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SYMPOSIUM ARTICLE

# Patterns of Raccoon Craniodental Morphology under Urbanization

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**Synopsis** Urbanization is one of the fastest and most extreme processes creating novel conditions and affecting persistence of animals in the Anthropocene. Documenting behavioral and morphological changes in urban wildlife is difficult because few studies account for non-urban sources of variation. As a result, multiple hypotheses have emerged. These hypotheses implicate the influence of cognitive demands (cognitive buffer hypothesis), human–wildlife interactions (self-domestication hypothesis), and diet (diet composition hypothesis) on morphology under urban conditions. We investigated craniodental morphological change in raccoons (*Procyon lotor*) with 98 specimens collected across the continental USA based on these hypotheses. Raccoons occur in rural and urban habitats, facilitating the exploration of these hypotheses in a single species under multiple conditions. Using modeling of linear measures, as well as 3-dimensional meshes and geometric analysis, and stable isotope diet estimation, we found that the occlusal area of the first molars and mandibular fourth premolar, in addition to the cranial vault shape, were most responsive to urbanization. Rostral shape showed limited variation across the urban and ecological gradients. Some structures, while variable, did not respond to any of the predictors tested. Our results provide the highest support to the self-domestication hypothesis, although multiple other pressures co-occur, including effects of sex, age, individual size, and geography. Our results also suggest that some craniodental structures may be evolutionarily fixed and promote the raccoon's generalist ecology.

## Introduction

Nearly all urbanization in the United States (USA) has occurred over the last 200 years and is globally expected to double by 2050 (Simkin et al. 2022). Under such novel conditions, species predisposed to urban success often respond with behavioral adaptations, such as increased tolerance of humans (Samia et al. 2015), use of anthropogenic foods (Newsome et al. 2010), and avoidance of novel dangers such as traffic and pets (Thurfjell et al. 2015). While behavioral changes in response to urbanization are well documented (Ritzel and Gallo 2020), fewer studies address changes in morphological traits, often with conflicting results.

For example, Parsons et al. (2020) found that urban foxes (*Vulpes vulpes*) in London, England, have shorter and wider muzzles and smaller braincases relative to rural individuals. In contrast, Stepkovitch et al. (2019) found that urban foxes in Sydney, Australia, had larger skulls than their rural counterparts. Similarly, DePasquale et al. (2020) found larger relative endocranial volumes in urban white-footed mice (*Peromyscus leucopus*) in Pennsylvania, while Pergams and Lacy (2008) found shallower braincases (presumably of lower volume) in urban individuals of the same species in Illinois. These differences may highlight the limitations of drawing conclusions from a few, unique geo-

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graphic regions. Indeed, some of these opposing results can be attributed to inconsistent definitions of urbanization, variations in age of the urban gradient, influence of climatic zones, differences in basic ecology and phylogeny across the taxa studied, or differences in the focal morphological structures of the study. These variations limit our ability to understand the global effects of urbanization, requiring the use of one species across a gradient of conditions to resolve these issues. Here we present a comprehensive analysis of morphological responses to urbanization across a large geographical area while controlling for several confounding ecological conditions that vary regionally.

Three main hypotheses have been forwarded to explain patterns in mammalian skull morphology seen across urban gradients. The cognitive buffer hypothesis (CBH) proposes that larger brains provide the cognitive skills needed for navigating complex urban habitats (Sol et al. 2008; Benson-Amram et al. 2016). For example, when introduced to novel environments, birds and mammals with larger brains exhibited higher survival compared with smaller brained species (Sol et al. 2008). While the CBH only predicts changes to the brain itself, allometric effects of increased brain size on skull shape could co-occur, as seen in white crested polish chickens (*Gallus gallus*) and domestic cat (*Felis catus*) breeds with abnormal brain development (i.e., brachycephalic; Frahm and Rehkämper 1998; Schmidt et al. 2017).

The self-domestication hypothesis (SDH) suggests that decreased aggression confers higher fitness under natural selection when living close to human populations (HPs; Driscoll et al. 2009). Under the SDH, selection for lower aggression would favor individuals that can take advantage of anthropogenic subsidies, akin to the "trash-heap hypothesis" of early dog domestication (Coppinger and Coppinger 2001). Over time, indirect selection for reduced aggression would lead to morphological traits in line with the "domestication syndrome." This syndrome arises in domesticated mammals, possibly through developmental changes at the embryonic neural crest (Wilkins et al. 2014; Pendleton et al. 2018). This syndrome includes consistent morphological traits, including shorter rostrums, smaller teeth, smaller brains, as well as variable pelage coloration and shortened inter-birth intervals (Clutton-Brock 1999; O'Regan and Kitchener 2005).

Lastly, the diet composition hypothesis (DCH) suggests that soft anthropogenic diets can alter craniodental shape during growth (Curtis et al. 2018). Carnivoran skull shape is especially flexible during postnatal development, and multiple studies demonstrate broader zygomatic widths, wider palates, shorter and wider rostrums, constriction of the braincase along the frontal–parietal suture, and greater variation in geometric shape (Hollister 1917; Hartstone-Rose et al. 2014; Curtis et al. 2018) in captive carnivorans fed non-natural diets. Thus, carnivorans consuming anthropogenic subsidies that have low textural diversity could experience change in craniodental shape due to diet alone.

To investigate these hypotheses, we used craniodental morphology of raccoons (*Procyon lotor*) across space and time to assess the effects of ecoregion, urbanization, age, sex, and diet on these structures. Raccoons are mid-size carnivores native to North America and are ubiquitous across most of the continent, encompassing multiple habitats and the full extent of rural to urban gradients (Gehrt 2003). Their broad omnivorous diet includes both natural and anthropogenic resources and provides the opportunity to identify the influence of anthropogenic foods on cranial morphology (Zeveloff 2002; Rulison et al. 2012). Their cranial shape is responsive to life experiences due to late-fusing sutures, providing the flexibility needed to express variations in skull morphology (Grau et al. 1970; Law et al. 2018). Their versatile behavior and broad ecological niche provide the variability responsible for success in urban environments (Daniels et al. 2019; Lazure and Weladji 2024; Stanton et al. 2024) and can be linked to morphological change.

We expected that under the CBH, an increase in relative brain size would occur with increasing urbanization, but not with metrics related to diet or geography (Table 1). In contrast, a decrease in relative brain size with increasing urbanization would support the SDH. Similarly, reduced tooth size and shortened rostrums (i.e., domestication syndrome) with increasing urbanization are expected under the SDH. The DCH would be supported by any shape change associated most with anthropogenic diets, but especially structural changes to cheek teeth. This includes a decrease in carnassial blade size and an increase in molar size as *hypo*carnivory increases with anthropogenic resource use.

## Methods

To assess raccoon craniodental features across urbanization, we collected caliper measures and developed 3-dimensional (3D) meshes from 98 raccoon skull specimens (listed in the supplemental materials [SM], SM Tables 1–3). We also collected hair samples from associated pelts for carbon and nitrogen stable isotope analysis of diet (Newsome et al. 2010; Ben-David and Flaherty 2012). We collected data from 295 raccoon specimens, but limited our analysis to adult specimens with a complete skull and mandible, a pelt, and precise information on collection date and location to avoid the effects of missing data. We removed juveniles based on tooth eruption (Stuewer 1943) and

**Table 1.** List of derived caliper measures of raccoon skulls and their characteristic grouping under the three main hypotheses for effects of urbanization. For acronyms of measures see Fig. 2.

| Region | Measure | Definition | CBH | SDH | DCH |
|---|---|---|---|---|---|
| **Cranial** | **relBCV** | Relative Braincase Volume; BCV/(ZW ∗ CBL). | Complex or novel habitats select for larger brains (Sol et al. 2008) and brain growth can influence cranial shape (Frahm and Rehkämper 1998; Schmidt et al. 2017). | Domestic animals have smaller brains than their wild counterparts (Garamszegi et al. 2023; Hare et al. 2002). | Cranial shape is altered by diet texture and quality (Hollister 1917; Curtis et al. 2018). |
| **Dental** | **relBL** | Relative Blade Length; BL/M1LL | NA | Domestic animals have smaller teeth than their wild counterparts (Morey 1992; Clutton-Brock 1999). | Carnassial blade size and grinding surfaces are constrained by diet across Carnivora, limiting variation (Raia 2004; Curtis et al. 2018; Van Valkenburgh 1991). |
| | **relUP4** | Relative upper PM4; PUL ∗ PUW/CBL | | | |
| | **relLP4** | Relative lower PM4, PLL ∗ PLW/CBL | | | |
| | **relUM1** | Relative upper M1; M1UL ∗ M1UW/CBL | | | |
| | **relLM1** | Relative lower M1, M1LL ∗ M1LW/CBL | | | |
| | **relUM2** | Relative upper M2; M2UL ∗ M2UW/CBL | | | |
| | **relLM2** | Relative lower M2; M2LL ∗ M2LW/CBL | | | |
| **Rostral** | **relRL** | Relative Rostral Length; PL/CBL | NA | Domestic animals have shorter rostrums than their wild counterparts (Clutton-Brock 1999; Trut et al. 2009). | Rostral shape and length is related to bite speed and force requirements of the diet constraining these structures within species (Law et al. 2018; Randau et al. 2019). |
| | **relDAO** | Relative distance from orbit to anterior edge of the upper 4th premolar; DAO/CBL. | | | |
| | **RWL** | Rostral Width to Length Ratio; PL/MZB | | | |

young yearlings based on a visible frontal–parietal suture (not yet obliterated; Junge and Hoffmeister 1980). The final dataset included 51 males and 47 females collected between 1885 and 2005 across 26 states. To account for craniodental variations due to evolutionary history and ecological conditions, we separated our samples into four groups based on the level I ecoregions for North America (Fig. 1, Environmental Protection Agency—EPA, Commission for Environmental Cooperation 1997). For each county, we defined urbanization as the proportion of the HP considered urban at the time of the census for the decade the animal was collected (% Urban Population, Manson et al. 2020). The US census defined "urban" persons as those living in incorporated cities/towns of at least 4,000 people in the 1880, 1890, and 1900 censuses and lowered this threshold to 2,500 persons in any area (including unincorporated suburbs) in the 1910 census (Ratcliffe 2015). We chose an urbanization metric based on HP, as this is the only variable common to all cities. Other characteristics like city design, building type, traffic volume, degree of industrialization, and greenspace distribution and management vary across states and countries and are inconsistently recorded, if at all. The history of urbanization in each collection area was also described by calculating the average age of each county's urban landscapes (Urban Age). These data were extracted from a raster describing the decade in which each cell surpassed a development threshold of 35 structures per $km^2$ with 1 indicating the development threshold was passed in 2010, 2 indicating the threshold was met in 2000, and so on up to 8 corresponding to the census taken in 1940 (Falcone 2017). This value describes the average decade in which each county surpassed the development threshold and offers perspective on the history of urbanization in each region, independent of the collection date and HPs.

We collected 19 measures with digital calipers from raccoon skull specimens (Fig. 2, SM Table 4) and converted these into 11 derived variables corrected for size (Table 1). Braincase volume (BCV, $mm^3$) was measured by filling the cranium with 4 mm diameter beads, with light shaking to settle beads into smaller interstices, and then measuring the beads' volume with a graduated cylinder (Logan and Palmstrom 2015).

To evaluate the effect of diet on skull morphology, we pulled 1–3 milligrams (mg) of hair from the dorsal pelvic region of each raccoon pelt for carbon ($\delta^{13}C$) and

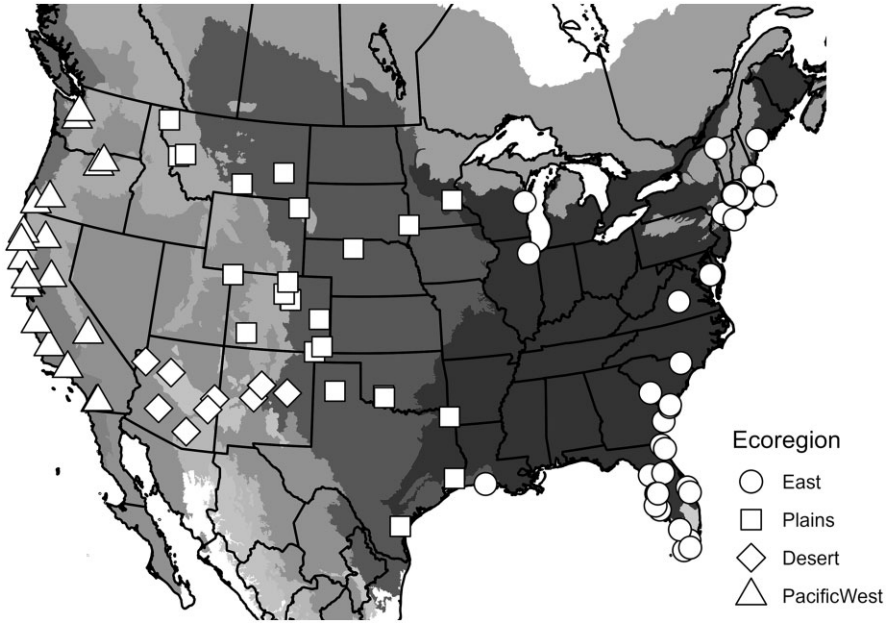


**Fig. 1** Collection locations and ecoregion groupings for the 98 raccoon specimens. Level I ecoregions indicated with shading (EPA, Commission for Environmental Cooperation 1997).

nitrogen ($\delta^{15}$N) stable isotope analysis (Ben-David and Flaherty 2012). Hairs were washed and dried before weighing a subsample into tin boats. Stable isotope analysis was conducted by the University of Wyoming Stable Isotope Facility using a continuous flow Delta Plus mass spectrometer, and $\delta^{13}$C was corrected for the Suess Effect based on Long et al. (2005). For each specimen, we calculated the difference between the observed $\delta^{13}$C ‰ and the estimated landscape $\delta^{13}$C ‰ from plant communities ($\Delta\delta^{13}$C) with the R package *grassmapr* and its included data (Powell et al. 2019). This value records the deviation in raccoon diet from that available on the surrounding natural landscape and was used as a marker of anthropogenic resource use (SM Fig. 2, Newsome et al. 2010).

To assess the effect of urbanization on skull shape, we created 3D meshes using the smartphone photogrammetry app *Abound* (formerly *Metascan*, https://aboundlabs.com) on an Apple iPhone XR. All meshes were produced by the same device. Each skull was placed on a turn table and imaged from 4 angles (~ 0°, 30°, 60°, and 90°) at a rate of 1 photo per second for a minimum of 25 photos per angle and 100 photos per skull (SM Fig. 1). Photos were uploaded to the cloud service of the Abound app for automatic mesh creation procedures. The app then provided a mesh for each photo set. We created a separate dorsal and ventral model of each skull to fully capture both sides in detail. Meshes were processed before landmarking to merge and remove extraneous surfaces. Further details on imaging and model processing methods are available in the supplemental materials.

A single person (for consistency) placed 13 fixed landmarks (fixed LMs, Fig. 2, SM Table 5), 25 points evenly spaced along the sagittal midline, and 50 points evenly spaced along the right zygomatic (curve LMs) on each skull mesh using the software *3D Slicer* version 5.6.2 (www.slicer.org, Kikinis et al. 2013). We then placed 399 surface landmarks (surface LMs) using a semi-automated method based on (Bardua et al. 2019). We use "landmarks" when describing all points and refer to each type individually (fixed LMs, curve LMs, and surface LMs) when necessary.

After aligning landmarks with Generalized Procrustes Analysis (GPA; with sliding semi-landmarks [semis] on curves; Bookstein 1989), we kept only those falling on the right side to remove duplicated information due to bilateral symmetry (Cardini 2017; Bardua et al. 2019). After dividing the landmarks at the midline, the set consisted of 13 fixed LMs, both curves (25 semis on the sagittal crest and 50 semis on the zygomatic arch), and 152 surface LMs across the skull surface for a total of 240 points. We used the GPA-transformed coordinates as the dependent variable describing skull shape and the log-transformed centroid size to account for skull size variation (Bookstein 1989). Detailed descriptions of all mesh processing methods are provided in the supplemental materials.

To determine if cranial modules vary independently under urbanization pressures, we also divided the land-

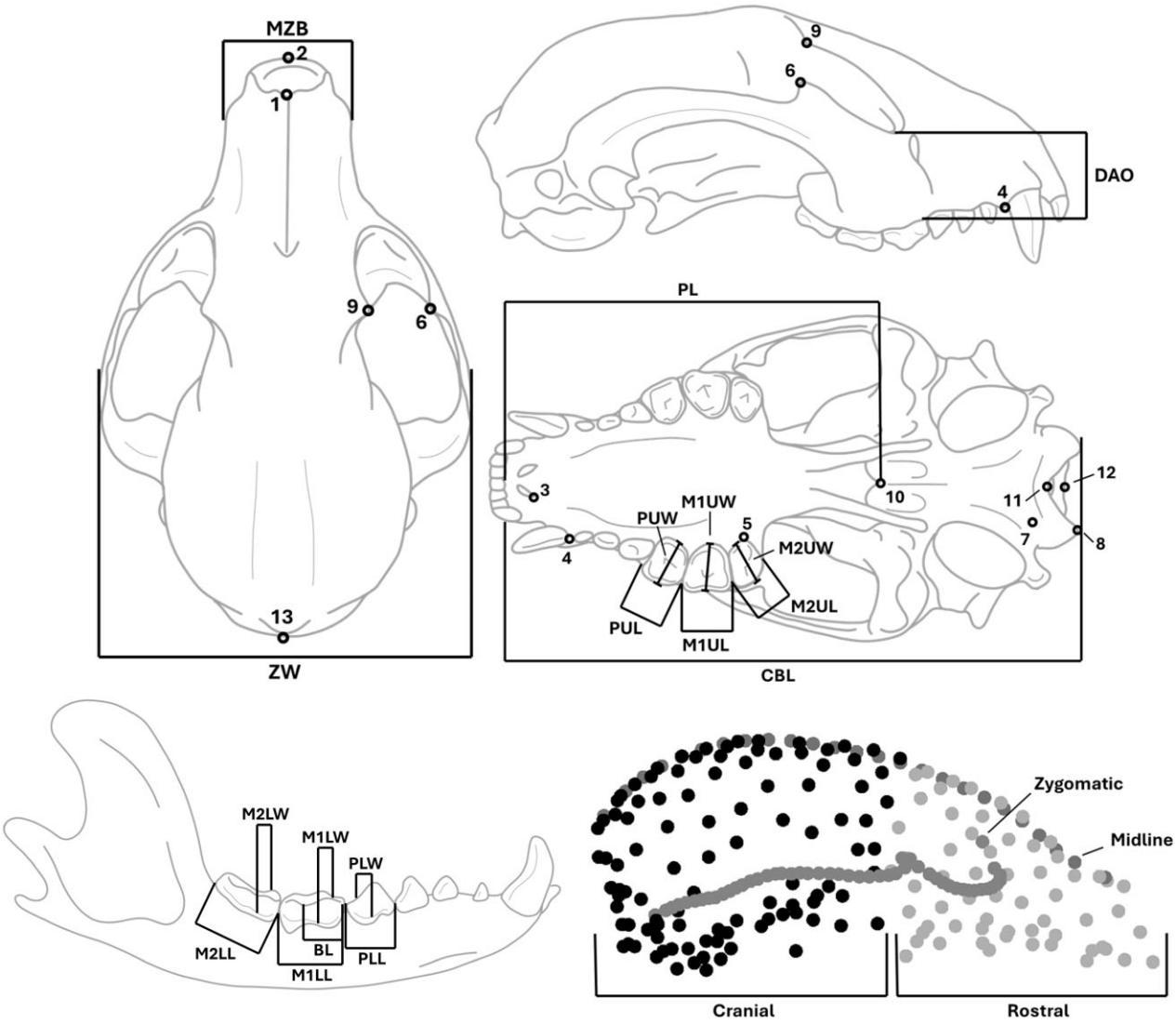


**Fig. 2** Illustration of three views of a raccoon skull with fixed landmarks (numbered points), caliper measures (text labels) indicated as well as an illustration of the four module groups used.

marks into four modules: rostral, cranial, zygomatic, and midline based on previous studies (Fig. 2, Goswami and Finarelli 2016; Randau et al. 2019). Modules were verified by a modularity test with 1000 permutations for the covariance ratio between named and randomized modules (CR = 0.651; effect size = -9.3579; *P*-value = 0.001, pairwise comparisons in SM Table 6). Subsetting these modules was done after superimposition in accordance with a "within configuration" design used in previous studies (Klingenberg 2011; Bardua et al. 2019; Goswami et al. 2019; Randau et al. 2019). This method was used to avoid warping caused by superimposition after splitting a bilaterally symmetric object at the biological midline (Cardini 2016, 2017; Bardua et al. 2019) and to maintain the size and orientation of modules in the shape space (but see Cardini et al. 2019 and Zelditch and Swiderski 2023).

To assess the validity of the three hypotheses, we compared the compared the performance of two test models to a null (Table 2). We used linear models for the derived measures while the 3D geometric data was assessed with Procrustes analysis of variance (ANOVA) with residual randomization in permutation procedures (RRPP models) and type III sum of squares (Collyer and Adams 2018). Significant predictors and the best fit models were determined by summaries, diagnostic plots, variance inflation factors, and *F*-tests between the three models. For each model, the response variable included all landmarks, only fixed and curve LMs, only fixed and surface LMs, only surface LMs, or only curve LMs. This method allowed us to parse which set of landmarks best described the data and the influence of other landmark types on the results (Goswami et al. 2019).

**Table 2** Equations for the null and two test models applied to raccoon cranial measures.

| Model Name | Type | Data | Model |
|---|---|---|---|
| Null | Linear | Caliper measures | $measure \sim Sex + Sutures + \delta 15N + Ecoregion + UrbanAge$ |
| Human Population (HP) | Linear | Caliper measures | $measure \sim Sex + Sutures + \delta 15N + \%UrbanPopulation + Ecoregion + UrbanAge$ |
| Urban Diet (UD) | Linear | Caliper measures | $measure \sim Sex + Sutures + \delta 15N + \Delta\delta 13C + Ecoregion + UrbanAge$ |
| Null | RRPP | 3D Shape | $3D\ Shape \sim log(Centroid\ Size) + Sex + Sutures + \delta 15N + Ecoregion + UrbanAge$ |
| Human Population (HP) | RRPP | 3D Shape | $3D\ Shape \sim log(Centroid\ Size) + Sex + Sutures + \delta 15N + \%UrbanPopulation + Ecoregion + UrbanAge$ |
| Urban Diet (UD) | RRPP | 3D Shape | $3D\ Shape \sim log(Centroid\ Size) + Sex + Sutures + \delta 15N + \Delta\delta 13C + Ecoregion + UrbanAge$ |

In all models, we included sex to account for dimorphism in cranial morphology (Ritke and Kennedy 1993), status of the frontal–parietal suture (fused or partial) as a measure of age at death (Geiger and Haussman 2016), $\delta^{15}$N to indicate diet and trophic level associated with difference in precipitation and temperature (Ben-David and Flaherty 2012), ecoregion to account for shape variation across geography (Ritke and Kennedy 1988), and Urban Age as a metric of urban expansion across the US (Table 2). Since $\delta^{15}$N and Urban Age were closely related to ecoregion, we grouped these in the null model as descriptions of ecological variation underlying trends in urbanization. Correlations between all model coefficients are reported in supplemental materials (SM Table 7).

In the diet composition (Urban Diet [UD]) model we included $\Delta d^{13}C$ as a metric of anthropogenic resource use (Table 2). If variation in craniodental measures responds to anthropogenic foods, this model will rank higher than the null, and $\Delta\delta^{13}C$ would emerge as a significant variable. A good fit to the data of the HP model, which included % Urban Population at the time of specimen collection, would support both the CBH and the SDH (see Table 1). The distinction between the two hypotheses relates to the direction of change in the cranium and dental morphology (Table 2).

All statistical and morphometric analyses were performed in R Studio (v2024.04.2, Build 764) with language R (v4.2.2; R Core Team 2013; R Studio Team 2020) unless otherwise noted. Geometric analyses relied on the R packages *geomorph* (v4.0.6; Adams et al. 2016; Baken et al. 2021), *Morpho* (v2.12; Schlager 2017), *SlicerMorphR* (v0.0.2; Zhang and Maga 2024), and *RRPP* (v2.0.0; Adams and Collyer 2018; Collyer and Adams 2018).

## Results

We found a negative relationship between % Urban Population and relBCV in raccoons (Pearson's $r = -0.30$; $P < 0.01$) that was not explained by a relationship with $\Delta\delta^{13}C$ (Pearson's $r = 0.03$; $P = 0.800$). However, the best fit linear model for relBCV was the null rather than the HP, suggesting that variation in relBCV may be independent of urbanization (Table 3, SM Table 8). Three dental measures were best predicted by the HP model rather than the other two (Table 3). The first mandibular and maxillary molars and the fourth mandibular premolar decreased in size with % Urban Population (Fig. 3, SM Table 8). Based on the model estimates for these three teeth, one percent increase in % Urban Population corresponded to an average decrease in occlusal surface area of 3.6–6.3 mm$^2$ (SM Table 10). This constitutes a noticeable 4.9%–11.5% change in occlusal area where these teeth range in width between 3–10 mm and 4–12 mm in length. In contrast, both second molars and the fourth maxillary premolar were best predicted by the null model (Table 3). The second molars did not have any significant predictors, while the fourth maxillary premolars showed an increased UP4 size in animals from the Plains region (SM Table 8). We also found that the relative blade length of the first mandibular molar (the "carnassial blade") was only predicated by age (i.e., the frontal–parietal suture status), and did not vary with diet or urbanization as expected under the DCH and SDH.

We found no evidence of a reduced rostrum in raccoons relative to urbanization, with most support for the null rostral models (Tables 3 and 4). The relRL was predicted solely by $\delta^{15}$N in the best fit model while RWL varied across sex, sutures, and ecoregion, with similar effect sizes. The relDAO varied with sutures and ecoregion, again with consistent effect sizes (SM Table 8). Similarly, ecoregion was the best predictor of rostral 3D shape (effect size = 4.63) in the RRPP models, comparable to cranial sutures (3.19) and size (3.71), but four times larger than sex (1.03) and more than 10 times larger than Urban Age (0.35) and $\delta^{15}$N (0.44; SM Table 9). The combined results of the linear measure and 3D analyses suggest that geography has a larger

**Table 3** Results of the *F*-test comparisons between the null model and each of the two test models for each caliper measure.

| | | Human Population Model | | | Urban Diet Model | | |
|---|---|---|---|---|---|---|---|
| **Group** | **Measure** | **Residual DF** | ***F*** | ***P*-value** | **Residual DF** | ***F*** | ***P*-value** |
| Cranial | relBCV | 70 | 3.46 | 0.067 | 70 | 0.9 | 0.347 |
| Rostral | reRL | 89 | 1.69 | 0.197 | 89 | 0.38 | 0.542 |
| Rostral | relDAO | 87 | 0.77 | 0.382 | 87 | 2.87 | 0.094 |
| Rostral | RWL | 89 | 0 | 0.986 | 89 | 0.09 | 0.77 |
| Dental | relLP4 | 80 | 7.74 | **0.007** | 80 | 0.38 | 0.542 |
| Dental | relLM1 | 80 | 4.3 | **0.041** | 80 | 1.74 | 0.191 |
| Dental | relLM2 | 78 | 0.16 | 0.693 | 78 | 1.53 | 0.22 |
| Dental | relUP4 | 81 | 1.72 | 0.193 | 81 | 0.56 | 0.455 |
| Dental | relUM1 | 80 | 7.73 | **0.007** | 80 | 0.13 | 0.722 |
| Dental | relUM2 | 83 | 0.87 | 0.354 | 83 | 0 | 0.981 |
| Dental | relBL | 80 | 0.01 | 0.913 | 80 | 1.36 | 0.247 |

*Note*: Significant *P*-values are indicated in bold text.

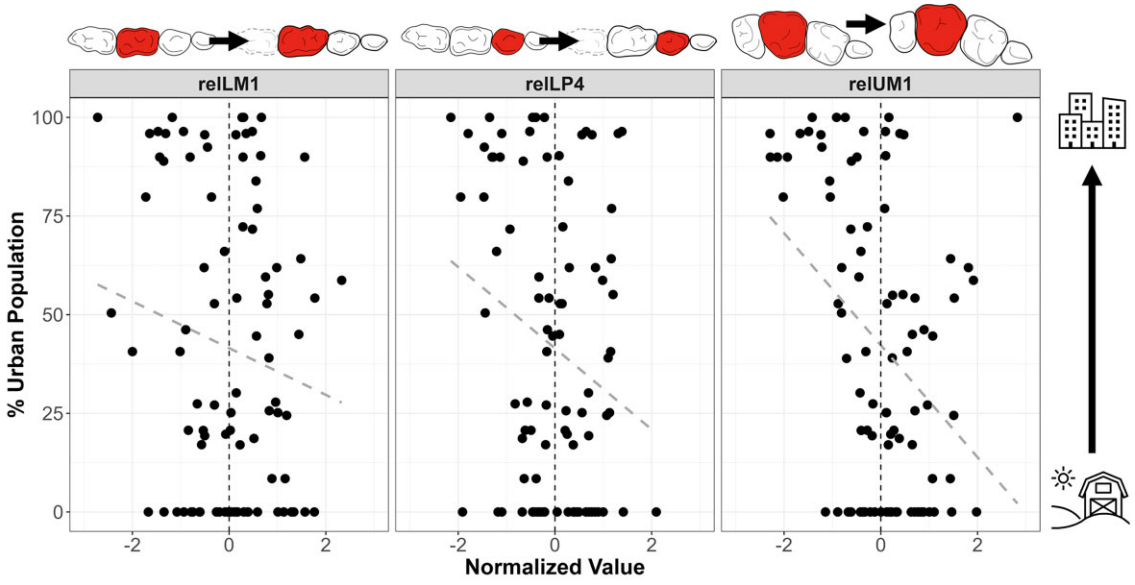


**Fig. 3** Relation (represented as a dashed linear regression line) between % Urban Population and three normalized dental measures (scaled to the means and divided by the standard deviations). Dashed outlines in illustrations above indicate missing structures in the reference specimens.

**Table 4** Results of the comparisons of the two test models to the null for each point combination for each module.

| | | Human Population Model | | | Urban Diet Model | | |
|---|---|---|---|---|---|---|---|
| **Module** | **LM set** | ***F*** | **Z** | ***P*-value** | ***F*** | **Z** | ***P*-value** |
| All | Fixed LMs + curves | 1.14 | 0.6 | 0.267 | 0.8 | −0.41 | 0.661 |
| All | Fixed LMs + curves + surfaces | 1.46 | 1.3 | 0.097 | 1.15 | 0.55 | 0.294 |
| All | Surfaces only | 2.12 | 1.93 | **0.033** | 1.76 | 1.45 | 0.076 |
| Cranial | Fixed LMs + surfaces | 1.99 | 1.74 | **0.047** | 2.06 | 1.64 | 0.055 |
| Cranial | Surfaces only | 2.5 | 1.89 | **0.035** | 2.14 | 1.56 | 0.064 |
| Rostral | Fixed LMs + surfaces | 1.31 | 0.95 | 0.167 | 0.74 | −0.65 | 0.741 |
| Rostral | Surfaces only | 1.53 | 1.26 | 0.104 | 0.91 | −0.01 | 0.507 |
| Midline | Curves only | 1.04 | 0.33 | 0.369 | 0.54 | −0.98 | 0.832 |
| Zygomatic | Curves only | 1.24 | 0.74 | 0.225 | 0.79 | −0.49 | 0.57 |

*Note*: Significant *P*-values are indicated in bold text.

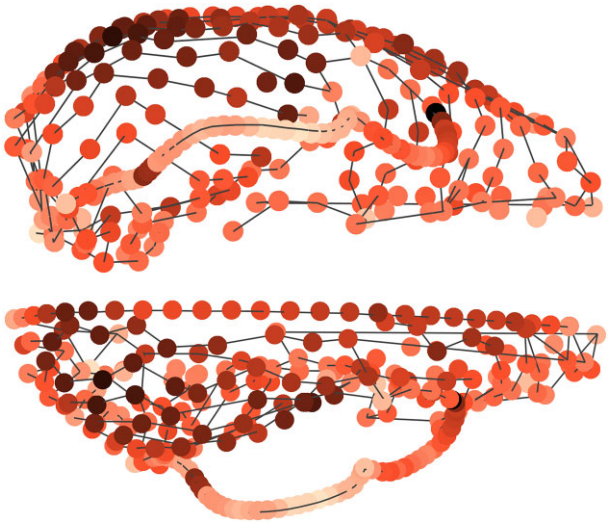

**Fig. 4** Difference between the mean landmark orientations of raccoons from 0% to 33% Urban Population counties and raccoons from 66% to 100% counties relative to the centroid. Darker points represent landmarks from the 66% to 100% mean shape that fell closer to the centroid (shrinkage) than the 0% to 33% raccoons and lighter points represent landmarks from the 66% to 100% mean shape that fell further from the centroid (expansion) than the mean 0% to 33% landmarks.

effect on rostral shape and size than any urban or diet metric, contrasting with the SDH.

As discussed above, we found mixed support for a decrease in overall brain size in urban raccoons. Nonetheless, the best fit model to cranial shape was the HP model (Table 4). The HP model for cranial module shape included % Urban Population as a significant predictor with an effect size of 1.92, comparable to that from sex and Urban Age but lower than that of sutures (2.92), size (3.42), and ecoregion (3.91). Raccoons collected from counties with more than 66% urban population had shallower cranial vaults at the dorsal surface and expanded occipital regions than those collected in counties with less than 33% urban population (Fig. 4), suggesting that opposing trends of the dorsal and occipital surfaces could maintain a static overall brain size.

While we used two correlated metrics of urbanization (% Urban Population and $\Delta\delta^{13}C$; Pearson's $r = 0.23$, $P = 0.0217$), we did not find that both equally predicted raccoon cranial morphology. Specifically, % Urban Population was predictive of size in some cheek teeth and the shape of the cranial module, while $\Delta\delta^{13}C$ did not significantly predict any measure. This suggests that while the two measures were correlated, they describe different aspects of the urban habitat.

The Urban Age variable was a significant predictor in only the relBCV model (SM Table 8). With lower Urban Age values indicating more recent development, a 1-decadal increase in the average development age of the county was related to a 0.91 $mm^3$ decrease in relBCV (SM Table 8). This suggests that relBCV was smaller in raccoons from counties with urban areas that surpassed the development threshold earlier in the 20$^{th}$ century. This is consistent with the correlation between relBCV and % Urban Population discussed earlier, although still unsupported by the relBCV models.

## Discussion

Our results suggest that the rapid development of urban spaces has a measurable effect on raccoon skull morphology across timescales of only 120 years, although the influence of urbanization is easily masked by ecological conditions across geography. We demonstrate the need to consider the effects of multiple drivers, including sex, age, diet, and geography, on cranial shape to accurately parse the effect of urbanization alone. In addition, we show that morphological adaptations to novel environments may not follow the predictions of these simple hypotheses because pressures likely influence cranial structures simultaneously.

While the changes we observed in relBCV may contradict the CBH, we caution against directly comparing brain size to cognitive ability, especially when also assessing domestication-like effects. While Sol et al. (2008) found a positive relationship between brain size and urban success in mammals, domesticated species, including dogs (*Canis* familiaris) and horses (*Equus equus*), demonstrate increased human–animal social cognition regardless of their relatively smaller brains (Miklósi et al. 2007; Fureix et al. 2009). With variation in cranial shape but not relBCV across urbanization, it is not clear how the observed changes in cranial module shape would influence brain shape or size. While we used a finite definition of the CBH from the literature, it is possible that these changes in braincase shape are indicative of changes to brain structure or regional size that could not be assessed in this study.

The reduced tooth size in two of the three mandibular cheek teeth (LP4 and LM1) and one of the three maxillary cheek teeth (UM1) is consistent with the shorter molar tooth rows found in urban rats (Puckett et al. 2020) and the shorter premolars in dogs compared to wolves (Morey 1992). This is also consistent with Wayne (1986), who showed variation between many dental measures of domestic dogs and wild canid species, except for that of the second molar, similar to our findings for raccoons. However, correlation between tooth size and domestication (i.e., support for SDH) has been questioned as small teeth also occur in some modern and ancient wolves (e.g., Dimitrijević and Vuković 2015). Morey (1992) suggests that reduced tooth size in modern domestic dogs could be the result of a develop-

mental lag relative to rapid dwarfing of body and skull size in early domesticated lineages. Raccoons could be experiencing an opposite trend where body size rapidly increases with access to high-calorie anthropogenic foods, leaving small teeth lagging (like large modern dogs, McKeown 1975). This explanation appears unlikely, however, as we found no evidence that raccoon size scales with urbanization based on the 45 specimens with body length measures (SM Figs. 3–5). Thus, the most plausible explanation for the variation we observed in these dental measures is currently the SDH. The reduced tooth size found here could affect food manipulation and survival in urban habitats. Smaller teeth are likely sufficient for processing soft textured foods, but may be detrimental if smaller teeth are more susceptible to breakage on objects like packaging, as suggested by the opposite trend in bone-crushing carnivorans (Kupczik and Stynder 2012).

In contrast to the dental measures, none of the three rostral measures (relRL, RWL, and relDAO) nor the 3D shape supports the SDH directly. These rostral results partially contradict the dental results since rostrum length is expected to decrease with domestication-like pressures (Wilkins et al. 2014), although the influence of diet may mask this trend (Law et al. 2018). The rostral module also showed less variation from the mean shape than the cranial module suggesting that raccoon rostral shape is largely constrained (SM Fig. 6). The low variability in the rostral module could be related to diet as constraint on rostral shape preserves the mechanical properties of the oral region like closing speed and bite strength in conjunction with the mandible. The conservation of this region could also indicate the maintenance of the olfactory structures that raccoons use for navigation and social communication even in urban habitats (Ough 1982; Kent and Tang-Martínez 2014).

The adaptation to a broad and variable diet in raccoons may explain why we found no significant relationship between stable isotopes and the shape of the skull. The DCH suggests high cranial variability in carnivorans in response to diet composition and texture (Curtis et al. 2018; Law et al. 2018) and Hollister (1917) even provided evidence that dietary texture influences cranial shape within the lifetime of individual carnivorans. It is unlikely, therefore, that raccoons would be resistant to morphological changes under masticatory stress from different dietary textures. Instead, $\Delta\delta^{13}C$ may be an imperfect metric of anthropogenic diets or may misrepresent the diversity of texture of human-derived foods. While values of $\delta^{13}C$ are reliably used as a marker of anthropogenic diets in wildlife studies, especially when compared to local plant communities (Newsome et al. 2010), it is possible that other factors may have masked the effects of diet. This includes the unresolved influence of pelt preservation techniques on carbon and nitrogen isotope values. Several of our specimens were collected as early as 1885, when preservation techniques were vastly different from modern protocols. Hair keratin is considered a non-reactive tissue for atom exchange of carbon and nitrogen (Ben-David and Flaherty 2012; Koehler and Hobson 2018), although Brabcová et al. (2024) found evidence that multiple stages of the tanning process influence both $\delta^{13}C$ and $\delta^{15}N$ of hair keratin. The effects of preservation, post-preservation treatments (e.g., pesticides), and duration of storage in museum collections on carbon and nitrogen isotopes merit further investigation. Alternatively, other methods to determine the effects of diet on skull morphology, like microwear analysis, should be explored (Schulz et al. 2013).

Two explanatory variables, ecoregion and Urban Age, emerged as important in several models. While Urban Age was dependent on ecoregion (SM Figs. 7–9), these measures describe both climatic and vegetation differences (Fig. 1) and the history of human settlement across geography in the USA (Dobson 2013; Falcone 2017). For example, areas with a longer history of urbanization could influence the genetic components of morphology and produce greater variation between urban and rural habitats. Ecoregions also reflect the genetic diversity of raccoons in North America, but we were unable to account for subspecies designations of the sampled raccoons because genetic information on this species is unavailable. While studies have assessed genetic support for subspecies identifications in the eastern USA (Cullingham et al. 2008; Trujillo and Hoffman 2017) and some have explored diversity along an urban–rural gradient in Illinois (Santonastaso et al. 2012), no study has provided information on the genetic diversity of raccoons across the continent. Associating morphological variation with known genetic patterns is therefore currently impossible, although Goldman (1950) suggests there may be little morphological variation between raccoon subspecies even if genetic differences exist.

Our selection of specimens based on suture obliteration may have introduced some bias because raccoon suture fusion rates may differ across ecoregions (Fiero and Verts 1986). Since we lack understanding of the relationship between obliteration rates and cranial shape (Geiger and Haussman 2016; Bieraugle et al. 2025), it is not clear how life experiences (like masticatory stress) could influence cranial shape before and after obliteration. The age of the animal could then influence measured morphology since frontal–parietal obliteration occurs during raccoon dispersal from the natal range (Gehrt and Fritzell 1998). This means that the col-

lection location of raccoons with a partially obliterated frontal–parietal suture (i.e., yearlings) could poorly describe the conditions that produced the given craniodental morphology. This is further complicated because suture closure rate can vary with domestication-like effects as sutures close earlier in domesticated dogs than in wolves (Bieraugle et al. 2025). Indeed, closure rate has been connected to some cranial morphologies like that in brachycephalic breeds (Geiger and Haussman 2016) and so suture closure rate could influence morphology through multiple avenues.

It is important to note the current controversy about superimposition prior to subsetting modules (i.e., "within-configuration" method, Klingenberg 2011) and its violation of Procrustes method assumptions (Cardini et al. 2019). While these issues are not yet resolved, it is possible that the results of our modularity assessment and subsequent analysis of module shape are skewed based on this superimposition procedure, exaggerating modularity and shape differences (but see Zelditch and Swiderski 2023). Nonetheless, our conclusions are based on the results of both the linear measures and the shape analysis and thus are unlikely to change if geometric analyses are amended. While we did not explore asymmetry across the raccoon skull, such future assessment would be valuable. Wigley et al. (2024) suggest that developmental stress can influence fluctuating asymmetries in human dental structures. It is possible that a similar developmental pathway could alter morphology in raccoons that experience human–wildlife conflict and associated stressors.

Given the limitation of museum collections of raccoon specimens (incomplete and broken skulls, predominance of juveniles, lack of reliable geographic data, and paucity of skins), our sample size was smaller than anticipated. However, our dental results, like the change in cheek tooth occlusal area, demonstrate a difference that was detectible by our sample size.

Understanding the evolutionary history of raccoons may be particularly important given their behavioral flexibility and some of their conserved ancestral morphological traits. Similar to $\Delta\delta^{13}C$, $\delta^{15}N$ values, which describe trophic level (Post 2002), were unrelated to measures of the carnassial blades (UP4 and LM1) as expected based on other studies (Van Valkenburgh 1988; Raia 2004; 2009). This too suggests that raccoons may rely on the conservation of the omnivore dental plan for behavioral flexibility. This generalist trait is consistent with the conservation of an ancestral trait or convergent evolution. The raccoon's lower cheek teeth are most similar to the lower molar form of basal carnivoramorphs in Viverravidae and Miacidae and carnivorans in Herpestidae and Viverridae (Vankelst 2024) rather than to the lower molars of the phylogenetically related Ursidae (Zeveloff 2002). In contrast, the derivation of cheek teeth towards morphotypes seen in the Felidae appears evolutionarily inflexible and is thought to have contributed to extinction of multiple hypercarnivorous groups; so, avoidance of dental specialization appears to provide raccoons with the flexibility needed to adapt to novel environments (Holliday 2010).

## Conclusion

We found evidence for shifts in morphological phenotype in response to urbanization, regardless of other factors like sex, size, and geography. This demonstrates that either raccoons alone are predisposed to respond similarly to urbanization even in disparate populations or that these patterns are indicative of a deeper evolutionary pattern. Of the three hypotheses we tested, our results are most consistent with the domestication syndrome produced through incidental self-domestication, a morphotype apparent across mammalian taxa and suggestive of an evolutionary bias (Wilkins et al. 2014). In contrast, our results suggest that as generalist omnivores, some aspects of raccoon morphology are adapted to resist drastic morphological shifts even under disparate conditions; a constrained generalism. These patterns in a wild carnivoran are clear indications that human influence on the landscape is profound, occurs rapidly, and could occur indirectly through incidental domestication.

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## Supplementary data

Supplementary Data available at *ICB* online.

## Conflict of interest

We declare no conflicts of interest.

## Data availability

The numeric data underlying this article are available in the article's online supplementary material. Landmark data are available upon reasonable request. The

3D meshes were produced by permission of each collection institution and are available upon request to the corresponding museum institutions.

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