JZAR www.jzar.org JOURNAL OF ZOO AND AQUARIUM RESEARCH

Research article

Biomechanical evaluation of the upper beak of Neotropical birds

Gabriel C. Camargo[1], Sheila C. Rahal[1], Cesar A.M. Pereira[2], Daniel S. Silva[1], Jeana P. Silva[1], Maria Cristina R. Castiglioni[1], Maria J. Mamprim[1] and Ricardo Shoiti Ichikawa[1]

[1]Department of Veterinary Surgery and Animal Reproduction, School of Veterinary Medicine and Animal Science, São Paulo State University (UNESP), Botucatu, São Paulo, Brazil
[2]Department of Orthopaedics and Traumatology, School of Medicine, University of Sao Paulo (USP), Sao Paulo, Sao Paulo, Brazil

Correspondence: Gabriel Corrêa de Camargo, e-mail; gabriel.c.camargo@unesp.br

Keywords: avian, imaging methods, rhamphotheca, trauma

Article history:
Received: 01 Feb 2025
Accepted: 31 Mar 2026

Abstract
Understanding the mechanical forces acting on the beak is crucial to enhancing the management of maxillary beak avulsion cases. Therefore, this study aimed to biomechanically evaluate the upper beaks of five Neotropical bird species and analyze Hounsfield units (HU) values using computed tomography (CT). Analysis was performed on white-eyed parakeet *Psittacara leucophthalmus*, red-legged seriema *Cariama cristata*, black-headed vulture *Coragyps atratus*, buff-necked ibis *Theristicus caudatus*, and toco toucan *Ramphastos toco*. A mechanical bending test was performed with a load applied perpendicularly to the distal third of the maxillary rostrum in the ventrodorsal direction. HU values were determined at three points of interest in the same area where the actuator was applied. There were no statistical differences in the HU values between parakeet and seriema beaks, while all other bird species exhibited statistical differences. The maximum force was highest for the parakeet (682.2 N) and toco toucan (126.6 N) beaks, followed by the seriema (65.3 N) and black-headed vulture (57.6 N), with the buff-necked ibis having the lowest force (21.2 N). Statistical analysis revealed differences in maximum force between the parakeet's beak and those of all other species. Significant differences occurred in maximum deformation between the black-headed vulture and buff-necked ibis beaks, and between the seriema and buff-necked ibis beaks. Statistical differences were also observed in the moment of the toco toucan's beak compared to the other bird's beaks. In conclusion, the data obtained may support future studies on prosthetic materials for the species analysed, taking into account the differences identified through the mechanical test.

Introduction

Bird beaks exhibit significant morphological variation in size, shape, and curvature, enabling birds to exploit diverse food sources, regulate body temperature, and engage in various social and communicative behaviors, including singing (Tattersall et al. 2017; Friedman et al. 2019; Darrow and Bennett 2022). Despite this variation in size, shape, curvature, and coloration, bird beaks share a consistent architectural framework (Wang et al. 2020). The beak is a dynamic structure that undergoes continuous growth (Fecchio 2021). Anatomically, it comprises two bony projections known as the maxillary and mandibular rostrums (King and McLelland 1984; Speer and Powers 2016). These projections are covered by a keratinized sheath called the rhamphotheca, which serves as a protective barrier against external environmental factors and is further divided into the rhinotheca and gnathotheca, corresponding to the upper and lower beak coverings, respectively (Olsen 2003; Gelis 2006; Gill 2007; Huynh et al. 2019).

The maxilla is a hollow, flat, bony cone reinforced internally by a complex network of trabeculae (Gill 2007). In many avian species, including those within the order Charadriiformes, the upper beak exhibits flexibility—a feature known as kinesis—enabling partial flexion or bending (Gill 2007; Huynh et al. 2019). Psittacines, for example, possess a prokinetic maxilla, allowing independent movement of the upper and lower beaks

http://doi/org/10.19227/jzar.v14i2.925

(Gelis 2006). Conversely, limited kinesis is observed in species such as ratites, penguins, and toucans (Huynh et al. 2019).

Traumatic injuries to the beak may result from aggression, accidents, predation, or iatrogenic causes (Gelis 2006). The morphological diversity of beaks predisposes certain species—such as long-billed waders, hummingbirds, and birds with large beaks like toucans and hornbills—to a higher risk of trauma (Huynh et al. 2019). Fractures and avulsions of the rhinotheca present significant treatment challenges (Gelis 2006). The primary objectives of beak repair are to achieve structural stability, restore normal functionality, and reestablish a protective barrier against microbial invasion (Huynh et al. 2019).

The growth rate of beak keratin varies by species (Olsen 2003). Avulsions affecting less than the rostral third of the maxilla often allow for regrowth of the affected portion, whereas more extensive injuries typically result in permanent deformities (Huynh et al. 2019). Regeneration is notably more common in psittacines, while species like ostriches exhibit no such capacity due to the cessation of beak growth upon reaching adulthood (Gelis 2006).

Birds with beak avulsions can benefit from the surgical application of prosthetic beaks (Huynh et al. 2019; Speer and Powers 2016). Replacement of lost segments can be accomplished using materials such as acrylic, metal, or natural substitutes (Gelis 2006; Fecchio 2021). Prostheses can be affixed using pins, wires, or screws in combination with adhesive materials, including resins or composites (Speer and Powers 2016; Fecchio 2021).

Beak prostheses are generally temporary due to the ongoing remodeling of the lightweight trabecular bone and dermal layer, as well as the exposure to significant mechanical forces during normal function (Huynh et al. 2019). Consequently, in cases of permanent injuries, prosthetic beaks require regular remodeling, replacement, or reapplication (Gelis 2006). Additionally, designing prostheses that replicate the mechanical properties of the natural beak remains a considerable challenge (Fecchio 2021).

Understanding the mechanical forces acting on the beak is crucial to enhancing the management of maxillary beak avulsion cases. Despite its clinical relevance, the mechanical resistance of bird beaks remains underexplored, with most notable studies focused on toco toucans (Seki et al. 2006; Fecchio et al. 2008; Fecchio et al. 2010). Moreover, the Hounsfield scale—a quantitative measure of radiodensity used in computed tomography (CT)—provides valuable insights into tissue density (Bibb et al. 2015, DenOtter and Schubert 2023) and has recently been employed to assess the maxillary and mandibular rostra in birds (Silva et al. 2024).

Therefore, this study aimed to biomechanically evaluate the upper beaks of five species of Neotropical birds and analyze Hounsfield unit (HU) values using computed tomography (CT). The hypothesis was that birds exhibit interspecific variation in biomechanical properties, which may be related to beak morphology and HU values.

Materials and Methods

Sample selection

This study was approved by The Ethics Committee for the Use of Animals from School of Veterinary Medicine and Animal Science, UNESP, Botucatu, São Paulo, Brazil under the number 0417/2023. Beaks (maxillary rostrum) from birds that had died or were euthanized for reasons unrelated to this study were used. The cadavers were identified and stored in a horizontal freezer at -20°C until biomechanical testing was conducted. The bird species analyzed included the white-eyed parakeet *Psittacara leucophthalmus*, red-legged seriema *Cariama cristata*, black-headed vulture *Coragyps atratus*, buff-necked ibis *Theristicus caudatus*, and toco toucan *Ramphastos toco*. These species were chosen due to their frequent occurrence in wildlife clinics and morphological differences in their beaks, as they belong to distinct families. Five beaks from each species underwent CT scanning, and six beaks from each species were subjected to mechanical testing.

Computed tomography

Cross-sectional images were acquired from the tip of the beak to its base using a 16-channel scanner (Canon Medical Systems, Barueri, São Paulo, Brazil). The scanning protocol included a tube voltage of 120 kVp, current of 60 mA, slice thickness of 1 mm, and a pitch of 1. Multiplanar reconstruction (MPR) was performed for each beak using sagittal and transverse planes with RadiAnt DICOM Viewer software (Medixant, Poznan, Poland). Hounsfield units (HU) values were measured at three points of interest - right lateral, left lateral, and dorsal -corresponding to the area where the actuator was applied (Figures 1 and 2). On the Hounsfield scale, air is assigned a value of −1000 HU, while bone ranges from approximately +700 HU for cancellous bone to +3000 HU for dense cortical bone (Bibb et al. 2015).

Biomechanical testing

Before testing, the cadavers were thawed at room temperature. The beaks were isolated along with their points of attachment to the skull. A universal testing machine (Kratos, model K5002) equipped with a 981 N load cell was used. The proximal end of the maxillary rostrum, including its insertion into the skull, was secured in a standard mold using acrylic resin (Figure 3). The mold was mounted onto a cylindrical clamp at the machine base. A perpendicular load was applied to the distal third of the maxillary rostrum in the ventrodorsal direction using a cylindrical actuator connected to the load cell (Figures 1, 2 and 3). The lever arm was calculated by subtracting the cemented portion of the beak (at the base) and the position of the actuator (relative to the beak's tip) from the total beak length. These lever arm values were used to compute the bending moment (torque) (Table 1). Each beak was subjected to bending test at a speed of 20 mm/min until structural failure occurred. Values of maximum force (maximum load that beak can withstand before failure), maximum deformation (greatest change experienced by beak under loading) (D) and moment (torque) were obtained. The data from a white-eyed parakeet's beak could not be included due to a system failure during analysis.

Statistical analysis

For each variable within each group, the Shapiro–Wilk test was used to assess normality. Variables with a normal distribution were compared using one-way ANOVA followed by Tukey's post hoc test, while non-normally distributed variables were analyzed using the Kruskal–Wallis test followed by Dunn's post hoc test. Statistical significance was set at $P<0.05$. Additionally, the correlation between dorsal HU values and force (N) was evaluated using Pearson's correlation coefficient. All statistical analyses and graph plotting were performed using R software, version 4.4.3 (R Core Team 2025), with the ggplot2 package (Wickham 2016).

Results

The HU values for each bird species are presented in Figure 4. The black-headed vulture's beak had the highest positive HU value (1459±368.5 for dorsal point, 1308±371.6 for right lateral point and 1263±300.4 for left lateral point), followed by the buff-necked ibis (912.8±292.6 for dorsal point, 743±304.8 for right lateral point and 738.4±284.3 for left lateral point), and white-eyed parakeet (244±37.18 for dorsal point, 192.8±48.8 for right lateral point and 195.4±30.61 for left lateral point) and red-legged seriema (268.2±10 for dorsal point, 274.2±43.35 for right lateral point and 239.8±44.07 for left lateral point) beaks having the lowest values.

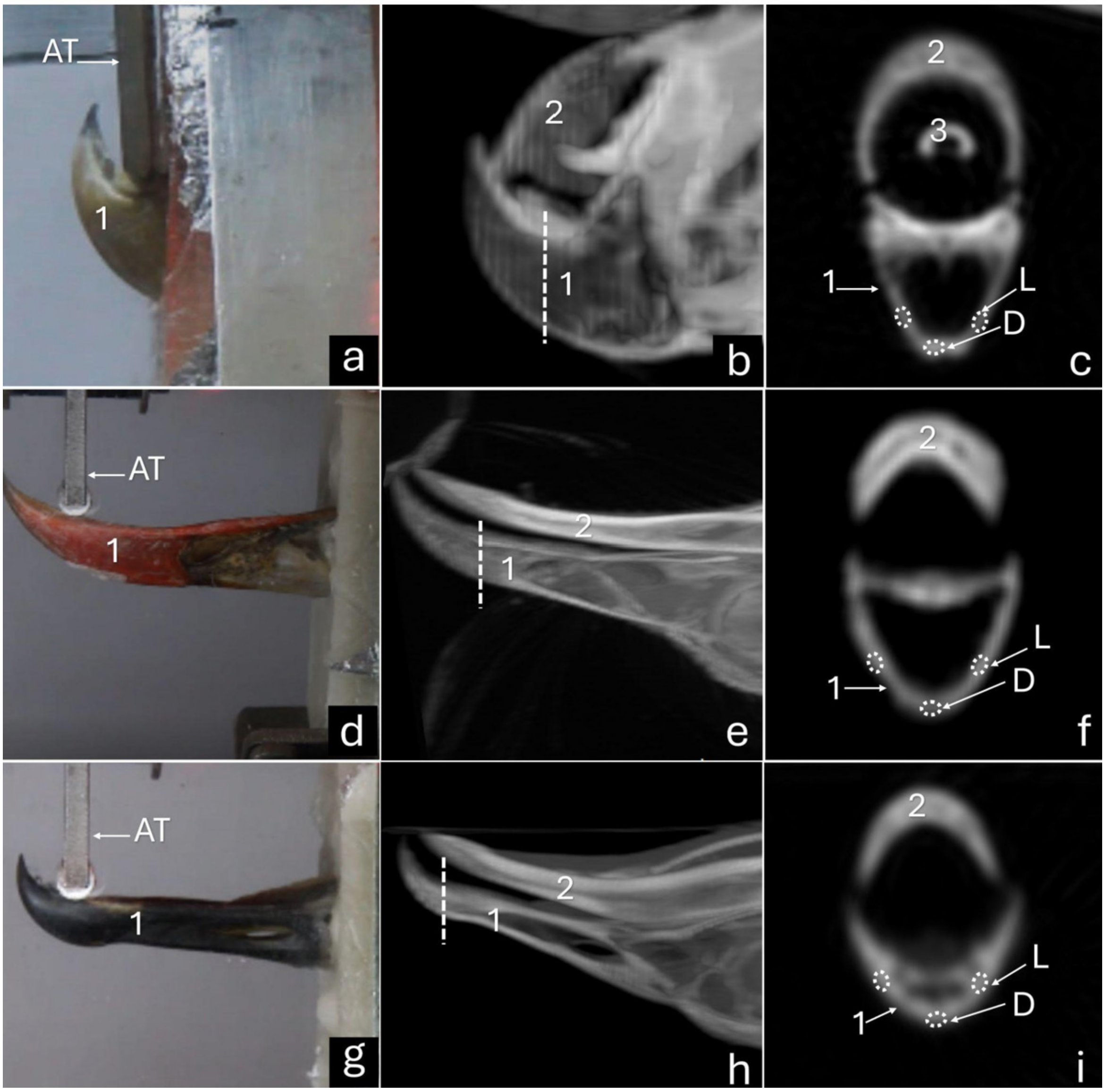

Figure 1. Actuator (AT) positioned on the ventral portion of the beak to conduct the bending test on the beaks of white-eyed parakeet (a), red-legged seriema (d), and black-headed vulture (g). Computed tomography images in sagittal (b, e, h) and transverse (c, f, i) planes showing the points of interest (L - lateral, D - dorsal) to determine Hounsfield units on beaks of the same birds. 1 - Maxilla, 2 – Mandible, dotted line (same area where the actuator was applied)

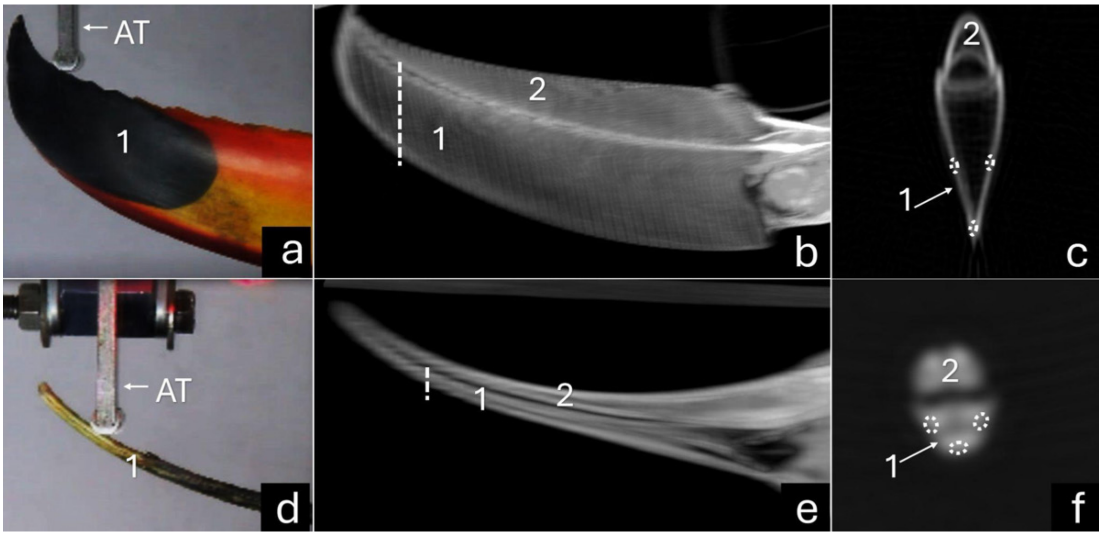

Figure 2. Actuator (AT) positioned on the ventral portion of the beak to conduct the bending test on beaks of a toco toucan (a) and a buff-necked ibis (d). Computed tomography images in sagittal (b, e) and transverse (c, f) planes showing the points of interest (dotted circles) used to determine Hounsfield units on the beaks of the same birds. 1 - Maxilla, 2 – Mandible, dotted line (same area where the actuator was applied)

Table 1. Measurements of the upper beaks of five Neotropical birds.

Birds	No	Beak total length (cm)	Percentage actuator to beak end	Cemented beak percentage	Lever arm (mm)
White-eyed parakeet	1	14.8	30	30	3.9
White-eyed parakeet	2	14.2	30	30	4.5
White-eyed parakeet	3	13.2	30	30	5.0
White-eyed parakeet	4	15.9	30	30	5.1
White-eyed parakeet	5	16.8	30	30	6.7
Red-legged seriema	1	60.0	15	15	42.0
Red-legged seriema	2	79.3	15	15	55.5
Red-legged seriema	3	77.5	15	15	51.9
Red-legged seriema	4	75.8	15	15	53.1
Red-legged seriema	5	71.8	15	15	43.1
Red-legged seriema	6	69.3	15	15	48.5
Black-headed vulture	1	55.0	15	15	38.5
Black-headed vulture	2	60.8	15	15	42.6
Black-headed vulture	3	60.0	15	15	44.2
Black-headed vulture	4	60.5	15	15	41.8
Black-headed vulture	5	60.2	15	15	43.4
Black-headed vulture	6	59.5	15	15	41.7
Buff-necked ibis	1	126.0	15	10	94.5
Buff-necked ibis	2	143.9	15	10	96.4
Buff-necked ibis	3	148.4	15	10	105.4
Buff-necked ibis	4	134.0	15	10	91.5
Buff-necked ibis	5	124.0	15	10	87.3
Buff-necked ibis	6	149.0	15	10	102.4
Toco toucan	1	148.9	15	15	119.0
Toco toucan	2	165.4	15	15	106.7
Toco toucan	3	173.1	15	15	138.2
Toco toucan	4	198.3	15	15	155.7
Toco toucan	5	175.5	15	15	139.5
Toco toucan	6	153.9	15	15	118.3

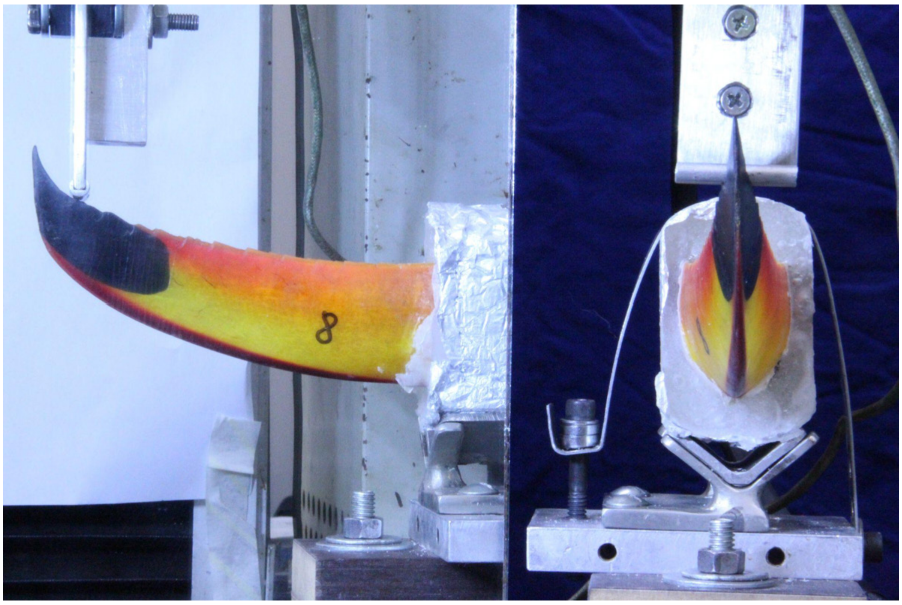

Figure 3. Bending test performed on toco toucan beak. Note the proximal end of the maxillary rostrum secured in an acrylic resin and the perpendicular load applied to the distal third of the maxillary by a cylindrical actuator.

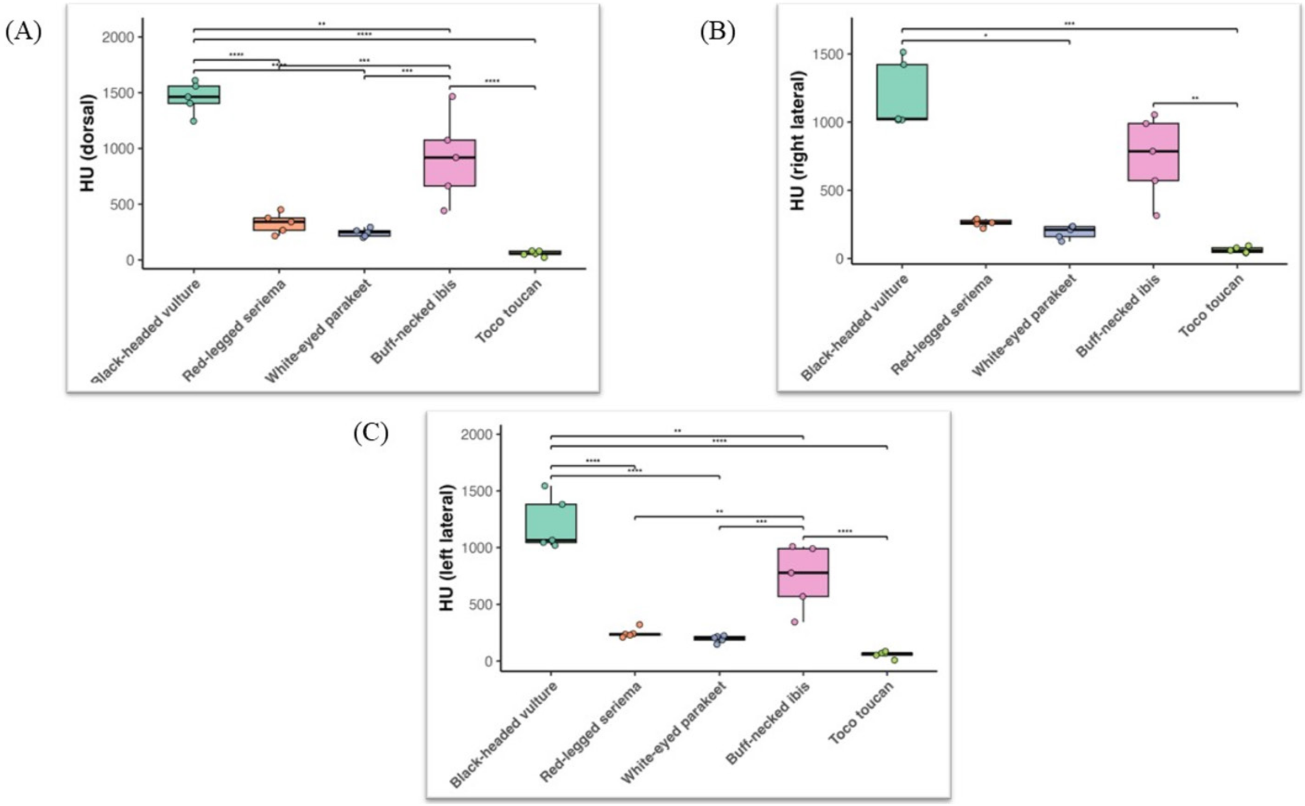

Figure 4. (A) Comparison of dorsal HU values among five bird species (black-headed vulture, red-legged seriema, white-eyed parakeet, buff-necked ibis, and toco toucan). (B) Comparison of right lateral HU values among the same species. (C) Comparison of left lateral HU values among the same species. In all panels, boxes indicate the interquartile range (IQR), horizontal lines represent the median, and whiskers extend to 1.5 × IQR. Dots correspond to outliers. Significant differences between species are indicated (*: P≤0.05; **: P≤p0.01; ***: P≤0.001; ****: P≤0.0001). Statistical tests: one-way ANOVA with post hoc comparisons for HU dorsal and HU left lateral, and Kruskal–Wallis test with post hoc comparisons for HU right lateral.

Negative HU values were recorded for the toco toucan's beak (-558.2±23.76 for dorsal point, -463.2±21.49 for right lateral point and -456.6±29.71 for left lateral point). There were no statistically significant differences in HU values at the three points of interest between the beaks of the white-eyed parakeet and the red-legged seriema, whereas all other bird species showed statistically significant differences ($p < 0.05$) (Figure 4). , as illustrated in the boxplot.

The mechanical testing data is presented in Figure 5. The maximum force (N) was highest for the white-eyed parakeet (682.2±157.8) and toco toucan (126.63±16.8), followed by the red-legged seriema (65.3±18.1) and black-headed vulture (57.6±43.2), with the buff-necked ibis having the lowest force (21.2±11.1). Maximum deformation (D) was highest for buff-necked ibis (20.3±3.7), followed by toco toucan (13.2±3.7), white-eyed parakeet (7.29±1.3), black-headed vulture (6.34±2.4) and red-legged seriema (5.35±1.8), Bending moment (N.mm) was the highest for toco toucan (17856.6±2755), followed by white-eyed parakeet (3496.2 ±1193), red-legged seriema (3275.5±1214.7), black-headed vulture (2438.8±1829.2) and buff-necked ibis (2063.7±1061). Statistical analysis revealed significant differencesin maximum force between the beak of the white-eyed parakeet and those of all other species (P<0.0001), with the white-eyed parakeet exhibiting the highest value, as shown in the boxplot. Regarding maximum deformation, significant differences were found between the beaks of the black-headed vulture and the buff-necked ibis (P<0.05), as well as between the red-legged seriema and the buff-necked ibis (P<0.001), with the latter showing higher values, as displayed in the boxplot. Statistically significant differences in bending moment (P<0.0001) were also observed between the toco toucan's beak and those of the white-eyed parakeet, red-legged seriema, black-headed vulture, and buff-necked ibis, with the toco toucan exhibiting the highest value (Figure 5).

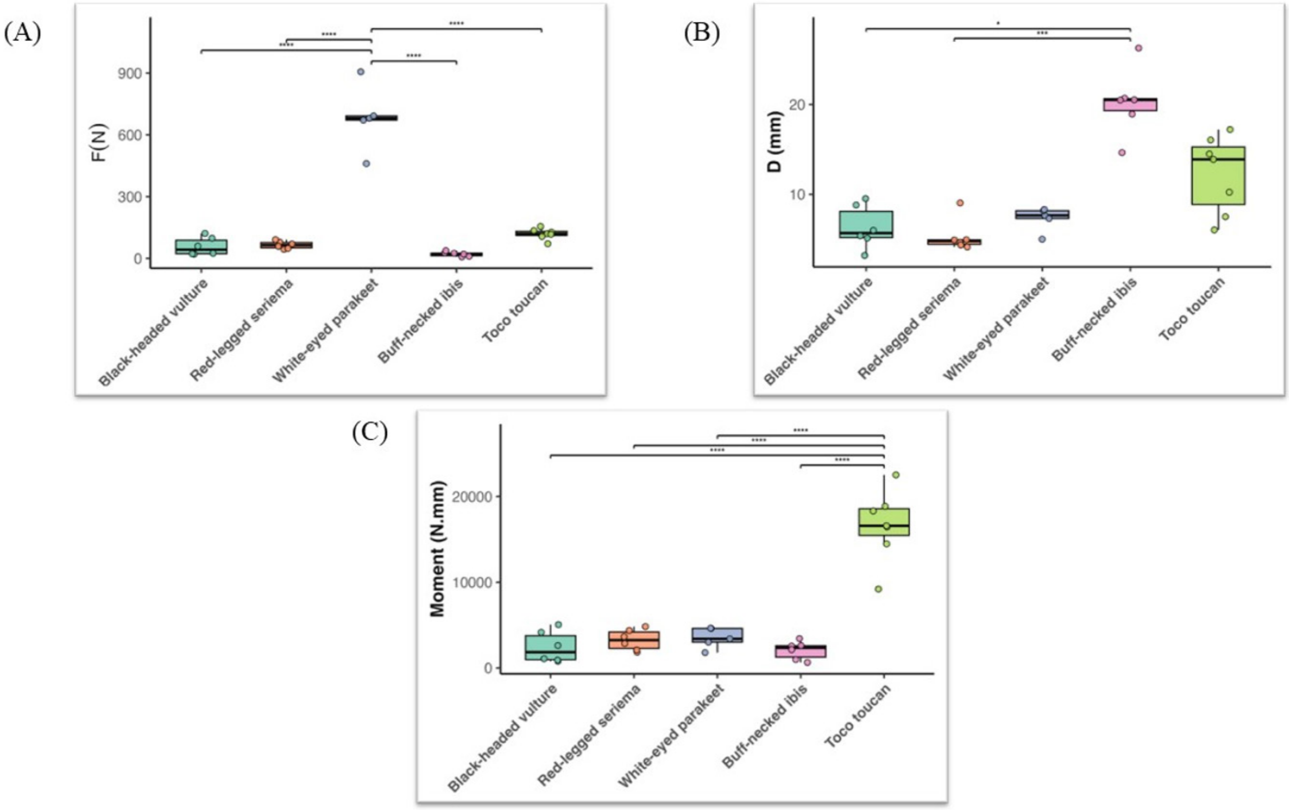

Figure 5. (A) Comparison of maximum force (F, N) among five bird species (black-headed vulture, red-legged seriema, white-eyed parakeet, buff-necked ibis, and toco toucan). (B) Comparison of maximum deformation (D, mm) among the same species. (C) Comparison of torque (Moment, N·mm) among the same species. In all panels, boxes indicate the interquartile range (IQR), horizontal lines represent the median, and whiskers extend to 1.5 × IQR. Dots correspond to outliers. Significant differences between species are indicated (*: $P<0.05$; **: $P<0.01$; ***: $P<0.001$; ****: $p < 0.0001$). Statistical tests: one-way ANOVA with post hoc comparisons for F and Moment, and Kruskal–Wallis test with post hoc comparisons for D.

Discussion

The present study conducted a mechanical evaluation of the maxillary rostrum due to its significance in trauma cases. Maxillary beak avulsion can hinder food grasping and self-feeding (Huynh et al. 2019; Speer and Powers 2016). The hypothesis was partially confirmed, as the birds exhibited interspecific variation in beak biomechanical resistance; however, this variation could not be related to HU values.

In the bending test, ventrodorsal load was applied to the distal third of the maxillary rostrum to simulate prehending force and standardize the methodology across different beak sizes. This approach differed from studies on the toco toucan beak, where flexure tests were conducted using traction perpendicular to the rostrocaudal axis (Fecchio et al. 2008; Fecchio et al. 2010), or by sectioning a portion of the beak's outer shell, which was then inserted into a laser cutting machine to produce dog-bone-shaped specimens used to assess tensile and compressive responses (Seki et al. 2006). However, the direction of the force used in the present study was consistent with that applied in the toco toucan beak traction studies (Fecchio et al. 2008; Fecchio et al. 2010).

Compared to the beaks of red-legged seriemas, black-headed vultures, and buff-necked ibises, the white-eyed parakeet's beak exhibited maximum force values that were 9.6, 844, and 3.1 times higher, respectively. Parrots have strong, hook-shaped beaks resembling nutcrackers, enabling them to climb trees, scrape and pick fruits, and engage in "beakiation" - a form of locomotion in which they use their beaks to swing from branch to branch (King and McLelland 1984; Kricher 1997; Dickinson et al. 2024). A study demonstrated that the parrot's beak can generate propulsive and tangential forces comparable to—or even greater than—those produced by the forelimbs of humans and non-human primates during vertical climbing (Young et al. 2022). Additionally, research on rosy-faced lovebirds *Agapornis roseicollis* verified that the maxilla plays a primary role in generating these forces during locomotion (Young et al. 2023). Parakeets primarily feed on seeds (30.4%) and fruits (39.1%), with a smaller proportion of flowers (17.4%) (Benavidez et al. 2018). The correlation between beak curvature and force has been previously demonstrated (Al-Mosleh et al. 2021).

The bending moment values of the white-eyed parakeet's beak were comparable to those of the red-legged seriema's beak, with no significant differences from the black-headed vulture and buff-necked ibis beaks. The thick, short, and decurved morphology of parrot beaks allows them to consume mechanically demanding foods, contributing to the relatively high bending moment values (Huynh et al. 2019). Additionally, the craniofacial hinge enhances upper beak mobility and strength (Harcourt-Brown 2005; Huynh et al. 2019). Finite-element analyses have demonstrated that beak shapes are generally well-suited to mitigating the risk of fracture in accordance with a species' predominant feeding habitat (Soons et al. 2015), with deep and wide beaks being better adapted for dissipating stress (Soons et al. 2010).

Despite its high maximum force value, the toco toucan's beak exhibited lower values than the white-eyed parakeet's beak. The maximum force of 126.6 N differed from previous studies, where fractures occurred at 270.4 N, likely due to methodological differences (Fecchio et al. 2008; Fecchio et al. 2010). The toucan's beak, proportionally one-third of its body mass (Fecchio et al. 2010; Fecchio 2021), is light yet highly energy-absorbent before fracturing (Seki et al. 2005). The beak's sandwich-like structure, featuring an outer β-keratin layer, trabecular bone core, and hollow interior, contributes significantly to its mechanical resistance (Seki et al. 2006; Seki et al. 2010). These structural traits appear more critical to mechanical resistance than dietary habits. Toucans are primarily frugivorous but also consume insects, lizards, snakes, eggs, and nestlings (Kricher 1997).

The maximum force values for the black-headed vulture and red-legged seriema beaks were similar, likely due to their comparable shapes. Both species possess curved, hook-shaped beaks typical of raptors, although they lack prokinetic capacity (Gelis 2006). Beak shape and strength may reflect dietary needs (Gill 2007), although one study found that diet accounts for less than 12% of the variation in beak shape (Navalón et al. 2019). Additionally, beak curvature and sharpening rates have been linked to dietary adaptations (Mosleh et al. 2023). Red-legged seriemas, with their strong, red beaks, feed on grasshoppers, arthropods, rodents, lizards, and snakes (Sick 1984; Favretto 2021). In contrast, black-headed vultures rely on their robust beaks to tear carrion and consume various animal remains (Sick 1984; Favretto 2021). The red-legged seriema's beak bending moment was 1.3 times greater than the black-headed vulture's, suggesting higher resistance to rupture despite the lack of statistical significance.

The buff-necked ibis' beak exhibited the lowest maximum force, reflecting its lower mechanical resistance. Classified as long and thin, the buff-necked ibis' curved, elongated beak is less resistant to bending forces (Sick 1984; Chen et al. 2008). Evolutionary pressures and dietary needs influence its shape and function (Fecchio 2021). The buff-necked ibis' beak, which withstood the greatest deformation, demonstrated lower rigidity compared to other species. This flexibility is essential for feeding behaviors, such as immersing the beak to extract larvae and preying on various animals (Sick 1984; Favretto 2021). The species possesses the ability to bend its upper jaw—a specialized movement known as rhynchokinesis (Zusi 1984).

Hounsfield Unit (HU) values in the actuator region did not correlate with maximum force. Although the toco toucan's beak displayed the second-highest maximum force, it had negative HU values, likely due to its thin bone shell (Seki et al. 2006). The black-headed vulture's beak had the highest HU values but much lower maximum force compared to the white-eyed parakeet and toco toucan. Except for the black-headed vulture, most beaks exhibited densities closer to spongy bone (+700 HU) (Bibb et al. 2015).

The study's primary limitation was the use of a single mechanical test. Additional tests, such as axial compression and torsion, are needed to fully understand beak mechanical properties under various loading conditions. The findings provide valuable insights for future research on prosthetic materials tailored to the mechanical properties of different bird species.

Conclusions

Biomechanical testing of the upper beak revealed some interspecific variation in mechanical properties, likely influenced by beak morphology, but no association with HU values. The white-eyed parakeet exhibited the highest maximum force, consistent with its robust, hook-shaped beak, followed by the toco toucan, red-legged seriema, black-headed vulture, and buff-necked ibis—the latter showing the lowest value, reflecting its elongated, flexible beak. These findings contribute to the understanding of functional adaptations in avian beaks and provide a basis to support future studies on prosthetic materials for the species analyzed, considering the differences identified through mechanical testing.

Acknowledgments

Grant information: FINEP (Financiadora de Estudos e Projetos): 01.12.0530.00; Capes (Coordination for the Improvement of Higher Education Personnel); National Council for Scientific and Technological Development: CNPq – PQ 305813/2023-4; and Biomechanics Laboratory of the Medical Research Laboratory of the Musculoskeletal System (LIM-41) of the Department of Orthopedics and Traumatology (DOT), School of Medicine, University of Sao Paulo (USP).

References

Al-Mosleh S., Choi G.P.T., Abzhanov A., Mahadevan L. (2021) Geometry and dynamics link form, function, and evolution of finch beaks. *Proceedings of the National Academy of Sciences of the United States of America* 118(46): e2105957118. doi:10.1073/pnas.2105957118

Benavidez A., Palacio F.X., Rivera L.O., Echevarria A.L., Politi N. (2018) Diet of Neotropical parrots is independent of phylogeny but correlates with body size and geographical range. *Ibis International Journal of Avian Science* 160(4): 742-754. doi:10.1111/ibi.12630

Bibb R, Eggbeer D, Paterson A (2015) Medical imaging. In: Bibb R., Eggbeer D., Paterson A. (eds.). *Medical Modelling. The Application of Advanced Design and Rapid Prototyping Techniques in Medicine*. 2nd ed. Cambridge, UK: Woodhead Publishing, 7-34.

Chen P.Y., Lin A.Y., Lin Y.S., Seki Y., Stokes A.G., Peyras J., Olevsky E.A., Meyers M.A., McKittrick J. (2008) Structure and mechanical properties of selected biological materials. *Journal of the Mechanical Behavior of Biomedical Materials* 1(3): 208-226. doi:10.1016/j.jmbbm.2008.02.003

Darrow B., Bennett R.A. (2022) Avian orthopedics. In: Bennett R.A, Pye G.W (eds.). *Surgery of Exotic Animals*. Hoboken, NY: Wiley-Blackwell, 112–153.

DenOtter T.D., Schubert J. (2023). Hounsfield Unit. In: *StatPearls. Treasure Island*, FL: StatPearls Publishing.

Dickinson E., Young M.W., Granatosky M.C. (2024) Beakiation: how a novel parrot gait expands the locomotor repertoire of living birds. *Royal Society Open Science* 11(1): 231397. doi:10.1098/rsos.231397

Favretto M.A. (2012) *Aves do Brasil, vol. I: Rheiformes a Psittaciformes*. Florianópolis, Brasil: Clube de Autores.

Fecchio R.S., Gomes M.S., Kolososki J., Petri B.S.S., Rossi Jr. J.L., Gioso M.A. (2008) Study of the occlusion biomechanics and adherence of acrylic resin (polimetilmetacrilate) in fractures of rhinotheca in toucans (*Ramphastos toco*). *Pesquisa Veterinária Brasileira* 28(7): 335-340.

Fecchio R.S., Seki Y., Bodde S.G., Gomes M.S., Kolososki J., Rossi Jr. J.L., Gioso M.A., Meyers M.A. (2010) Mechanical behavior of prosthesis in Toucan beak (*Ramphastos toco*). *Materials Science and Engineering: C* 30(3): 460–464. doi:10.1016/j.msec.2010.01.001

Fecchio R.S. (2021) Beakistry. In: Emily P.P., Eisner E.R. (eds.). *Zoo and Wild Animal Dentistry*. Hoboken, NY: Wiley Blackwell, 99-117.

Friedman, N.R., Miller, E.T., Ball, J.R., Kasuga, H., Remeš, V., Economo, E.P. (2019) Evolution of a multifunctional trait: shared effects of foraging ecology and thermoregulation on beak morphology, with consequences for song evolution. *Proceedings. Biological Sciences* 286(1917): 20192474. doi:10.1098/rspb.2019.2474

Gelis S. (2006). Evaluating and treating the gastrointestinal system. In: Harrison G.J., Lightfoot T. (eds.). *Clinical Avian Medicine*. Palm Beach, FL: Spix Publishing Inc., 412-440.

Gill F.B. (2007) *Ornithology. 3rd ed*. New York, NY: Freeman.

Harcourt-Brown N.H. (2005) Anatomy and physiology. In: Harcourt-Brown N.H., Chitty J. (eds.). *BSAVA Manual of Psittacine Birds. 2nd ed*. Gloucester, UK: British Small Animal Veterinary Association, 7-21.

Huynh M., González M.S., Beaufrére H. (2019) Avian skull orthopedics. Veterinary Clinics of North America: *Exotic Animal Practice* 22(2): 253-283. doi:10.1016/j.cvex.2019.01.006

Kricher J.C. (1997) Neotropical birds. In: Kricher J.C. (ed.). A Neotropical Companion: *An Introduction to the Animals, Plants, and Ecosystems of the New World Tropics. 2nd ed*. New Jersey, NJ: Princeton University Press, 251-294.

King A.S., McLelland J. (1984) *Birds: Their Structure & Function*. 2nd ed. London, UK: Bailliere Tindall.

Mosleh S., Choi G.P.T., Musser G.M., James H.F., Abzhanov A., Mahadevan L. (2023) Beak morphometry and morphogenesis across avian radiations. *Proceedings of the Royal Society - Biological Sciences* 290(2007): 20230420. doi:10.1098/rspb.2023.0420

Navalón, G., Bright, J.A., Marugán-Lobón, J., Rayfield, E.J. (2019) The evolutionary relationship among beak shape, mechanical advantage, and feeding ecology in modern birds. *Evolution; International Journal of Organic Evolution* 73(3): 422–435. doi:10.1111/evo.13655

Olsen G.H. (2003) Oral biology and beak disorders of birds. Veterinary Clinics of North America: *Exotic Animal Practice* 6(3): 505-vi. doi:10.1016/s1094-9194(03)00030-6

Seki Y., Schneider M.S., Meyers M.A. (2005) Structure and mechanical behavior of a toucan beak. *Acta Materialia* 53(20): 5281–5296. doi:10.1016/j.actamat.2005.04.048

Seki Y., Kad B., Benson D., Meyers M.A. (2006) The toucan beak: structure and mechanical response. *Materials Science and Engineering* C 26(8): 1412-1420. doi:10.1016/j.msec.2005.08.025

Seki Y., Bodde S.G., Meyers M.A. (2010) Toucan and hornbill beaks: a comparative study. *Acta Biomaterialia* 6(2): 331-343. doi:10.1016/j.actbio.2009.08.026

Sick H. (1984) *Ornitologia Brasileira. 2nd ed*. Brasília, Brasil: Editora Universidade de Brasília.

Silva D.S., Rahal S.C., Silva J.P., Mamprim M.J., Camargo G.C., Cassanego G.R., Ichikawa, R.S. (2024). Radiologic and computed tomography evaluation of the beaks from three bird species. *Anatomia, Histologia, Embryologia* 53(2): e13027. doi:10.1111/ahe.13027

Soons J., Herrel A., Genbrugge A., Aerts P., Podos J., Adriaens D., de Witte Y., Jacobs P., Dirckx J. (2010) Mechanical stress, fracture risk and beak evolution in Darwin's ground finches (Geospiza). *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences,* 365(1543): 1093–1098. doi:10.1098/rstb.2009.0280

Soons J., Genbrugge A., Podos J., Adriaens D., Aerts P., Dirckx J., Herrel A. (2015) Is beak morphology in Darwin's finches tuned to loading demands? *PloS One* 10(6): e0129479. doi:10.1371/journal.pone.0129479

Speer B., Powers L.V. (2016) Anatomy and disorders of the beak and oral cavity of birds. *Veterinary Clinics of North America: Exotic Animal Practice* 19(3): 707-736. doi:10.1016/j.cvex.2016.04.003

Tattersall, G.J., Arnaout, B., Symonds, M.R.E. (2017) The evolution of the avian bill as a thermoregulatory organ*. Biological Reviews of the Cambridge Philosophical Society* 92(3): 1630–1656. doi:10.1111/brv.12299

Young M.W., Wilken A.T., Manafzadeh A.R., Schurr A.F., Bastian A., Dickinson E., Granatosky M.C. (2023) The dual function of prokinesis in the feeding and locomotor systems of parrots. *The Journal of Experimental Biology* 226(24): jeb246659. doi:10.1242/jeb.246659

Young M.W., Dickinson E., Flaim N.D., Granatosky M.C. (2022) Overcoming a 'forbidden phenotype': the parrot's head supports, propels and powers tripedal locomotion*. Proceedings Biological Sciences* 289(1975): 20220245. doi:10.1098/rspb.2022.024

Wang S., Stiegler J., Wu P., Chuong C-M. (2020) Tooth vs. beak: the evolutionary developmental control of the avian feeding apparatus. In: Pittman M, Xu X (eds.). *Pennaraptoran Theropod Dinosaurs: Past Progress and New Frontiers*. New York, NY: Bulletin of the American Museum of Natural History, 205–228.

Zusi R.L. (1984) A Functional and Evolutionary Analysis of Rhynchokinesis in *Birds*. Washington, DC: Smithsonian Institution Press.