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RESEARCH ARTICLE

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The effect of captivity on craniomandibular and calcaneal ontogenetic trajectories in wild boar

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Abstract

Deciphering the plastic (i.e., nonheritable) changes induced by human control over wild animals in the archeological record is challenging. Previous studies detected morphological markers associated with captivity in the cranium, mandible, and calcaneus of adult wild boar (*Sus scrofa*) but the developmental trajectories leading up to these changes during ontogeny remain unknown. To assess the impact of growth in a captive environment on morphological structures during postnatal ontogeny, we used an experimental approach focusing on the same three structures and taxon. We investigated the form and size differences of captive-reared and wild-caught wild boar during growth using three-dimensional landmark-based geometric morphometrics. Our results provide evidence of an influence of captivity on the morphology of craniomandibular structures, as wild specimens are smaller than captive individuals at similar ages. The food resources inherent to anthropogenic environments may explain some of the observed differences between captive-reared and wild specimens. The calcaneus presents a different contrasted pattern of plasticity as captive and wild individuals differ in terms of form but not in terms of size. The physically more constrained nature of the calcaneus and the direct influence of mobility reduction on this bone may explain these discrepancies. These results provide new methodological perspectives for bioarchaeological approaches as they imply that the plastic mark of captivity can be observed in juvenile specimens in the same way it has been previously described in adults.

KEYWORDS

domestication, geometric morphometrics, growth, ontogeny, phenotypic plasticity

1 | INTRODUCTION

Animal domestication is an ongoing process (Vigne, 2011; Zeder, 2012) associated with substantial phenotypic changes that form part of the so-called domestication syndrome (Lord, Larson, Coppinger, et al., 2020; Sánchez-Villagra et al., 2016; Zeder, 2012). Exploring the developmental mechanisms associated with the emergence of domestic phenotypes is crucial to document the roots of animal domestication over the last 15,000 years (Zeder, 2018). Zooarchaeologists previously considered that morphological changes observed in the archeological record, such as bone shape and size modifications, were subsequent to the integration of animals into human society (Clutton-Brock, 1992) through adaptations to the new constraints of the anthropogenic environment (Price, 1999). Therefore, morphological markers have been deemed irrelevant to document the early processes of domestication (e.g., population control trough captivity; Vigne et al., 2011), as they would only be detectable when genetic isolation and breeding selection are already in place (Frantz et al., 2015; Marshall et al., 2014). Yet, a series of recent experimental studies with wild boar (*Sus scrofa*) have demonstrated that early domestication steps, such as the control of wild animals, can be detected and quantified. These studies further showed that a lifetime in captivity induces changes in the functional demands (e.g., locomotor, foraging, or feeding behaviors), modifying the shape of craniomandibular (Neaux, Blanc, Ortiz, Locatelli, Laurens, et al., 2021; Neaux, Blanc, Ortiz, Locatelli, Schafberg, et al., 2021) and postcranial (Harbers, Neaux, et al., 2020; Harbers, Zanolli, et al., 2020) bony structures. More importantly, these studies showed that captivity leaves an anatomical imprint on the musculoskeletal system beyond the phenotypic variation range observed in animals in their natural habitat. These results have been confirmed by studies on reindeer (*Rangifer tarandus*) comparing wild and captive populations (Pelletier et al., 2020, 2021).

While previous studies detected morphological markers associated with captivity in the cranium, mandible (Neaux, Blanc, Ortiz, Locatelli, Laurens, et al., 2021; Neaux, Blanc, Ortiz, Locatelli, Schafberg, et al., 2021), calcaneus (Harbers, Neaux, et al., 2020), and humerus (Harbers, Zanolli, et al., 2020) of adult specimens, the tempo of these changes during postnatal ontogeny remains unknown. Substantial differences in terms of shape and size between wild and captive animals have already been identified in mammals during growth but with contradictory results (O'Regan & Kitchener, 2005). While some studies found greater cranial dimensions in captive lion cubs (*Panthera leo*; Smuts et al., 1978) and captive-bred chinchillas (*Chinchilla lanigera*; Crossley & del Mar Miguélez, 2001), others showed a decrease in cranial dimensions in captive Indian rhinoceroses (*Rhinoceros unicornis*; Groves, 1982) and equids (*Equus* spp.; Groves, 1966). The morphological ontogenetic changes associated with captivity therefore remain to be understood.

To assess the impact of growth in a captive environment on morphological structures during postnatal ontogeny, we used an experimental approach focusing on the same bones and taxon on which morphological markers associated with captivity were detected, that is, the cranium, mandible (Neaux, Blanc, Ortiz, Locatelli, Laurens, et al., 2021; Neaux, Blanc, Ortiz, Locatelli, Schafberg, et al., 2021), and calcaneus (Harbers, Neaux, et al., 2020) of wild boar. We collected weaned wild boar piglets from a genetically homogenous population and raised them in a captive anthropogenic environment from the age of 6 months. We scanned them in vivo at five different age classes and compared them with wild-caught wild boar populations.

To determine the influence of captivity on the growth and development of the wild boar skeleton, we compared ontogenetic changes in form (i.e., size and shape) and size between captive-reared and wild-caught specimens. We predicted that form and size differences should not differ significantly at an early age but should rather start diverging in later age classes, when the effect of captivity on morphological structures becomes more prominent. Next, we investigated differences in ontogenetic allometry, that is, the relationship between shape and size over the course of ontogeny at different ages (Alberch et al., 1979; Klingenberg, 2016), as allometry has been shown to affect postnatal ontogenetic trajectories in domesticated clades when compared to their wild counterparts (Sánchez-Villagra et al., 2017; Wilson, 2018). We hypothesized that differences in ontogenetic allometry should be significant between captive-reared and wild-caught wild boar, indicative of a plastic effect of captivity upon developmental trajectories.

2 | METHODS

2.1 | Experimental design

Captive wild boar groups (Appendix S1) consist of wild boar from the DOMEXP project: a multidisciplinary experiment aiming to assess the effect of captivity on the musculoskeletal system (http://anr-domexp.cnrs.fr/). They include the same specimens that were studied as adults by Neaux, Blanc, Ortiz, Locatelli, Laurens (2021) and Neaux, Blanc, Ortiz, Locatelli, Schafberg et al. (2021) and Harbers, Neaux et al. (2020) and Harbers, Zanolli et al. (2020). We relied on a control population of wild boar living in a 100,000 m^2 fenced forest in Urciers (France). These specimens came from a wild boar farm, where human interactions are intentionally kept to a minimum to ensure that the behavior of the wild boar remains as natural as possible. They are free to forage for food in the woods. From this population, we sampled 24 piglets that were divided into two groups of 12 specimens of equal sex ratio (6 males and 6 females). These groups were raised from the age of 6 months at the zoological reserve of La Haute-Touche (France) in two different contexts of mobility reduction: a 3000 m^2 wooded pen ("enclosure" group) and an indoor stall of 100 m^2 ("stall" group). These space restrictions, respectively, represent a reduction of 97% and 99.9% of the range of the control population and do not allow the captive specimens to roam as freely as animals from natural populations of wild boar (Palencia et al., 2019; Russo et al., 1997). We supplied individuals from both groups with processed dry food pellets including 15.5% of raw proteins adapted for domestic pig diet. These specimens were repeatedly scanned in vivo at the age of 6, 8, 11, 14, and 20 months, using a computed tomography scanner with a spatial resolution of between 100 and 500 µm at the Chirurgie et Imagerie pour la Recherche et l'Enseignement platform of the Institut National de Recherche pour l'Agriculture, l'Alimentation et l'Environnement. This experiment received ethics approval from the French Ministère de l'Enseignement Supérieur, de la Recherche et de l'Innovation (APAFIS#5353-201605111133847).

2.2 | Comparative wild-caught wild boar samples

For comparison with the two captive groups, we collected free-ranging specimens ("wild-caught" group). This group included six individuals from the control free-ranging population of Urciers (100,000 m^2) mentioned previously. Also included in the "wild-caught" groups are 15 free-ranging wild boar that were sampled in the forests of Chambord and Compiègne (approximated at 54,400,000 m^2 and 150,000,000 m^2, respectively; Harbers, Neaux, et al., 2020), belonging to similar geographic and climatic environment (i.e., temperate central France), to reduce the confounding effects of geographic and climate-induced morphological variation known to exist in *Sus scrofa* (Albarella et al., 2009; Groves, 1981; Iannuci et al., 2020). Like most wild boar in western Europe, these free-ranging specimens likely had an omnivorous diet consisting mostly of plants (e.g., acorns, roots, and crops) supplemented with animal matter (e.g., insects and earthworms) as a primary source of protein (Schley & Roper, 2003). These specimens were wild-caught either between 8 and 10 months or between 16 and 18 months of age. We based age estimation on the mandibular tooth eruption and wear stages in occlusal view comparing our specimens with the charts developed by Grant (1982) and Horard-Herbin (1997). The selection of wild-caught specimens has been performed to match at best the age variation of captive specimens. Due to the inherent difficulty of collecting juvenile wild-caught specimens, the individuals from our study do not cover fully this variation.

2.3 | Data acquisition and analyses

We used homologous landmarks and semilandmarks placed on three-dimensional surfaces to describe the morphology. Digitization and landmark definition were performed following published protocols (Appendix S2; Harbers, Neaux, et al., 2020; Neaux, Blanc, Ortiz, Locatelli, Laurens, et al., 2021; Neaux et al., 2020). We performed all the analyses in the R environment (R Core Team, 2019). Coordinates were aligned using a generalized Procrustes superimposition (Rohlf & Slice, 1990), implemented in the procSym function of the package "Morpho" (Schlager & Jefferis, 2020).

We chose to work on form, that is, the combination of size and shape (Dryden & Mardia, 1998), rather than shape as form is a more comprehensive description of an object than shape alone in the context of ontogenetic studies (Mitteroecker et al., 2013). We constructed the form space by augmenting the Procrustes coordinates by the logarithm (log) of centroid size (CS; Mitteroecker et al., 2004). The exploratory approach of the major directions of variation in this form space relies on a principal component analysis (PCA) on form variables performed on the mean form of each age class of each of the three groups. We visualized the deformations between negative and positive scores on the first two principal components (PCs) as well as the deformations between age classes for each of the three groups using heatmaps through the meshDist function of "Morpho." The lack of congruence in age class among wild-caught groups and the two captive groups prevented us from directly comparing the ontogenetic trajectories (Adams & Collyer, 2009). We, therefore, tested the difference in form between captive-reared and wild-caught groups using a factorial multivariate analysis of variance (MANOVA) through the procD.lm function of the package "geomorph" (Adams et al., 2019). We also tested the difference in CS and in body mass (Appendix S3) between captive-reared and wild-caught groups with a pairwise test and visualized it graphically with a bivariate plot. Body masses were measured on a scale before each scan in vivo for the captive-reared specimens and on uneviscerated specimens for the wild-caught ones.

To estimate and compare ontogenetic allometries between the three groups, we used a multivariate regression (Drake & Klingenberg, 2008) between shape (Procrustes coordinates) and size, computed as log CS (Collyer et al., 2015). We displayed graphically the difference in ontogenetic trajectories among our three mobility groups using a biplot of regression shape scores against log CS and tested it with a multivariate analysis of covariance through the procD.lm function.

3 | RESULTS

3.1 | Form

The factorial MANOVA (Table 1) showed that the "8-10 month wild-caught" cranium, mandible, and calcaneus forms are not significantly different from the 6- and 8-month old captive forms (i.e., stall and enclosure). Those structures are different from those of all the older captive groups. The "16-18 month wild-caught" group is not significantly different from the 11- and 14-month captive groups for any of the studied structures. The mandible and calcaneus of this age class do not differ from those of the 8-month "enclosure" nor from the 8-month "stall" groups for the mandible. They are different from those of all the other captive groups (see Appendix S4 for the factorial MANOVA between all groups).

For the PCA (Figure 1), PC1 for the cranium, mandible, and calcaneus show, respectively, 79.8%, 86.1%, and 75.5% of the total variance. For the three studied structures, PC1 displays mostly changes associated with growth as the younger specimens have the lower PC scores and the older ones have the higher scores. The cranium form changes associated with positive scores involve (1) an anteroposteriorly longer and more concave rostrum, (2) more robust zygomatic arches, and (3) smaller orbits relative to the overall cranium size (Figure 1a). For the mandible, the associated form changes towards positive scores include (1) a reduction of the gonial

TABLE 1 MANOVA *p*-values of the form coordinates between captive (stall and enclosure) and wild-caught groups of wild boar (*Sus scrofa*) computed for the cranium, mandible, and calcaneus

	Cranium		Mandible		Calcaneus	
	8–10 m wild-caught	16–18 m wild-caught	8–10 m wild-caught	16–18 m wild-caught	8–10 m wild-caught	16–18 m wild-caught
6 m— enclosure	0.21	**<0.01**	0.55	**<0.01**	0.49	**<0.01**
6 m—stall	0.27	**<0.01**	0.74	**<0.01**	0.35	**0.01**
8 m— enclosure	0.11	**0.02**	0.27	0.09	0.13	0.09
8 m—stall	0.22	**0.01**	0.38	0.05	0.22	**0.03**
11 m— enclosure	**<0.01**	0.12	**0.01**	0.42	**0.01**	0.35
11 m—stall	**0.01**	0.13	**0.01**	0.30	**<0.01**	0.20
14 m— enclosure	**<0.01**	0.17	**<0.01**	0.21	**<0.01**	0.25
14 m—stall	**<0.01**	0.15	**<0.01**	0.12	**<0.01**	0.09
20 m— enclosure	**<0.01**	**0.01**	**<0.01**	**0.01**	**<0.01**	**0.02**
20 m—stall	**<0.01**	**0.01**	**<0.01**	**0.01**	**<0.01**	**0.01**

Note: Significant values ($p < 0.05$) are in bold.

Abbreviations: m, months; MANOVA, multivariate analysis of variance.

angle, (2) a longer corpus and mandibular symphysis, and (3) a mediolateral reduction of the space between the two mandibular rami in dorsal view (Figure 1b). For the calcaneus, the changes towards positive scores consisted in (1) a shift of the sustentaculum tali and of the calcaneal sulcus towards the distal extremity, (2) a more dorsoplantarily curved calcaneus, and (3) a more elongated epiphysis that is orientated toward the plantar side (Figure 1c). PC2 bear less variation in form for the cranium, mandible, and calcaneus (respectively, 7.4%, 5.1%, and 9.1% of the total variance) but clearly distinguishes captive and wild-caught specimens. Cranial form changes along PC2 from wild-caught (low values) to captive individuals (high values) involved (1) a narrower cranium in dorsal view, specifically in the zygomatic region, (2) a less vertical occipital region, and (3) an anteroposteriorly shorter nasal and maxillary region (Figure 1a). The mandible form changes along PC2 are characterized by (1) a mediolateral narrowing, (2) a higher ramus, and (3) a ventrally orientated ramus (Figure 1b). The calcaneus form changes along PC2 mainly express (1) a downward shift of the sustentaculum tali and (2) an epiphysis more orientated toward the plantar side (Figure 1c). From 6 to 20 months, the main changes for captive specimens are localized on the zygomatic arches and on the occipital region for the cranium (Figure 1d), on the ramus and on the symphysis for the mandible (Figure 1e), and on the epiphysis, the sustentaculum tali, and the cuboid facet for the calcaneus (Figure 1f). From 8 to 10 months to 16–18 months, the changes for wild-caught specimens are localized on the same areas but are less prominent.

3.2 | Size

The size of the "8-10 month wild-caught" group is not significantly different from the 6- and 8-month captive groups for the cranium, mandible, and calcaneus (Figure 2; Table 2). It is different from all the older captive groups. The "16-18 month wild-caught" group is not significantly different from the 11- and 14-month captive groups for the cranium, the 8-, 11-, and 14-month captive groups for the mandible, and all the captive groups from 8 to 20 months for the calcaneus. The body mass of the "8-10 month wild-caught" is not significantly different from the 6-, 8-, and 11-month captive groups and the "16-18 month wild-caught" group is not significantly different from the 11- and 14-month captive groups and the "20 months–enclosure" group. All the other groups are statistically different.

3.3 | Ontogenetic allometry

We found overall ontogenetic allometry across all three structures in the three groups of mobility, which explains greater variation in calcaneus (26%) than in cranium (21%), and mandible (16%; Figure 3). The ontogenetic allometric trajectories depicted graphically are parallel between enclosure and stall captive groups across the three structures. They differ from the wild-caught group with a more positive allometry, although the interaction term was only significant for the calcaneus, indicative of a difference in allometric growth among the three groups for this structure.

4 | DISCUSSION

For the cranium, mandible, and calcaneus, we found that the form and size of the "8-10 month wild-caught" wild boar are similar to those of younger captive specimens aged between 6 and 8 months, but are significantly different from the 11-month-old animals and older ones. This may suggest that the growth in captivity of a wild

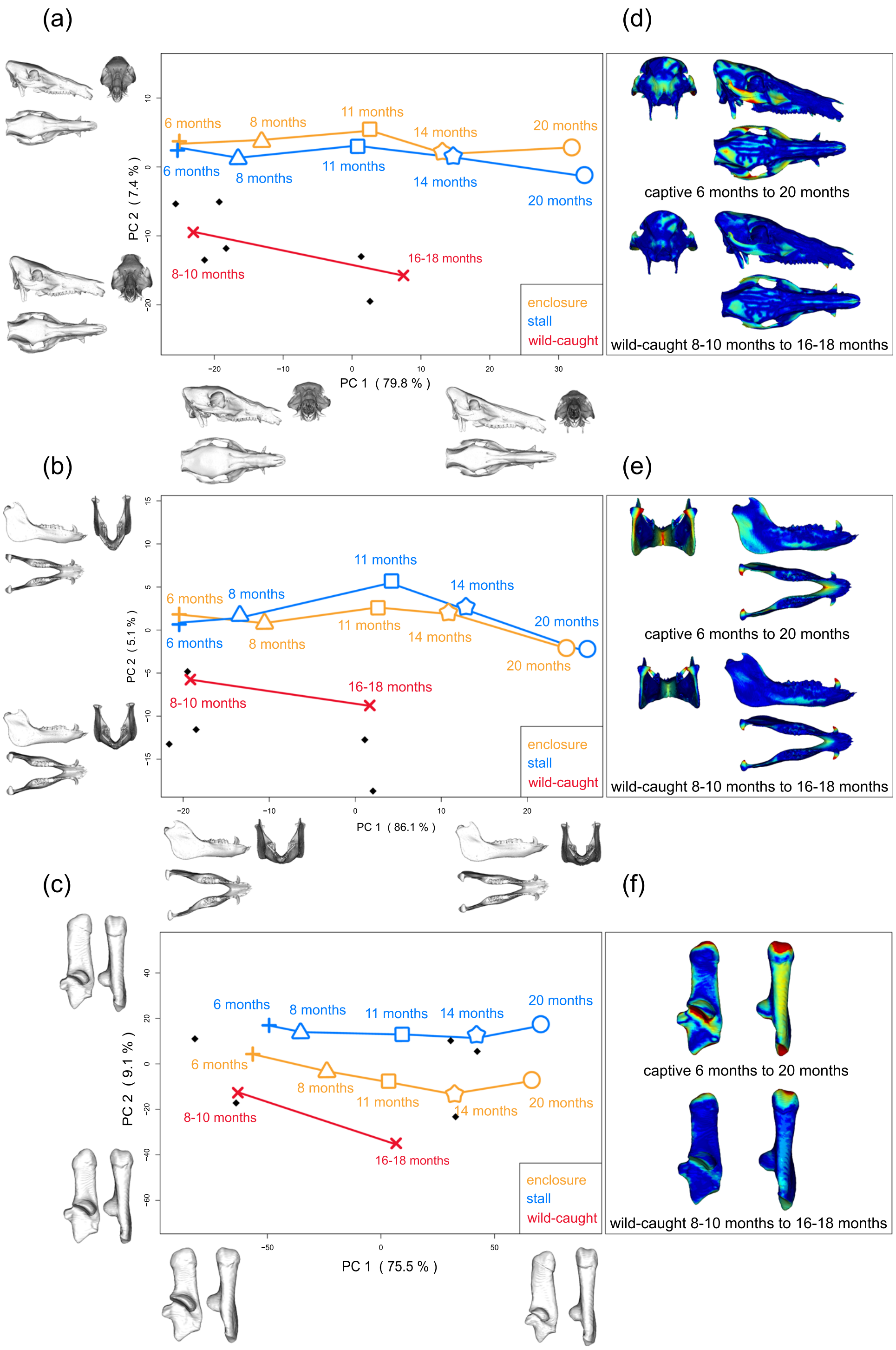

FIGURE 1 Principal component (PC) analyses for the (a) cranium, (b) mandible, and (c) calcaneus of wild boar (*Sus scrofa*) in the PC1–PC2 form space. Symbols represent the mean form for each group. Black dots represent the "control' specimens from the wild-caught group, that is, the specimens belonging to the same initial population as the individuals from the stall and enclosure groups. Form changes are depicted in lateral, dorsal, and frontal views for the cranium and the mandible, and in medial and plantar views for the calcaneus. Heatmap of the intensity of form variation between captive (i.e., enclosure and stall) groups (6 and 20 months) and between wild-caught groups (8–10 and 16–18 months) for the (d) cranium, (e) mandible, and (f) calcaneus. Blue indicates a low intensity of variation and red indicates a high intensity of variation. Form changes are depicted in lateral, dorsal, and frontal views for the cranium and the mandible, and in medial and plantar views for the calcaneus

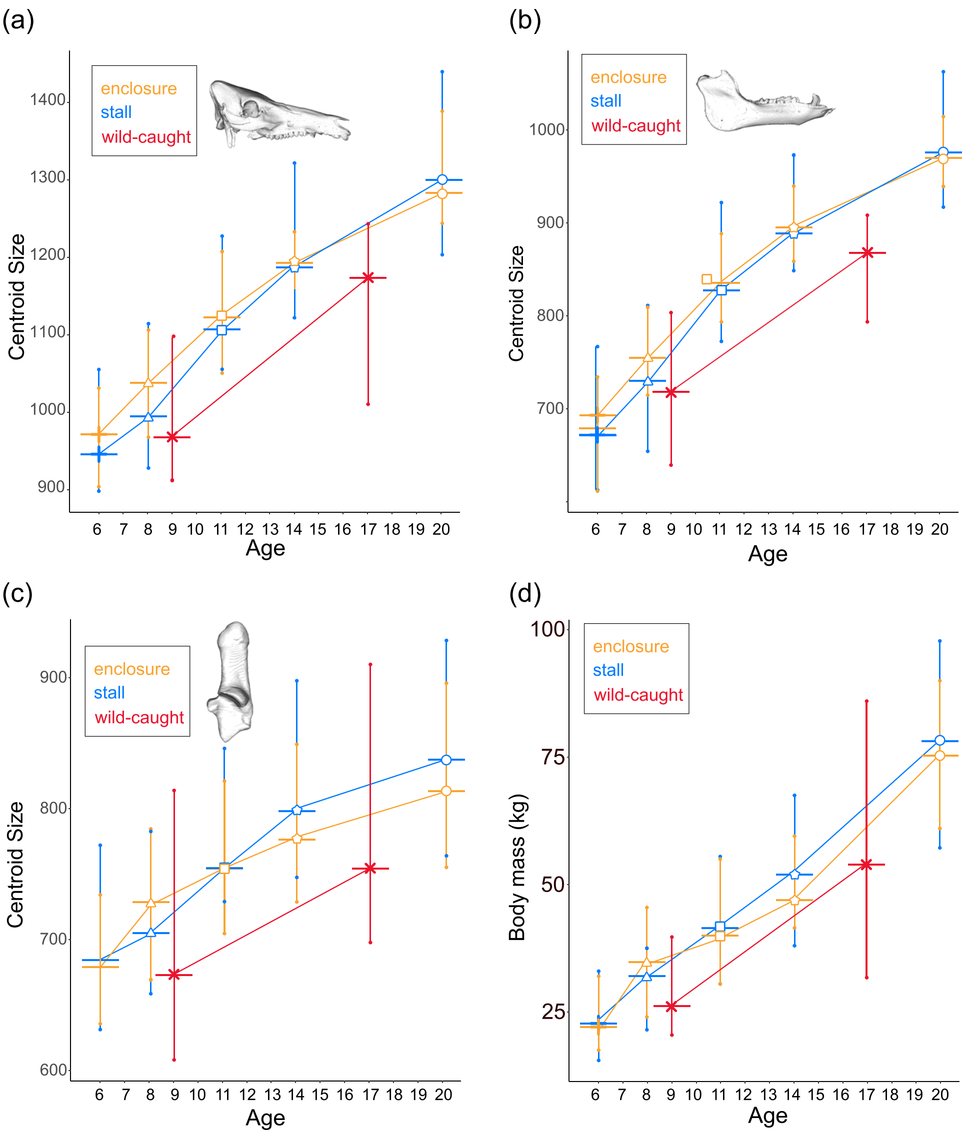

FIGURE 2 Boxplots of centroid size for the (a) cranium, (b) mandible, and (c) calcaneus and of (d) body mass of wild boar (*Sus scrofa*). The vertical lines represent all the values within 1.5 times of the interquartile range accounting for 50% of the data, from the 25th percentile to the 75th percentile. The horizontal lines are the median values

ungulate impacts the development of the three studied structures (O'Regan & Kitchener, 2005). Differences also exist later for the cranium and mandible, when the effect of the reduction of mobility on morphological structures becomes more prominent. Indeed, the form and size of the "16-18 month wild-caught" group are similar to the 11- and 14-month-old captive specimens but statistically different from the 20-month-old ones. The same results are observed when comparing body mass between wild-caught and captive specimens. These results are strengthened by the fact that the wild-caught control specimens, belonging to the same initial herd as the captive ones, follow the same trend as the other wild-caught wild boar (see Figure 1a,b). Unfortunately, 6-month-old wild-caught wild boar were not available. Yet, since the "8-10 month wild-caught" group is similar to the 6-month-old captive specimens, we could speculate that 6-month-old wild-caught wild boar would be similar to younger specimens. This suggests that captive growth in wild boar induces a morphological divergence driven by an acceleration of changes in the size and form of the skull. This developmental delay in wild-caught wild boar compared to captive ones is characterized by a retention of more juvenile traits observed in younger wild specimens as evidenced by the MANOVA. This implies an increase in the developmental rate of captive wild boar when compared to that of wild-caught specimens. These findings are in line with previous studies on postnatal growth assessing that, for a given age, captive specimens are often significantly larger than wild-caught individuals. Comparing skeletal measurements, Zihlman et al. (2007) found that the tempo of growth in wild chimpanzees (*Pan troglodytes*) contrasts sharply with the rate demonstrated for captive individuals that can mature as much as 3 years earlier. Cheverud et al. (1992) also found a significant increase of the growth rate in toque macaques (*Macaca*

TABLE 2 ANOVA *p*-values of the centroid size (CS) between captive (stall and enclosure) and wild-caught groups of wild boar (*Sus scrofa*) computed for the cranium, mandible, and calcaneus and ANOVA *p*-values of body mass

	CS cranium		CS mandible		CS calcaneus		Body mass	
	8–10 m wild-caught	16–18 m wild-caught	8–10 m wild-caught	16–18 m wild-caught	8–10 m wild-caught	16–18 m wild-caught	8–10 m wild-caught	16–18 m wild-caught
6 m— enclosure	0.75	**<0.01**	0.54	**<0.01**	0.93	**<0.01**	0.50	**<0.01**
6 m—stall	0.67	**<0.01**	0.58	**0.01**	0.78	**0.01**	0.45	**<0.01**
8 m— enclosure	0.37	**0.03**	0.39	0.09	0.18	0.12	0.81	**0.01**
8 m—stall	0.60	**0.00**	0.61	0.05	0.32	0.06	0.64	**<0.02**
11 m— enclosure	**0.01**	0.42	**<0.01**	0.79	**0.01**	0.62	0.20	0.12
11 m—stall	**0.02**	0.37	**0.02**	0.81	**<0.01**	0.95	0.16	0.22
14 m— enclosure	**<0.01**	0.71	**<0.01**	0.49	**<0.01**	0.63	**<0.02**	0.60
14 m—stall	**<0.01**	0.60	**<0.01**	0.33	**<0.01**	0.28	**0.01**	0.99
20 m— enclosure	**<0.01**	**0.04**	**<0.01**	**0.02**	**<0.01**	0.12	**<0.01**	0.06
20 m—stall	**<0.01**	**0.02**	**<0.01**	**0.01**	**<0.01**	0.08	**<0.01**	**0.03**

Note: Significant values ($p < 0.05$) are in bold.

Abbreviations: ANOVA, analysis of variance; m, months.

sinica) raised in the laboratory when compared to wild specimens. Finally, captive-raised lion cubs were reported as being nearly twice the size of wild cubs of the same age (Schaller, 1973). The more consistently available food is probably the main cause of these differences (Turner et al., 2016). Indeed, one of the consequences of the spatial control of wild animals by humans is the presence of more constantly available food resources. As it is the case in the context of our experimental study, animals in captivity are regularly provisioned and do not need to spend energy searching for food, hence removing intragroup feeding competition. In addition, intrasexual competition is removed in stall specimens and drastically reduced for the pen specimens. Differences in cranial size during the postnatal development were previously described between domestic pigs and wild boar, especially in the neurocranial region, surrounding and protecting cerebral structures (Evin et al., 2017). Our study stresses that this increase of the size of neurocranial structures is not necessarily a product of the long selective breeding leading to the morphology observed in domestic pigs. Indeed, we observe a similar increase as a plastic response to captivity, considered as one of the earliest domestication steps (Vigne, 2011), most likely due to an unrestricted access to food leading to a faster growth (Kimura & Hamada, 1996). Furthermore, these findings are consistent with recent studies suggesting that the commonly assumed reduction of brain size associated with domestication should be questioned (Lord, Larson, Coppinger, et al., 2020; Lord, Larson, & Karlsson, 2020). Indeed, both early domestication steps, in the context of our study, and long-term selective processes (Evin et al., 2017) result in a size increase and not a reduction of the structures surrounding the brain. Yet, although described previously (Finarelli, 2006, 2011), the presence of a clear positive relationship between brain size and cranial structures size is still unclear (Logan & Palmstrom, 2015), highlighting the need for future studies directly addressing the evolution of endocranial shape and size in relation to domestication.

The calcaneus presents a different pattern when the specimens are older, that is, when the effect of captivity becomes prominent as the "16-18 month wild-caught" group is similar to the 11-, 14-, and 20-month-old captive specimens in size. This result is supported by the fact that the wild-caught control specimens follow the same trend as the captive ones (see Figure 1c). The more physically constrained nature of the calcaneus, articulating with both the talus and the cuboid bones, may partly explain this difference. In this sense, Hanot et al. (2017) described a strong and significant morphological integration between the calcaneus and talus in horses (*Equus caballus*). In comparison, lower level of integration were found between the cranium and mandible of wild boar, specifically for captive individuals (Neaux, Blanc, Ortiz, Locatelli, Schafberg, et al., 2021). This comparatively loose integration in the skull may allow more size variation, and a greater and more rapid growth of these structures in captive individuals. Further covariation studies of the tarsus of less specialized taxa than horses, such as wild boar, will help untangle the role of morphological integration in the observed differences between the craniomandibular and postcranial structures.

The calcaneus is subjected to high tensile, bending, and compressive forces (Su et al., 1999) and has often being described has a key proxy to assess terrestrial mammal locomotor behaviors (Bassarova et al., 2009; Ginot et al., 2016; Panciroli et al., 2017). In this respect, the phenotypic plasticity in shape (but not the size) of the calcaneus has been shown to capture the direct influence of the anthropogenic control of wild boar locomotor behavior (Harbers, Neaux, et al., 2020). Conversely, the morphological modifications associated with the mandible in captive animals are not the direct consequence of mobility reduction but may rather be related to functional demands resulting from the anthropogenic environment

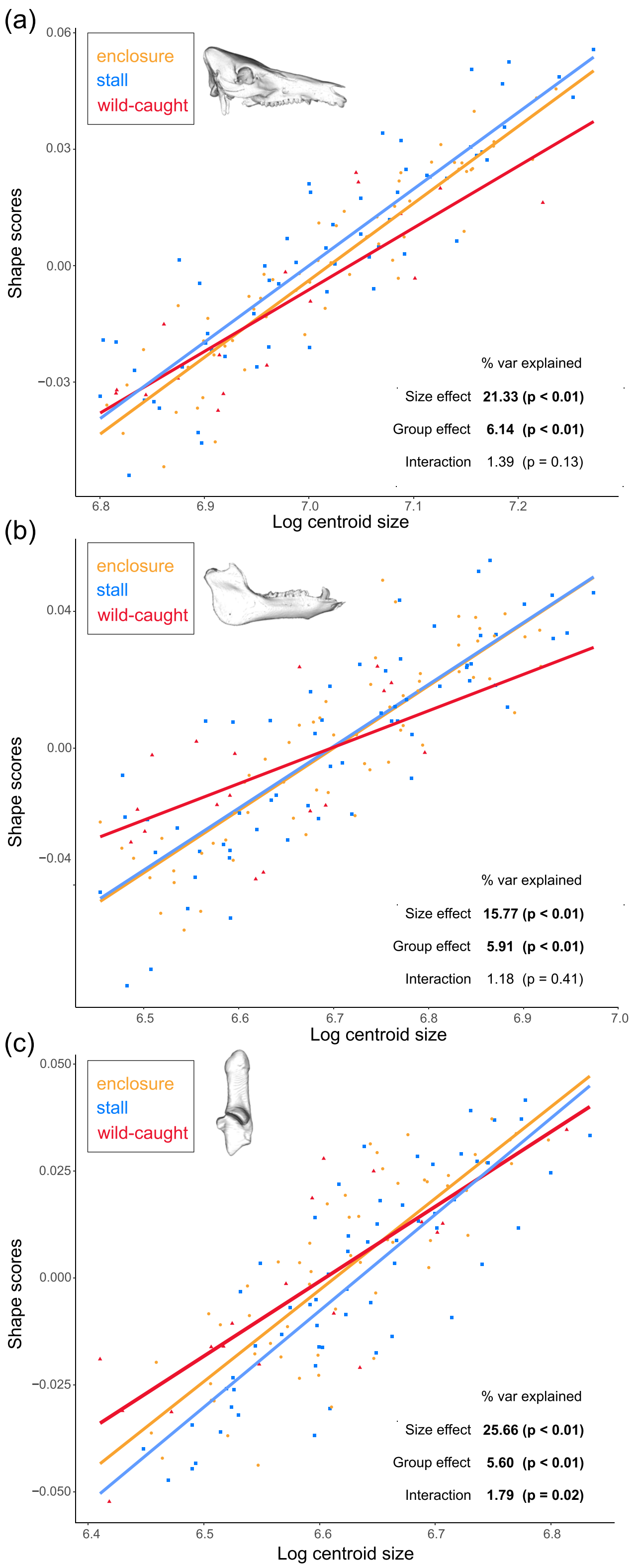

FIGURE 3 Regression of log centroid size (CS) on shape scores for the (a) cranium, (b) mandible, and (c) calcaneus of wild boar (*Sus scrofa*) and effects of size, group, and interaction between size and group on the regression of log CS on shape scores. Significant values ($p < 0.05$) are in bold.

(Neaux, Blanc, Ortiz, Locatelli, Laurens, et al., 2021). They include the increase of feeding activity (Turner et al., 2016), the reduction of foraging behavior (Mason & Mendl, 1997), and the appearance of stereotypy (Rhodes et al., 2005), that is, repeated sequences of movements with no obvious purpose, particularly common in captive animals (Fraser & Broom, 1990). In this sense, in PC2 of the PCA on the form space for the calcaneus, from negative to positive values, there is a clear gradient from wild-caught, to enclosure, to stall specimens (Figure 1c), while for the cranium (Figure 1a) and mandible (Figure 1b) captive individuals (i.e., enclosure and stall) are similar. This result is consistent with the hypothesis that the calcaneus captures mainly locomotor behavior as the habitats of the wild-caught group is the larger (≥100,000 m^2), followed by the enclosure group (3000 m^2) and finally the stall group (100 m^2). The PC2 for the cranium and mandible form space primarily records changes between the captive specimens (i.e., enclosure and stall) under anthropogenic control on the one hand and the wild-caught group on the other. This result is in line with the hypothesis that craniomandibular changes are not directly associated with a reduced mobility but rather with functional requirements resulting from the anthropogenic environment (e.g., feeding activity, foraging behavior, stereotypy). The difference in the way captivity affects the calcaneus (direct influence) and the cranium and mandible (indirect influence) may explain this distinction and should be further explored.

The slope of the ontogenetic allometry for the cranium and mandible is not significantly different between captive-reared and wild-caught specimens. This result is in line with previous findings that ontogenetic allometry generally does not evolve on short evolutionary time scales and that modifications of ontogenetic trajectories are usually achieved by heterochronic shifts along a shared slope rather than directional changes (Voje et al., 2014; Wilson, 2018). Moreover, previous results (Sánchez-Villagra et al., 2017; Wilson, 2018) found no significant differences in the ontogenetic slopes between domestic pigs and wild boar contrary to dogs (*Canis lupus familiaris*) and wolves (*C. lupus*), and llamas (*Lama glama*) and guanacos (*L. guanicoe*). This is congruent with our results on wild boar captivity, as the control of mobility is considered one of the first steps of the domestication process leading to the morphology observed in modern pigs (Vigne, 2011). The differences in the direction of the slope for the calcaneus shows that some level of directional change can nevertheless occur on a short-time scale. The distinctions between the skull and the calcaneus may once again arise from how mobility reduction influences these structures, that is, respectively indirectly and directly.

5 | CONCLUSION

Our results provide evidence that captivity influences the morphology of craniomandibular and postcranial structures of wild boar, as wild specimens are significantly smaller than captive individuals of a similar age. Consistently available food resources and the reduction of stress associated with the search for food and intragroup feeding competition may explain the distinction between captive-reared and wild specimens. The calcaneus presents a different pattern as captive and wild individuals differ in terms of form but not in terms of size. Furthermore, it is the only structure presenting differences in ontogenetic allometry. The more physically constrained nature of the calcaneus and the direct influence of mobility reduction on this bone may explain these specificities. These results provide new methodological perspectives for bioarchaeological approaches as they imply that the plastic mark of captivity can be observed in juvenile specimens as well as in adults (Cucchi et al., 2021; Harbers, Neaux, et al., 2020; Neaux, Blanc, Ortiz, Locatelli, Laurens, et al., 2021; Neaux, Blanc, Ortiz, Locatelli, Schafberg, et al., 2021). Further studies need to explore the morphological integration during growth in captive conditions for both craniomandibular and postcranial structures to decipher the role of developmental and functional correlates between structures in generating the differences observed in our study.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All analytical codes and data are freely available at https://zenodo.org/record/5547335 (Neaux, Harbers, et al., 2021).

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