ficetola, G. F., Gonçalves, J., Kuzmin, S., Lymberakis, P., de Pous, P., Rodríguez, A., Sindaco, R., Speybroeck, J., Toxopeus, B., Vieites, D. R., Vences, M. 2014. Updated distribution and biogeography of amphibians and reptiles of Europe. *Amphibia-Reptilia*, 35(1), pp. 1-31. doi:10.1163/15685381-00002935
- Snyder, N. F., & Wiley, J. W. 1976. Sexual size dimorphism in hawks and owls of North America. *Ornithological Monograph*. Washington DC: American Ornithologists' Union. no. 20; doi: 10.2307/40166710
- StatSoft, Inc. 2011. Statistica (data analysis software system). version 10, www.statsoft.com
- Vincent, S.E., Herrel, A., & Irschick, D.J. 2004. Sexual dimorphism in head shape and diet in the cottonmouth snake (*Agkistrodon piscivorus*). *Journal of Zoology*, 264(1), pp. 53-59. doi: 10.1017/S0952836904005503
- Vladić, Ž. J., Benítez, H. A., Pirnat, A., Hristovski, S., & Jelaska, L. Š. 2019. Variations in body shape of mountain habitat specialist *Carabus croaticus* and its sister species *Carabus caelatus* (Coleoptera: Carabidae) populations across Dinaric

- Alps. *Zoomorphology*, 138(1), pp. 85-96. doi: 10.1007/s00435-018-0428-5
- Vukov, T., Krstičić, J., Petrović, T., & Tomašević, K. N. 2018. Patterns of cranial sexual dimorphism in the yellow-bellied toad (*Bombina variegata*, Bombinatoridae). *North-Western Journal of Zoology*, 14(1), pp. 44-49.
- Woolbright, L. L. 1983. Sexual Selection and Size Dimorphism in Anuran Amphibia. *The American Naturalist*, 121(1), pp. 110-119. doi:10.1086/284042
- Zhang, L., & Lu, X. 2013. Sexual size dimorphism in anurans: ontogenetic determination revealed by an across-species comparison. *Evolutionary Biology*, 40(1), pp. 84-91. doi: 10.1007/s11692-012-9187-2