Research Article

A surprising pattern of Sexual Dimorphism in the Eurasian otter (*Lutra lutra*) in Sweden

Federica Pontieri[1,2], Luca Francesco Russo[1,*], Pasquale Raia[2], Anna Loy[1,3]

[1]*EnvixLab, Department of Biosciences and Territory, Università degli Studi del Molise, Pesche, Italy*
[2]*Department of Earth Sciences, Environment and Resources, University of Naples Federico II, 80138 Naples, Italy*
[3]*IUCN Species Survival Commission, Otter Specialist Group, Rue Mauverney 28, 1196 Gland, Switzerland*

Abstract

Sexual dimorphism is a very common strategy in polygamous mammals. In mustelids, sexual size dimorphism (SSD) is present in several species, while sexual shape dimorphism (SShD) is not as common. The Eurasian otter is a semiaquatic mustelid, exclusively feeding on aquatic prey, mainly fish, amphibians, and crustaceans. It is well-known that male otters tend to be larger, whereas information on SShD is contrasting. We used a 3D geometric morphometric approach to investigate SSD and SShD in three genetically distinct populations of otters located in Northern, Central and Southern Sweden. We analyzed 71 otter skulls (M=41, F=30), using photogrammetric techniques to produce 3D models of each skull, placing 30 3D landmarks on each model. We found that sexual dimorphism varies among populations. Neither SSD nor SShD occurred in the North, only SSD occurred in the Centre, and both SSD and SShD are present in the South of Sweden. Allometric trajectories of males and females from the North population differed from those of the other two populations. Our results highlighted a great variability in sexual dimorphism in Swedish Eurasian otters, that probably derives from different responses to prey availability and historical contingencies.

Introduction

The Eurasian otter (*Lutra lutra*) is a semi-aquatic mustelid, inhabiting a variety of habitats, from inland freshwater to coastal environments (Loy et al., 2022). It is the most widespread species among Lutrinae, occurring over Eurasia and Northern Africa (Hung and Law, 2016; Loy et al., 2022).

The Eurasian otter is a *mouth-oriented* predator, meaning it captures prey by using the mouth (Carss, 1995; Timm-Davis et al., 2015). The otter diet typically includes fish, crustaceans, amphibians, and to a lower extent birds and small mammals (Russo et al., 2023; Clavero et al., 2003; Hung and Law, 2016; Lanszki et al., 2016; Remonti et al., 2010). Yet, diet greatly varies depending on the season and prey availability (Clavero et al., 2003; Moorhouse-Gann et al., 2020). The Eurasian otter has a polygynous mating system (Loy et al., 2022) with males larger than females and owing territories overlapping with those of several females (Kruuk, 2006). Male-oriented sexual size dimorphism (SSD) is typical of mustelids and may promote intersexual niche differentiation (Law and Mehta, 2018; Loy et al., 2004). Beyond SSD, a number of studies also reported Sexual Shape Dimorphisms (SShD) in mustelids (Gálvez-López et al., 2022; Loy et al., 2004), even among individual populations (Galatius et al., 2021; Russo et al., 2022).

Herein, we focused on cranial shape and size variability in the Swedish populations of *Lutra lutra*. The genetic variation of Swedish otters was explored by Arrendal et al. (2004), who found sizeable genomic differences occurring among populations living in different geographic areas. Yom-Tov et al. (2010) further reported a significant difference in cranial size associated with latitude. Moreover, otters in

Sweden suffered a strong population decline during the last century due to hunting, water pollution, and habitat degradation (Roos et al., 2001). In the late '80s, otters still occurred in Northern Sweden, although scattered in fragmented groups, whereas the species was virtually absent from the Southern portion of the country (Roos et al., 2001). Following legal protection, habitat restoration, and the ban on harmful pollutants, the species is now recovering throughout Sweden (Björklund and Arrendal, 2008). Hence, by using geometric morphometrics (GMMs) on 3D models of otter skulls we investigated whether: *i)* both SSD and SShD could be detected in the Swedish otter populations and *ii)* if any geographic shape and size variation of the skull was detectable according to genetic differences found by Arrendal et al. (2004) in Swedish otters.

## Materials and Methods

Data collection

We analysed 71 otter skulls (M = 41, F = 30) stored in the Swedish Museum of Natural History. We included only adult specimens for which information on sex and sample locality were available from the museum labels. Skulls were aged according to the degree of obliteration of the following cranial joints: nasal, frontoparietal, zygomatic, squamous-parietal, and pre-basisphenoid-basioccipital (Lynch.ea.1996). Sample localities were pooled into three geographic regions based on ecoregions (Olson et al., 2001) and genetic clusters found by (Arrendal et al., 2004). In particular: 11 individuals from Northern (M=7 and F=4), 30 from Central (M=18 and F=10), and 30 from Southern (M=16 and F=16) population (Fig. 1).

Each skull was placed on a turntable and photographed at regular 10° intervals from the dorsal, ventral, and vertical views, summing to 108 pictures (36 pictures per view ∗ 3 different views). Pictures were
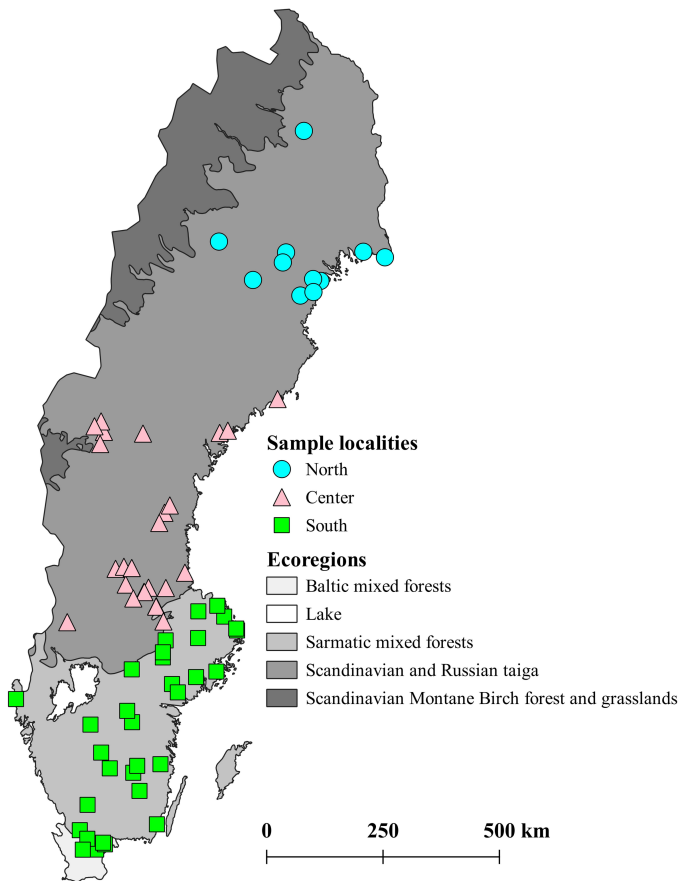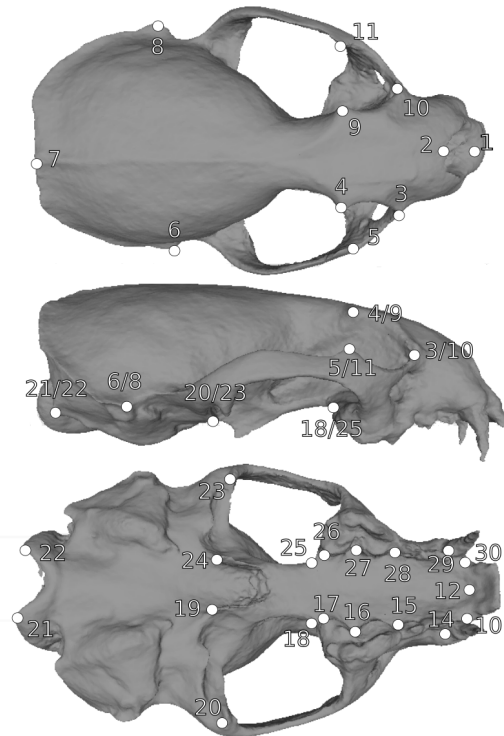
Figure 1 – Distribution of sample localities overlapped to ecoregions according to WWF (Olson et al., 2001). Coloured squares represent geographic regions North (blue), Centre (pink), South (green) .

Figure 2 – Selected landmarks. 1 = Superior premaxilla; 2= nasal suture; 3-10 = lacrimal; 4-9 = postorbital process 5-11; = zygomatic arch;6-8 = mastoid process; 7 = intersection of temporal line and sagittal crest; 12 = prosthion;13-30 = premaxilla and nasal bone suture;14-29 = canine alveoli; 15-28 = carnassial alveoli; 16-27 = carnassial alveoli; 17-26 = toothrow; 18-25 = palatine; 19-24 = pterygoid; 20-23 = glenoid cavity; 21-22 = occipital condyle.

shot with a Canon 30EOS camera with a 50 mm lens placed on a tripod at a fixed distance from the turntable. 3D models of the skull were then produced using photogrammetry (Giacomini et al., 2019; Loy et al., 2021; Sansalone et al., 2020), a method which is virtually as accurate as digital reconstructions performed with laser scanners (Evin et al., 2016; Giacomini et al., 2019). The 3D models reconstructions were implemented using the Agisoft software (Agisoft PhotoScan, www.agisoft.com). The scale factor was derived from 2D images according to the following procedure: on each image we recorded the total length of the skull in cm through TpsDig; the length was used to set the scale of the 3D model of the same skull in Meshlab (Cignoni et al., 2008), prior to landmarks recording. Thirty unique 3D landmarks were placed on 3D models using Meshlab (Fig. 2).

Morphometric analyses

Landmarks configurations were imported in the R environment (R Core Team, 2022) and the original landmark coordinates transformed through Generalized Procrustes Analysis (GPA, Rohlf et al., 1990) implemented in the function *gpagen()* of 'geomorph' package (Adams et al., 2021). GPA removes the effect of orientation, position, and size on shape variability. The centroid size, i.e. the square root of the sum of squared distances among landmarks (Bookstein, 1992), was extracted and log transformed (LnCS) to ensure normality. LnCS was used as a proxy of skull size (Rohlf et al., 1990).

To evaluate the presence of static allometry (*sensu* Klingenberg, 2016) we examined the allometric trajectories of each population using the function *procD.lm()* in 'geomorph' package. To investigate on sexual dimorphism we computed the size-adjusted shape by extracting the residuals from the Procrustes ANOVA output. We then run Procrustes ANOVA on adjusted shape coordinates to detect any sexual shape dimorphism (SShD), and ANOVA on LnCS to evaluate sexual size dimorphism (SSD) in the whole sample and among populations.
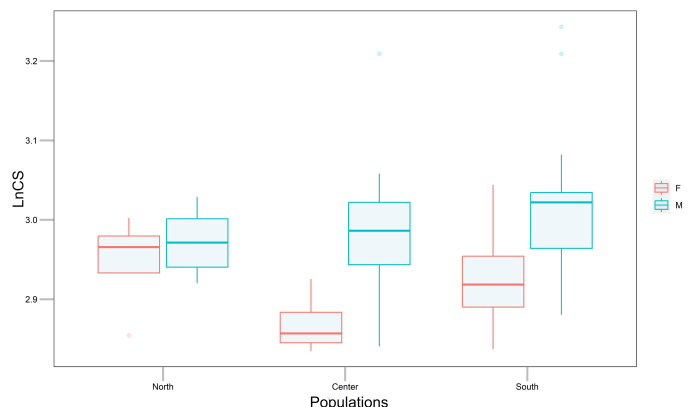
Results

Sexual dimorphism

ANOVAs performed on LnCS considering the effect of sex showed a significant difference in size between males and females (Rsq=0.256, p<0.01), confirming SSD as a significant component of sexual dimorphism of the Eurasian otter. A significant difference between sexes was equally found for skull shape (Procrustes ANOVA; Rsq=0.033, p<0.01), indicating that SShD occurs in Swedish otters. SSD and SShD were then analysed separately in the three populations. Box plots (Fig. 3) suggest that size difference between males and females is less marked in the Northern compared to both Central and Southern populations. ANOVA on LnCS performed separately within the three populations revealed that differences in size were significant only for the latter (Tab. 1).

Shape differences between males and females explored in each population showed significant differences only in the Southern population (Tab. 2). PCA run on shape coordinates of this population evidenced a

Figure 3 – Boxplot of LnCS between sexes and among the three different populations .

15

Table 1 – Results for ANOVA on differences in LnCS between sexes in Northern (a), Central (b), and Southern (c) populations.

Northern	Df	SS	MS	Rsq	F	Z	Pr(>F)
Sex	1	0.002	0.002	0.067	0.642	0.139	0.457
Residuals	9	0.022	0.002	0.933			
Total	10	0.024					
Central	**Df**	**SS**	**MS**	**Rsq**	**F**	**Z**	**Pr(>F)**
Sex	1	0.088	0.088	0.419	18.789	3.177	0.001
Residuals	26	0.121	0.005	0.581			
Total	27	0.209					
Southern	**Df**	**SS**	**MS**	**Rsq**	**F**	**Z**	**Pr(>F)**
Sex	1	0.071	0.071	0.275	11.379	2.606	0.002
Residuals	30	0.187	0.006	0.725			
Total	31	0.258					

clear distinction between males and females along the first component, explaining 15 % cumulative variance (Fig. 4). Wireframes related to the extreme of PC1 axis revealed that the main morphological changes between males and females are concentrated in the maxillary area and the posterior part of the braincase. Specifically, females have a more elongated basicranium, a narrower zygomatic arch, a narrower space between the tips of the pterygoid process, and a larger post-orbital constriction.

Table 2 – Results for Procrustes ANOVA on adjusted shape. SShD variation in in Northern (a), Central (b), and Southern (c) populations.

| Northern	Df	SS	MS	Rsq	F	Z	Pr(>F)
Sex	1	0.002	0.002	0.135	1.400	1.254	0.104
Residuals	9	0.010	0.001	0.865			
Total	10	0.011					
Central	**Df**	**SS**	**MS**	**Rsq**	**F**	**Z**	**Pr(>F)**
Sex	1	0.001	0.001	0.028	0.762	-0.690	0.761
Residuals	26	0.037	0.001	0.972			
Total	27	0.038					
Southern	**Df**	**SS**	**MS**	**Rsq**	**F**	**Z**	**Pr(>F)**
Sex	1	0.003	0.003	0.062	1.986	2.811	0.005
Residuals	30	0.041	0.001	0.938			
Total	31	0.044					

Allometry

Multivariate regression of shape coordinates *vs* LnCS highlighted that allometric trajectories differ both among populations and sexes (Tab. 3), with diverging directions between males and females in the Southern and Northern populations (Fig. 5). Specifically, males and females of the Northern population showed convergent trajectories, whereas in the Southern and Central population they run parallel, either shifted (South) or overlapped (Centre).

Discussion

Our results highlighted that the skull of the Eurasian otter from Sweden is characterized by sexual dimorphism of in both size (SSD) and shape (SShD). Yet, the extent and significance of these patters have a strong geographic underpinning. The degree of sexual dimorphism, the traits involved in sex differentiation, as well as allometric trajectories of males and females differed among North, Centre, and South of Sweden. Specifically, in the South both SSD and SShD occur. In the Centre
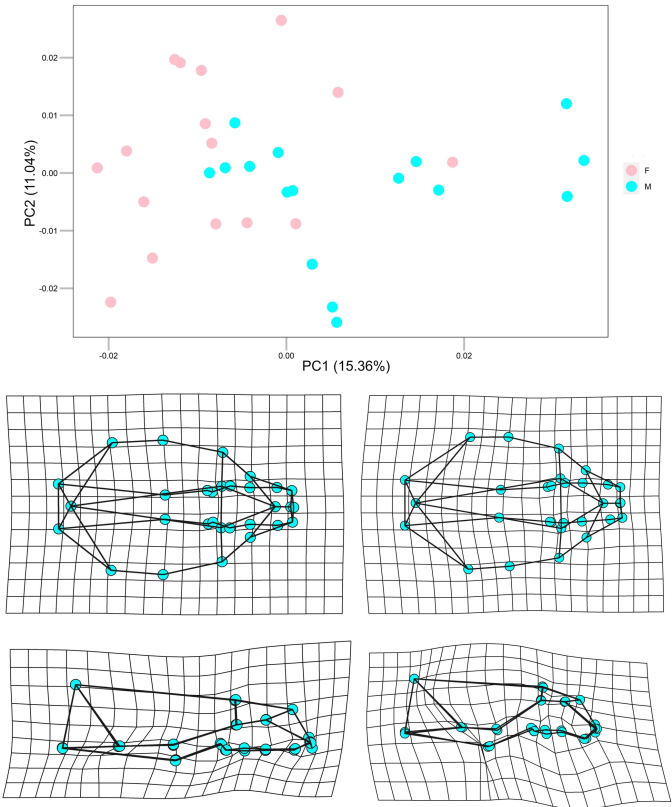
Figure 4 – Principal Component Analysis(PCA) run on aligned coordinates only of the South population. Blue dots represent males, pink dots females. Wireframes below the x axis show shape variation at extremes of PC1 axis .
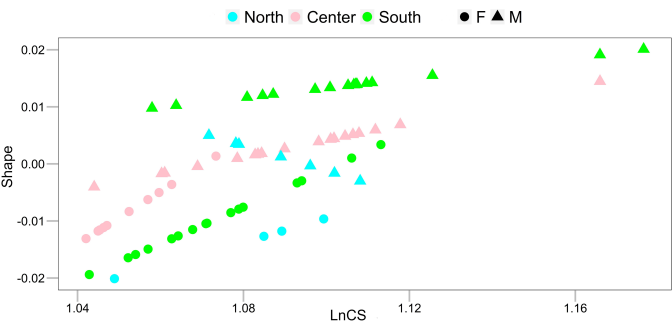
Figure 5 – Multivariate regression LnCS vs shape coordinates. Colours referrers to populations: North (blue), Centre (pink), South (green), triangles refer to males and circles to females symbols to sexes .

only SSD is present, whereas neither SSD nor SShD were detected in the Northern population. Although SSD is common in Mustelidae and known to occur in the Eurasian otter in relation to their polygynous

Table 3 – Results for Procrustes ANOVA testing allometry.

a) Allometry	Df	SS	MS	Rsq	F	Z	Pr(>F)
Size	ht1	0.006	0.006	0.055	4.287	4.588	0.001
Sex	ht1	0.004	0.004	0.042	3.249	3.489	0.002
Popul.	ht 2	0.005	0.002	0.045	1.754	2.825	0.002
Size:Sex	ht1	0.001	0.001	0.013	1.045	0.267	0.391
Size:Popul.	ht2	0.004	0.002	0.037	1.433	1.661	0.047
Sex:Popul.	ht2	0.003	0.001	0.028	1.077	0.430	0.332
Size:Sex:Popul.	ht2	0.003	0.001	0.027	1.037	0.311	0.384
Residuals	ht59	0.080	0.001	0.755			
Total	ht70	0.107					

mating system (Law, 2019; Law and Mehta, 2018), SShD was only described in a few species within the family (i.e. Gálvez-López et al., 2022; Loy et al., 2004). Moreover, differences observed in SSD, SShD among populations suggest that the three populations follow different strategies of resource partitioning between sexes (McNab, 2010).

In the South, males have larger skulls, wider zygomatic arches and higher skulls compared to females. These traits allow an increased masseter and temporalis mass, enhancing the bite force (Campbell et al., 2017; Law et al., 2016). In contrast, the slender, elongate skull of females allows for faster closure of the jaws (Timm-Davis et al., 2015). These difference are clearly suggestive of different abilities to catch prey items between males and females (Campbell et al., 2017; Senawi et al., 2015; Timm-Davis et al., 2015) that in turn may result in differences in their trophic niche aimed at reducing intraspecific competition (Law and Mehta, 2018; Loy et al., 2004). On the other hand, male otters from Central Sweden only showed larger skulls but no differences in skull shape, suggesting larger bite force compared to females (Law and Mehta, 2018). Differences in bite force might be related to different abilities in catching the same prey of different size, i.e. larger prey by males and smaller prey by females. In fact, availability of prey in Sweden is more stable and diversified at lower latitudes (Tammi et al., 2003; Yom-Tov et al., 2010), whereas biodiversity decreases at high latitudes, limiting the opportunities for niche differentiation between the sexes (Erlinge, 1979). On the other extreme, the North population did not show any evidence of sexual dimorphism, either in size or shape. As stated before, whereas shape dimorphism is rare in mustelids, lack of SSD was quite unexpected. However, Yom-Tov et al. (2010) found an inverse relation between otter body size and latitude in Sweden, and absence of sexual dimorphism in the small sized northern population would be in accordance to Rensch's rule, predicting that size dimorphism within a lineage decreases with decreasing body size when the male is the larger sex Rensch (1950).

The absence of both SSD and SShD in the northern population can therefore be attributed to both a lower diversity of prey, which limits the possibility of diet shifting between males and females, and to the effects of the Rensch's rule.

The North population also showed different allometric trajectories of males and females compared to the populations from central and southern Sweden, suggesting a different origin for this population. In fact, allometric trajectories are related to developmental processes and heterochrony, and have long been recognized as a key evolutionary pattern (Souquet et al., 2022). Yet, to date, little is known empirically whether static allometry (measured in adult forms only), or ontogenetic allometry, may be prevalent in what circumstances (Souquet et al., 2022). According to Mucci et al. (2010) the post glacial recolonization of Sweden occurred from two main directions, from Finland, the likely origin of the Northern population, and from Denmark, giving rise to the southern and central populations. However, Galatius et al. (2021), recently suggested that gene flow among populations in Denmark and Sweden has historically been low, likely promoting the genetic and adaptive divergence of the Southern, Central and Northern populations in Sweden evidenced by Arrendal et al. (2004) and confirmed by this study.

Our results evidenced that sexual dimorphism in the Eurasian otter varies among genetically different population, likely reflecting both their past history, and the response to resource availability and competitive intraspecific interactions. 🖎

References

Adams D.C., Collyer M.L., Kaliontzopoulou A., Baken E.K. 2021. Geomorph: Software for geometric morphometric analyses. R package version 4.0.

Arrendal J., Walker C.W., Sundqvist A.-K.K., Hellborg L., Vilà C., Vilà C. 2004. Genetic evaluation of an otter translocation program. Conserv. Genet. 5(1): 79–88. doi:10.1023/B:COGE.0000014059.49606.dd.

Björklund M., Arrendal J. 2008. Demo-genetic analysis of a recovering population of otters in Central Sweden. Anim. Conserv. 11(6): 529–534. doi:10.1111/j.1469-1795.2008.00214.x.

Bookstein F.L. 1992. Morphometric Tools for Landmark Data. Cambridge University Press(Ed.), Cambridge University Press, New York.

Campbell K.M., Santana S.E. 2017. Do differences in skull morphology and bite performance explain dietary specialization in sea otters? J. Mammal. 98(5): 1408–1416. doi:10.1093/jmammal/gyx091.

Carss N. 1995. Foraging behaviour and feeding ecology of the otter *Lutra lutra*: a selective review. Hystrix, Ital. J. Mammal. 7(1–2): 179–194. doi:https://doi.org/10.4404/hystrix-7.1-2-4069.

Cignoni P., Callieri M., Corsini, M., Dellepiane M., Ganovelli F., Ranzuglia G. 2008. MeshLab: An open-source mesh processing tool. 6th Eurographics Ital. Chapter Conf. 2008 - Proc. (February 2015): 129–136. doi:10.2312/LocalChapterEvents/ItalChap/ItalianChapConf2008/129-136.

Clavero M., Prenda J., Delibes M. 2003. Trophic diversity of the otter (*Lutra lutra* L.) in temperate and Mediterranean freshwater habitats. J. Biogeogr. 30(5): 761–769. doi:10.1046/j.1365-2699.2003.00865.x.

Erlinge S. 1979. Adaptive Significance of Sexual Dimorphism in Weasels. Oikos 33(2): 233. doi:10.2307/3544000.

Evin A., Souter T., Hulme-Beaman A., Ameen C., Allen R., Viacava P., Larson G., Cucchi T., Dobney K. 2016. The use of close-range photogrammetry in zooarchaeology: Creating accurate 3D models of wolf crania to study dog domestication. J. Archaeol. Sci. Reports 9: 87–93. doi:10.1016/j.jasrep.2016.06.028.

Galatius A., Christiansen C.D., Elmeros M., Lorenzen E.D. 2021. Salty divides: geometric morphometrics reveal Danish straits as barriers to otter migration. Mamm. Biol. 101(6): 1109–1114. doi:10.1007/S42991-021-00171-W.

Gálvez-López E., Kilbourne B., Cox P.G. 2022. Cranial shape variation in mink: Separating two highly similar species. J. Anat. 240(2): 210–225. doi:10.1111/JOA.13554.

Giacomini G., Scaravelli D., Herrel A., Veneziano A., Russo D., Brown R.P., Meloro C. 2019. 3D Photogrammetry of Bat Skulls: Perspectives for Macro-evolutionary Analyses. Evol. Biol. 46(3): 249–259. doi:10.1007/s11692-019-09478-6.

Hung N., Law C.J. 2016. *Lutra lutra* (Carnivora: Mustelidae). Mamm. Species 48(940): 109–122. doi:10.1093/mspecies/sew011.

Klingenberg C.P. 2016. Size, shape, and form: concepts of allometry in geometric morphometrics. Dev. Genes Evol. 226(3): 113–137. doi:10.1007/s00427-016-0539-2.

Kruuk H. 2006. Otters. Oxford University Press, New York.

Lanszki J., Lehoczky I., Kotze A., Somers M.J. 2016. Diet of otters (*Lutra lutra*) in various habitat types in the Pannonian biogeographical region compared to other regions of Europe. PeerJ 4(8): e2266. doi:10.7717/peerj.2266.

Law C.J. 2019. Solitary meat-eaters: solitary, carnivorous carnivorans exhibit the highest degree of sexual size dimorphism. Sci. Rep. 9(1): 1–10. doi:10.1038/s41598-019-51943-x.

Law C.J., Mehta R.S. 2018. Carnivory maintains cranial dimorphism between males and females: Evidence for niche divergence in extant Musteloidea. Evolution (N. Y). 72(9): 1950–1961. doi:10.1111/evo.13514.

Law C.J., Young C., Mehta R.S. 2016. Ontogenetic scaling of theoretical bite force in southern sea otters (*Enhydra lutris nereis*). Physiol. Biochem. Zool. 89(5): 347–363. doi:10.1086/688313.

Loy A., Ciucci P., Guidarelli G., Roccotelli E., Colangelo, P. 2021. Developmental instability and phenotypic evolution in a small and isolated bear population. Biol. Lett. 17(4). doi:10.1098/rsbl.2020.0729.

Loy A., Kranz A., Oleynikov A., Roos A., Savage M., Duplaix, N. 2022. *Lutra lutra* (amended version of 2021 assessment). IUCN Red List Threat. Species 2022 e.T12419A218069689. doi:https://dx.doi.org/10.2305/IUCN.UK.2022-2.RLTS.T12419A218069689.en.

Loy A., Spinosi O., Carlini R. 2004. Cranial morphology of *Martes foina* and *M. martes* (Mammalia, Carnivora, Mustelidae): The role of size and shape in sexual dimorphism and interspecific differentiation. Ital. J. Zool. 71(1): 27–34. doi:10.1080/11250000409356547.

Lynch J.M., Conroy J.W.H., Kitchener A.C., Jefferies D.J., Hayden T.J. 1996. Variation in cranial form and sexual dimorphism among five European populations of the otter *Lutra lutra*. J. Zool. 238(1): 81–96. doi:10.1111/j.1469-7998.1996.tb05380.x.

McNab B.K. 2010. Geographic and temporal correlations of mammalian size reconsidered: A resource rule. Oecologia 164(1): 13–23. doi:10.1007/s00442-010-1621-5.

Moorhouse-Gann R.J., Kean E.F., Parry G., Valladares S., Chadwick E.A. 2020. Dietary complexity and hidden costs of prey switching in a generalist top predator. Ecol. Evol. 10(13): 6395–6408. doi:10.1002/ece3.6375.

Mucci N., Arrendal J., Ansorge H., Bailey M., Bodner M., Delibes M., Ferrando A., Fournier P., Fournier C., Godoy J.A., Hajkova P., Hauer S., Heggberget T.M., Heidecke D., Kirjavainen H., Krueger H.-H., Kvaloy K., Lafontaine L., Lanszki J., Lemarchand C., Liukko U.-M., Loeschcke V., Ludwig G., Madsen A.B., Mercier L., Ozolins J., Paunovic M., Pertoldi C., Piriz A., Prigioni C., Santos-Reis M., Luis T.S., Stjernberg T., Schmid H., Suchentrunk F., Teubner J., Tornberg R., Zinke O., Randi E. 2010. Genetic diversity and landscape genetic structure of otter (*Lutra lutra*) populations in Europe. Conserv. Genet. 11(2): 583–599. doi:10.1007/s10592-010-0054-3.

Olson D.M., Dinerstein E., Wikramanayake E.D., Burgess N.D., Powell G.V.N., Underwood E.C., D'Amico J.A., Itoua I., Strand H.E., Morrison J.C., Loucks C.J., Allnutt T.F., Ricketts T.H., Kura Y., Lamoreux J.F., Wettengel W.W., Hedao P., Kassem K.R. 2001. Terrestrial ecoregions of the world: A new map of life on Earth. Bioscience 51(11): 933–938. doi:https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2.

R Core Team. 2022. R: A Language and Environment for Statistical Computing. Vienna, Austria.

Remonti L., Prigioni C., Balestrieri A., Sgrosso S., Priore G. 2010. Eurasian otter (*Lutra lutra*) prey selection in response to a variation of fish abundance. Ital. J. Zool. 77(3): 331–338. doi:10.1080/11250000903229809.

Rensch B. 1950. Die Abhängigkeit der relativen Sexual differenz von der Körpergrösse. Bonner Zool. beiträge 1: 58–69.

Rohlf F.J., Slice D. 1990. Extensions of the procrustes method for the optimal superimposition of landmarks. Syst. Zool. 39(1): 40–59. doi:10.2307/2992207.

Roos A., Greyerz E., Olsson M., Sandegren F. 2001. The otter (*Lutra lutra*) in Sweden — population trends in relation to ΣDDT and total PCB concentrations during 1968–99. Environ. Pollut. 111(3): 457–469. doi:10.1016/S0269-7491(00)00085-3.

Russo L.F., Fernández-González Á., Penteriani V., Delgado M.D.M., Palazón S., Loy A., Di Febbraro M. 2023. The Different Fate of the Pyrenean Desman (*Galemys pyrenaicus*) and the Eurasian Otter (*Lutra lutra*) under Climate and Land Use Changes. Animals 13(2): 274. doi:10.3390/ani13020274.

Russo L.F., Meloro C., De Silvestri M., Chadwick E.A., Loy A. 2022. Better sturdy or slender? Eurasian otter skull plasticity in response to feeding ecology. PLoS One 17(9): e0274893. doi:10.1371/journal.pone.0274893.

Sansalone G., Allen K., Ledogar J.A., Ledogar S., Mitchell D.R., Profico A., Castiglione S., Melchionna M., Serio C., Mondanaro A., Raia P., Wroe S. 2020. Variation in the

strength of allometry drives rates of evolution in primate brain shape. Proc. R. Soc. B Biol. Sci. 287(1930). doi:10.1098/rspb.2020.0807.

Senawi J., Schmieder D., Siemers B., Kingston T. 2015. Beyond size-morphological predictors of bite force in a diverse insectivorous bat assemblage from Malaysia. doi: 10.1111/1365-2435.12447.

Souquet L., Guenser P., Girard C., Mazza M., Rigo M., Goudemand N. 2022. Temperature-driven heterochrony as a main evolutionary response to climate changes in conodonts. Proc. R. Soc. B Biol. Sci. 289(1985): 1–10. doi:10.1098/rspb.2022.0614.

Tammi J., Appelberg M., Beier U., Hesthagen T., Lappalainen A., Rask M. 2003. Fish status survey of Nordic lakes: Effects of acidification, eutrophication and stocking activity on present fish species composition. Ambio 32(2): 98–105. doi:10.1579/0044-7447-32.2.98.

Timm-Davis L.L., DeWitt T.J., Marshall C.D. 2015. Divergent skull morphology supports two trophic specializations in otters (Lutrinae). PLoS One 10(12): 1–18. doi: 10.1371/journal.pone.0143236.

Yom-Tov Y., Roos A., Mortensen P., Wiig Ø., Yom-Tov S., Heggberget T.M. 2010. Recent Changes in Body Size of the Eurasian Otter *Lutra lutra* in Sweden. Ambio 39(7): 496. doi:10.1007/S13280-010-0074-8.

Associate Editor: L.A. Wauters