



SHORT COMMUNICATIONS

The Condor 107:445–449
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MANDIBULAR BOWING AND MINERALIZATION IN BROWN PELICANS

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Abstract. Brown Pelicans (*Pelecanus occidentalis*) plunge dive into water to capture fish with highly distensible pouches. During prey capture, the pouch may expand to hold 11 L of water and the mandibular rami may bow from a resting position of 5 cm to over 15 cm. We compared mineralization of two bending regions of the mandible with a nonbending region, and examined cross-sectional morphology to determine if mineral content and shape play a role in mandibular bending. A rostral bending zone, adjacent to the mandibular symphysis, possessed only about 20% mineral content, significantly less than the lateral bending zone and the rigid caudal mandible, both comprised of over 50% mineral content. Additionally, the rostral zone was solid in cross section, facilitating bending, whereas the lateral zone was made up of bones joined by connective tissue. This latter morphology permits movement between the bones even though there was relatively high mineralization. We suggest that mineral content may be an overlooked component to cranial kinesis in birds.

Key words: Brown Pelican, cranial kinesis, feeding, jaw mechanics, *Pelecanus occidentalis*, streptognathism.

Arqueamiento y Mineralización de la Mandíbula en *Pelecanus occidentalis*

Resumen. Los pelícanos *Pelecanus occidentalis* se zambullen en el agua para capturar peces utilizando bolsas bucales muy distensibles. Durante la captura de la presa, la bolsa bucal se puede expandir para contener hasta 11 litros de agua y las ramas mandibulares se pueden arquear desde una posición de descanso de 5 cm hasta más de 15 cm. En este estudio, comparamos la mineralización de dos regiones mandibulares que se arquean con una región rígida que no se arquea y examinamos la morfología transversal para deter-

minar si el contenido mineral y la forma desempeñan una función al arquear la mandíbula. Una zona de doblado rostral adyacente a la sínfisis mandibular posee un contenido mineral de aproximadamente el 20%, lo que representa una mineralización significativamente menor que la de la zona lateral de doblado y la sección caudal rígida de la mandíbula, las cuales contienen más de un 50% de minerales. Adicionalmente, la zona rostral tiene una sección transversal sólida que facilita su arqueamiento, mientras que la zona lateral está compuesta de huesos unidos por tejido conectivo. Esta última morfología permite el movimiento entre los huesos aunque exista una alta mineralización. Sugerimos que el contenido mineral puede ser un componente de la quinesis cranial de las aves que es frecuentemente ignorado.

Brown Pelicans (*Pelecanus occidentalis*) dive into water for fish from altitudes of 9–16 m (Allen 1923), often attaining speeds of up to 18 m sec⁻¹ before water impact (Johnsgard 1993). Their gular pouches are highly distensible, and can hold up to 11 L of water (Schreiber et al. 1975). Schreiber et al. (1975) estimated that when the mandibles bow (from a resting position of about 5 cm apart to over 15 cm apart) the opening created is approximately 500 cm². This bowing, termed streptognathism, is well-developed in birds that are able to swallow large objects (Judin 1961, Zusi 1993), such as pelicans. Mandibular bowing in pelicans may be produced by: (1) passive interaction between the water and the flexible mandibles (Schreiber et al. 1975), (2) contraction of pouch musculature (i.e., genioglossus muscle) pulling the chin caudally (Johnsgard 1993), or (3) action of the pterygoid musculature acting on the internal process of the mandible (Böker 1938, Judin 1961, Burton 1977).

When bowed, the mandible has two distinct pairs of bending zones: one pair on either side of the mandibular symphysis, and another occupying approximately the rostral two-thirds of the mandible (Fig. 1). Bending zones within the avian skull are typically described as being thin bony regions (Gussekloot et al. 2001) or multilayered bony laminae (Bühler 1981). Studies of

Manuscript received 11 November 2004; accepted 20 January 2005.

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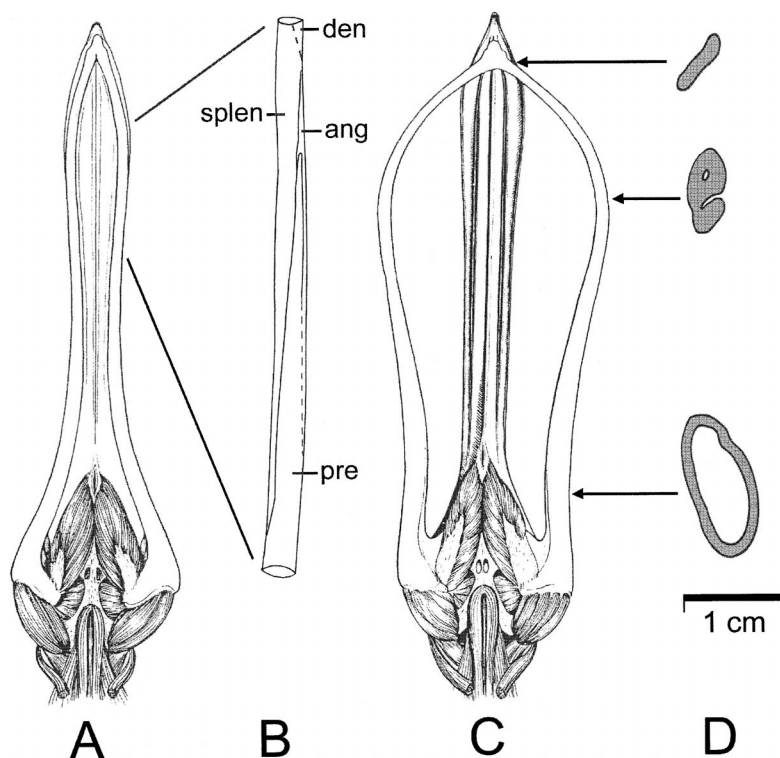


FIGURE 1. Mandibular bowing in the Brown Pelican (*Pelecanus occidentalis*). (A) Ventral view of pelican head and lower jaw in resting position, pouch removed (modified from Böker [1938]). (B) Medial view of left mandible, showing lower jaw bones that make up the "leaf spring" area of the lateral bending zone. ang = angular; den = dentary; pre = prearticular; splen = splenial. (C) Ventral view of pelican head and lower jaw in bowed position, pouch removed (modified from Böker [1938]). (D) Cross sections through the three lower jaw regions studied: top, solid rostral bending zone; middle, syndesmotomic lateral bending zone; bottom, caudal nonbending zone (scale = 1 cm).

avian cranial kinesis typically focus on the upper bill and not the lower jaw, though there have been exceptions (Judin 1961, Bock and Kummer 1968). Judin's (1961) detailed paper on the lower jaw describes a complex syndesmosis (a type of joint in which bones are joined by connective tissue) that accounts for lower jaw bowing in gulls and other species, including pelicans. In this paper, we examined the bending of the Brown Pelican lower jaw, and show that both mineral content and bone shape contribute to the high degree of bowing observed when this species dives into the water for food.

METHODS

Fresh specimens of four adult Brown Pelicans were obtained from the North Carolina State Museum of Natural History, Raleigh, NC, and from Pelican Harbor Seabird Station, Florida. Mandibles were removed, stripped of their keratinous rhamphothecae and underlying connective tissue, and dried. Cross sections were determined using a Siemens (BMI Medical, Lake Barrington, Illinois) Volume Access Multirow CT scanner with a field of view of 1024×1024 pixel images at McKay-Dee Hospital in Ogden, Utah. These images

were used to resolve cross-sectional shapes and to calculate second moments of area. The latter gives a measure of how bendable a beam or tube is. It takes into account the relative height to width as well as the thickness of the tube wall and its distance from the central axis (Panjabi and White 2001). Calculations were made on ellipses that closely approximate the shape of each jaw region.

Mineral content of three mandibular regions was determined by ashing fragments of dried bone from areas along the length of the lower jaw: the rostral bending zone adjacent to the symphysis, the syndesmotomic lateral bending zone, and the caudal non-bending part of the mandible (Fig. 1C, D). Small pieces of bone (Mean mass = 0.12 ± 0.10 g) were weighed using a Mettler (Columbus, Ohio) PE 360 milligram balance to determine initial mass (M_0) and then placed in a ceramic crucible. The samples were individually heated with a bunsen burner to over 600°C for periods of 20 min, after which all of the organic material in the bone should have been burned away, leaving only mineral behind. Once it was cool enough to handle, the crucible was weighed and its (pre-ashing) mass was sub-

TABLE 1. Mean mineral content (%) and number of samples (*n*) from each region of the mandible of four Brown Pelican individuals. Note that for the rostral zone, samples consisted of a single fragment from both sides of each mandible.

Individual	Mandibular Region					
	Rostral zone		Lateral zone		Caudal zone	
	Mineral content (%)	<i>n</i>	Mineral content (%)	<i>n</i>	Mineral content (%)	<i>n</i>
1	22.1	2	50.2	9	48.5	4
2	19.6	2	52.9	17	57.5	3
3	15.4	2	50.7	8	61.7	3
4	23.3	2	55.0	7	52.5	3

tracted out to obtain the bone fragment's final mass (*M*). The percent mineral content was determined using the following equation (Papadimitriou et al. 1996):

$$\text{Mineral content (\%)} = (MM_0^{-1}) \times 100.$$

Mean mineral content was calculated for each region per mandible, and then a grand mean was calculated for each region across the four individual mandibles (Table 1). A one-way analysis of variance (ANOVA) was conducted to compare mineral content among regions (SPSS Inc. 2001). An *a priori* contrast using the *t*-statistic was used as a *post-hoc* test to compare the mineral content of the rostral bending zone to the other mandibular regions. Alpha levels of 0.05 were considered significant and values are reported as mean \pm SD.

RESULTS

We found specializations for two distinct bending zones within the pelican lower jaw. The rostral bending zone, directly adjacent to the symphysis, is narrowly elliptical in shape and solid in cross section (Fig. 1D). This very small region only 2–3 mm long has a second moment of area of 0.29 mm⁴. Ash analysis determined that the rostral bending zone is an area of very low mineralization (20% \pm 4% mineral content, Fig. 2).

Occupying the rostral two-thirds of the mandible are lateral bending zones, which are composed of syndesmoses between the dentary and splenial bones, rostrally, and the prearticular and angular bones, caudally (Fig. 1B). This region is generally oval in cross sectional shape with small spaces corresponding to the location where connective tissue joins the bones, as well as an internal space between the bones. This region has a second moment of area of 25.1 mm⁴ and a mean mineral content of 52 \pm 2% (Fig. 2). The caudal one-third of the mandible is oval, rigid, and hollow with a second moment of area of 493.6 mm⁴. Its mineral content is similar to that of the lateral bending zone (56 \pm 5%; Fig. 2). Our data support the hypothesis that mineral content differs among regions ($F_{2,9} = 90.3$, $P = 0.0001$). The contrast follow-up test indicates that the rostral bending zone has a significantly lower mineral content than the other regions ($t_{1,9} = -13.4$, $P = 0.0001$).

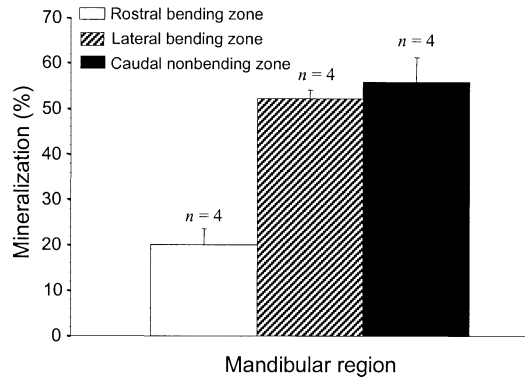


FIGURE 2. Average mineral content (\pm SD) of the rostral bending zone, lateral bending zone, and caudal nonbending zone from Brown Pelicans.

DISCUSSION

Although the mechanism of pouch expansion and mandibular bowing of the Brown Pelican is a subject that has been studied very little, there are conflicting results. Böker (1938), Judin (1961), and Burton (1977) suggested that the pouch expands due to contraction of the pterygoid muscles. Schreiber et al. (1975) explained that pouch expansion is likely passive, and is due to the interaction of the jaws with the water. Lastly, Johnsgard (1993) suggested that a (unspecified) pouch muscle could bow the jaws by pulling the chin caudally.

The mandibular bending zones are clearly essential to the Brown Pelican feeding apparatus. Judin (1961) described the morphology of the syndesmotomic lateral bending zone in gulls and compared it with many other species. He noted that three groups of birds could be distinguished based on this characteristic of the lower jaw: species with the lower jaw divided into cranial and caudal parts connected by syndesmotomic sutures capable of bending (e.g., gulls, pelicans), species with the bony elements of the lower jaw connected by syndesmoses but arranged such that no bending is possible (e.g., ostriches), and species whose lower jaw lacks sutures (e.g., raptors, parrots, passerines). Judin (1961) concluded that streptognathism probably evolved convergently many times within birds.

Bühler (1970) described in great detail the mechanism for lower jaw bowing in goatsuckers (Caprimulgidae) in which there are two bending zones: an "anterior intramandibular joint" (our rostral bending zone) and a "posterior intramandibular joint" (our lateral bending zone). Bühler (1970) describes the anterior intramandibular joint as a "kinetic synostosis" [a union of two bones to form a single bone] caudal to the symphysis and the posterior intramandibular joint as a "well-known hinge joint." The anatomical arrangement of bending zones in the Brown Pelican is somewhat similar to that of goatsuckers, although the extreme rotation seen in *Caprimulgus* does not occur in *Pelecanus* (Zusi 1993), nor is jaw depression linked to bowing (Judin 1961).

The decreased mineralization and solid cross section of the rostral bending zone make it extremely bendable. Bones typically function to resist bending, but mineral content and shape can affect the degree to which bones can bend (Currey 1984, 2002). Mineral content is correlated with the mechanical properties of bone, and it is well known that decreased mineral content makes a bone more flexible and less likely to break (Currey 1979, 1984, 2002, 2003, Papadimitriou et al. 1996). For example, the proximal and middle phalanges of bats (*Tadarida brasiliensis*) have a mineral content of about 30 percent; distal phalanges have no mineral content and are cartilaginous (Papadimitriou et al. 1996). These low mineral levels are interpreted as being useful for flexibility in wingtip deformation during flapping flight. Similarly, the low mineral content of deer antlers (59%) is viewed as an adaptation to resist breakage during fighting (Currey 1979, 2003).

In addition, shape plays an important role in the mechanical properties of bones. It is well known that given a tube and rod of similar material and equal mass, the hollow rod will resist bending more than a solid rod (McGowan 1999). The rostral bending zone, in addition to being only about 20 percent mineral content, is solid in cross section, and taller than wide, thus facilitating lateral bending (Vogel 1988). This is again similar to the distal phalanges of bats that are also solid in cross-section (Swartz 1998). Even though the rostral bending zone has only about one-third of the cross-sectional area (of bone) of the hollow caudal region, its second moment of area is still about 500 times less! Since the rostral bending zone is also 2.5 times less mineralized, this zone is even more bendable than it would be based on shape alone.

Mandibular bending is also not restricted by the presence of the overlying keratin. The keratin that overlies the rostral bending zone is much more skin-like and not at all like typical rhamphothecal keratin. Homberger and Brush (1986) described different categories of avian keratins based on mechanical properties and molecular weight of the keratin monomers. We suggest that the keratin overlying the rostral bending zone is likely to be more similar to skin keratin in its molecular weight.

The lateral bending zone is morphologically unlike the rostral bending zone. It is comprised of syndesmoses of the dentary, splenial, prearticular, and angular bones. Both Judin (1961) and Bühler (1981) reported that this bending zone is made up of bony laminae interspersed with connective tissue and Judin (1961) described how this separation of bones "increases space" within the pelican's zone of flexibility and allows this area of the mandible to bow. These bones are solid in cross section, and have a mineral content of about 52 percent. This syndesmotomic joint permits these bones to move relative to one another, much like a leaf-spring functions. Despite the relatively higher mineral content of this region, this movement of lower jaw bones contributes to the high degree of lateral bowing seen during pelican feeding.

In conclusion, we have described how very low mineralization and shape facilitates bending in the lower jaw of Brown Pelicans. Future work needs to

determine the type of keratin overlying the rostral bending zone, and to determine if reduced mineralization is associated with bending zones in both the lower jaws and skulls of other bird species.

We would like to thank Harry Kelton and Wendy Fox of Pelican Harbor Seabird Station and John Gerwin of the North Carolina State Museum of Natural History for providing specimens. Angie Ackerman-Martinez of McKay-Dee Hospital, Ogden, Utah graciously provided access to a CT scanner. Clint Webb assisted with mandibular ashing. Drs. John Cavitt and Adam Johnston provided technical assistance. DaLyn Erickson of the Ogden Nature Center provided access to a living and willing pelican for mandible manipulation. Nick Harris translated the Böker paper; Tyrun Ray translated excerpts from the Judin paper. Dr. D. G. Homberger made a full translation of the Judin paper available. Zach Warner and Dr. Diego Bernal provided the Spanish abstract. Two reviewers made helpful comments on the ms. This research was funded by a Thompson Research Fellowship (RPM) and a Hemingway Faculty Vitality Award in support of Undergraduate Research (RAM).

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The Condor 107:449–457
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TRANSFORMATIONS AT HIGH LATITUDES: WHY DO RED KNOTS BRING BODY STORES TO THE BREEDING GROUNDS?

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Abstract. We examined changes in body composition of Red Knots (*Calidris canutus islandica*) following arrival on their High Arctic breeding grounds at Alert, Ellesmere Island, Canada. Knots arrived in late May and early June with large fat and muscle stores. In the next two weeks, fat and protein stores (pectoral muscles) declined, while increases occurred in gizzard, proventriculus, gut length, heart, liver, and possibly gonads. Most stores were used before egg laying occurred and were therefore not available for egg formation. Early development of ova in some females suggests that body stores may be incorporated into the earliest eggs. While stores may be used for survival when conditions are difficult after arrival, their rapid loss and the concomitant increase in other organs suggests that a major function may be to facilitate a transformation from a physiological state suitable for mi-

gration to one suitable, and possibly required, for successful breeding.

Key words: body stores, *Calidris canutus*, High Arctic, migration, phenotypic flexibility, Red Knot, shorebirds.

Transformaciones a Altas Latitudes: ¿Por qué *Calidris canutus islandica* Lleva Reservas Corporales a los Sitios de Nidificación?

Resumen. Examinamos los cambios en la condición corporal de individuos de *Calidris canutus islandica* luego de que éstos llegaron a sus territorios reproductivos a altas latitudes en el Ártico en Alert, isla Ellesmere, Canadá. Los individuos de *C. c. islandica* llegaron a fines de mayo y comienzos de junio con grandes reservas de grasa y músculo. Durante las dos semanas siguientes, las reservas de grasa y proteína (músculos pectorales) disminuyeron, mientras que la molleja, los proventriculos, el largo del intestino, el hígado y posiblemente las gónadas aumentaron de tamaño. La mayoría de las reservas fueron usadas antes

Manuscript received 4 May 2004; accepted 17 December 2004.

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