Metacarpal Bone Strength of Pronghorn (*Antilocapra americana*) compared to Mule Deer (*Odocoileus hemionus*)

by

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Thesis directed by Associate Professor Jeffrey P Broker

**ABSTRACT**

Human-made barriers influence the migration patterns of many species. In the case of the pronghorn (*Antilocapra americana*), a member of the Order Artiodactyla and native to the central and western prairies of the United States, the presence of fences may completely inhibit movement. Depending on the fence a pronghorn will rarely decide to jump over it, instead preferring to crawl under, if possible, or negotiate around it until the animal finds an opening. Despite having been observed to jump an 8-foot-tall fence in a previous study, some block exists. This study investigated one possible block, being the risk of breakage on the lower extremity bones upon landing. The metacarpals of pronghorn and mule deer (*Odocoileus hemionus*), a routine jumper of fences that lives in relative proximity to the pronghorn, were tested using a three-point bending test. Upon bone failure, the ultimate force and deformation measurements were collected, and stiffness of the bones was calculated. A comparison of the two species showed that mule deer metacarpals resisted greater forces and flexed more before breaking. This could be the case because the bones need to support a much larger body weight. Both species have nearly equal measures of stiffness in their metacarpal. The strength of the pronghorn leg
bone seems to be great enough to allow the jump, which supports the supposition that the jumping block may be strictly behavioral for an ungulate that evolved on open plains.
DEDICATION

I would like to dedicate this thesis to Jon Pigage whose passion, which started this study, will be carried on as I explore more of the natural world for many years to come.
ACKNOWLEDGEMENTS

I would like to thank Dr. Helen Pigage for her extremely helpful work reading and editing this paper. Her determined attitude pushed me forward when I needed it most. I would also like to thank Dr. Jeffrey Broker for sharing his expertise and knowledge of a subject I started off knowing so little about. I would like to thank Dr. Emily Mooney for providing me with the tools and information to solve my analytical problems. Ted Baker Meat Processing generously provided the bones I used for my study. I appreciate Brandi Miller for not only lending a helping hand but also supporting me the whole way. Also, I would like to thank my wonderful friends and family for giving me a much-needed pat on the back or kick in the butt.
# TABLE OF CONTENTS

**CHAPTER**

I. LITERATURE REVIEW ................................................................. 1

II. METHODS AND MATERIALS ..................................................... 13

III. RESULTS ................................................................................. 21

IV. DISCUSSION ............................................................................ 30

LITERATURE CITED ........................................................................ 35

PHOTO CREDITS ............................................................................ 38
LIST OF TABLES

TABLE

1. Mean and standard deviation for 6 dimensions for the 3 bone groups…………..27
2. P-values for 6 dimensions comparing each bone group to another………………27
3. Means and standard deviations for 6 physical properties for the 3 bone groups…28
4. P-values for 6 physical properties comparing each bone group to another………29
LIST OF FIGURES

FIGURE

1. Male pronghorn (*Antilocapra americana*) seen in its native grassland habitat........1

2. Pronghorn buck crawling under a fence, the bottom strand of which is far enough off the ground to allow such movement.................................................................4

3. Anterior side of a pronghorn metacarpal (cannon bone) with the distal end on the left and the proximal end on the right.................................................................7

4. Posterior side of a pronghorn metacarpal (cannon bone). The large groove is visible.................................................................7

5. Close-up of the distal end of a pronghorn metacarpal featuring its highly-adapted, articular facets...............................................................8

6. The three-point bending test apparatus shows the locations of the supporting pins and the force as applied to the specimen.........................................................11

7. Frozen bones wrapped in gauze and placed in room temperature saline solution 24 hours before testing.................................................................14

8. The MTS 858 Mini Bionix II Table Top System used. The custom testing apparatus can also be seen fitted in the machine’s middle........................................15

9. The custom testing apparatus shown from an angled view................................15

10. The custom testing apparatus shown from the front view with a scale for size...16

11. Typical cross section of elliptical bone.........................................................17

12. The force-deformation curve for most materials........................................18

13. Force-deformation curves for the three bone groups. The mean stiffness for each group is shown with a colored line........................................22
14. Force-deformation curves of all three bone groups as well as their mean stiffness line………………………………………………………………………………………………..23
15. Ultimate force and deformation scatter plot for the Mule Deer metacarpal group………………………………………………………………………………………………..24
16. Ultimate force and deformation scatter plot for the pronghorn metacarpal group………………………………………………………………………………………………..25
17. Ultimate force and deformation scatter plot for the pronghorn metatarsal group………………………………………………………………………………………………..25
18. Combined ultimate force and deformation scatter plot for all three groups: mule deer metacarpal, pronghorn metacarpal, and pronghorn metatarsal……………26
CHAPTER I

LITERATURE REVIEW

Pronghorn

The pronghorn (*Antilocapra americana*) is a member of the Order Artiodactyla that is indigenous to the central and western prairies of North America. The species is named for the presence of pronged-horns on the males (Fig 1). The females have much shorter horns that are barely visible.

![Fig 1: Male pronghorn (*Antilocapra americana*) seen in its native grassland habitat.](image)

While usually referenced as the pronghorn “antelope”, the pronghorn is more closely related to the giraffe and is so named due to its parallel ecological niche to the antelopes of the Old World. It was first formally described by the expedition of Lewis and Clark in 1804, as a result of hunting:

“I walked on shore to find an old Vulcanoe . . . in my walk I killed a Buck Goat of this Countrey, about the height of the Grown Deer, its body Shorter the horns which is not very hard and forks 2/3 up one prong Short the other round & Sharp arched, and is immediately above its Eyes the Colour is a
The pronghorn’s body displays many adaptations that assist it for long-distance running. Cutright (2003) explained that the animal “can cover ground at a rate of close to 60 miles an hour and can maintain a speed of 40 miles for several minutes”. It is believed that the presence of a North American cheetah thousands of years ago was the primary selective force for this adaptation (Byers 1997). Pronghorn have large hearts, lungs, and windpipes as well as padded, pointed toes that help cushion the impact when running. They also run with their mouths open to maximize oxygen intake (O’Gara and Yoakum 2004).

Fencing Impact on Wildlife

Since the Neolithic, fences have been used to protect humans from outside threats (Hayward and Kerley 2009). For conservation biology, fences are one method to separate people and wildlife such as establishing wildlife preserves which assist in the protection of habitat or select species that would normally have higher risks of extinction (Woodroffe et al. 2014). They also postulate that fences may also restrict the spread of disease or invasive species. However, fencing can fragment existing contiguous habitat creating smaller “island” areas. These areas lower the possible number and density of populations due to smaller carrying capacities. Several predators have improved their hunting success by chasing their prey into fences or hunting near choke-points (Hayward and Kerley 2009).

Another effect of fencing, especially important to this study, is the blocking of migration routes. Seasonal movements of populations are timed with changes in resources
or assisting with gene flow (Hayward and Kerley 2009). In many cases, migration corridors have been established to connect areas of habitat. In North America, pronghorn and mule deer annually follow specific migratory routes (Sawyer et al. 2005). As humans have colonized along their routes, they have built fences to mark off parcels of land which has effectively diverted or eliminated certain migration paths. For mule deer and other larger ungulates, fencing (depending on dimensions) has only been a minor obstacle as they easily bound over, but pronghorn seem to show an unwillingness or inability to do the same.

“In the relatively fractional time since fencing of the West began, segmenting major proportions of pronghorn rangelands, pronghorn have not learned to go through most fences (as do bison) or vault them (as for elk and deer). Instead, many have learned to negotiate certain fences by crawling underneath. But, if the bottom wires of fences are too low, by virtue of design or buildup of vegetation or snow, pronghorn mobility can be impeded” (O’Gara and Yoakum 2004).

With entrapment by fences, pronghorn cannot respond to the same seasonal changes or environmental disasters (drought, blizzard, etc.) as they did before.

Fence Behavior

The selective behavior of the pronghorn was first described by John Caton (1881) while observing a buck in a fenced enclosure. He had been told previously that “the Prong Buck cannot, or rather I should say does not know how to leap over high obstructions”. Caton references this quote in another:

"Although I had observed this buck, whilst confined in the yard, when frightened by a person going in, dash against the palings not three feet from the ground, in his efforts to break through the fence, without attempting to leap over it, yet it never occurred to me that he could not make vertical leaps, till I met the statement above quoted. Subsequent observation of the conduct of these animals in my grounds convinced me that the statement might well be true, and that the Prong Buck may be restrained by a fence which would be sufficient to confine domestic sheep".
The behavior was best described by Einarsen (1948) as (Fig 2):

"During our field work on this species no instance was noted where antelope attempted to jump even a low fence. Usually they pass through by quickly wriggling under or between the wires near the ground. Often the excavations of a rabbit or coyote under the bottom wire will permit an antelope to squeeze through either netting or barbed wire fences. It has been observed from time to time that antelope traveling as fast as 40 miles an hour will not hesitate approaching a 4-strand fence, but will strike it in full stride and pass through, leaving a cloud of hair floating in the wind behind them."

![Image](image.png)

**Fig 2:** Pronghorn buck crawling under a fence, the bottom strand of which is far enough off the ground to allow such movement.

The fastest mammal in North America appears to be choosing not to jump fences but rather going under the lowest wire or between them, should sufficient gaps exist. During several experiments, however, pronghorn have been observed to leap over fences. In one trapping operation, Buechner (1950) observed a pronghorn jumping over a 1.52 or 1.83 m (5 or 6 ft) tall net from a standing position. A pronghorn has even been observed going over a 2.44 m (8 ft) tall obstacle, though it required goading (Spillett, Low, and Sill 1967). Buechner further noted:

“With few exceptions, they appeared to be unaware of their ability to jump vertical barriers and rarely jumped fences over 32 inches (0.82 m) high unless it was a result of active pursuit or severe stress induced by man”.
Even under stresses such as starvation from being trapped in an overgrazed area surrounded by a sheep-fence, pronghorn have been found dead (Buechner 1950). This is not to say pronghorn will never jump fences, it appears to be an uncommon event. Hunters have observed pronghorn jumping fences without any notable stresses provoking them to do so (Popowski and Pyle 1982).

Since Caton described the behavior in 1881, biologists have suggested that it originates from a behavioral block (Popowski and Pyle 1982). Precisely how this block manifests is not known. Spillett, Low, and Sill (1967) also noted that a pronghorn was more hesitant to jump if the animal could not see above the vertical barrier. Pronghorn have the ability to notice small movements in their environment miles away, so it has been also proposed that their ability to see the fence close-up is diminished. However, a horse, which has comparable visual acuity, does not have difficulty jumping or interacting with fences (Popowski and Pyle 1982). An observational study in Wyoming (Autenrieth 1983) also looked at the learning ability of pronghorn to jump fences as they matured. They found that “there has been no marked increase in the number of pronghorns learning to jump fences” but older individuals have a “greater tendency” to jump than fawns.

Another possible reason for pronghorn choosing to go under rather than over may be the prevention of physical damage. With the pronghorn living its entire lifespan on the plains and the highly adapted nature with its ability to run, an injury could easily lead to death. As the pronghorn’s primary mode of movement is horizontal, the bones or joints may not be able to withstand vertical impact following a high jump. The effect of fence height have been studied in animals that routinely jump obstacles for show. In horses, a study by Meershoek et al. (2001) concluded that increased fence height caused higher
loading on leg tendons, which therefore could increase injuries in those tendons. In dogs, a study by Birch and Lesniak (2013) found that increased fence height caused increased flexion of joints during take-off and at the peak of the jump. These higher joint angles can cause intensified stretching of muscles leading to a higher chance of injury. In addition, the pronghorn’s ability to run over uneven terrain has been noted:

"The apparent skill which pronghorns display in preventing accidents to limbs as they run over rough or broken ground is in a large degree due to the perfection of structural design which permits free movement, yet effectively binds and supports the articulated members, thus preventing strains, sprains or other injuries. The length of tendons and ligaments is so nicely adjusted that only in the rarest instance can bone be so forced beyond its usual position as to result in damage" (Einarsen, 1948).

“Rough or broken ground”, however, does not encapsulate the vertical difference a fence may present. The impact force against the front legs of the pronghorn during landing may be significant enough to cause damage to either bones or joints.

Pronghorn Leg Bones

Much like their enlarged heart, lung, and windpipe, a pronghorn’s leg bones have been adapted to maximize their running ability. In humans, the metacarpals and metatarsals are five short bones used in precise articulation. In pronghorn as well as other ungulates, the metacarpus and metatarsus have fused into a long bone called a cannon bone (O’Gara and Yoakum 2004) (Fig 3). They further describe that the cannon bone in pronghorn as nearly circular with a large groove on its posterior side running along the entire length of the bone (Fig 4). The proximal end of a metatarsal is divided into three articular facets, which move with the distal surfaces of the tarsals, rather than two which are present on a metacarpal (Fig 5), which move with the distal surfaces of the carpals. The cannon bone of
the hind limb is also slightly longer (0.5 cm) and is laterally flattened on the posterior side forming a D-shape.

Fig 3: Anterior side of a pronghorn metacarpal (cannon bone) with the distal end on the left and the proximal end on the right.

Fig 4: Posterior side of a pronghorn metacarpal (cannon bone). The large groove is visible.

Fig 5: Close-up of the distal end of a pronghorn metacarpal featuring its highly-adapted, articular facets.
The leg bone of a pronghorn is modified to account for its rapid movement as well. Einarsen (1948) compared it to a cow’s (*Bos taurus*) leg bone saying:

"Although the latter (pronghorn) may weigh only a tenth as much as the cow, its leg length is about the same, enabling it to forage in the sagebrush stands and yet have good visibility over the surrounding terrain. Cross sections of the antelope's metacarpus show that it has only about one-sixth the area of a mature cow. Both animals have a marrow space in the metacarpus, but in the antelope this space is very small and the bone is further strengthened by a finer texture and a peripheral layer, which functions as a firm support to the leg bone when it is subjected to unusual strains, as in jumping”.

Einarsen (1948) then went on to test the mechanical limits of both bones by determining the maximum load weight that led to the failure of the bone. He found that the foreleg of a cow failed at 41,300 lb/in² while a comparable section from a pronghorn’s foreleg failed at 45,300 lb/in². This was intriguing as the original weight of the cow was seven times greater than that of the antelope. The maximum load weight showed that the pronghorn’s bone is structured in such a way that it can withstand large impacts. The impact, however, is not felt solely by the bone, but also by the tendons, cartilage, and other tissues in between and around the bone that assist with articulation and function in motility.

A major problem with testing bones includes the individual differences from specimen to specimen. While homologous bones differ greatly in species that are closely-related evolutionarily, they can also differ substantially among members of the same species. Even samples on the same bone can be variable depending on the sampling site, and this can contribute to differences in mechanical properties (Martin and Boardman 1993). Bone material properties can vary little enough to matter among the bones of the same individual or between groups of individuals of similar ages (Cointry et al. 2014). Nielsen et al. (2014) also found that in pigs (*Sus scrofus*), for the variables tested, there
was no significant difference between the left and right limbs. By extension, pronghorn limbs can be expected to behave in a similar manner. Consistent sampling along the same bone should give similar results regardless of whether the bone is from the left or right.

Testing the bone in its most natural condition can be problematic, because these tests go to failure, thus the specimens must be collected after the pronghorn’s death. Several other studies of bones have demonstrated that testing while the bone is wet, usually in a solution considered as a proxy to normal bodily solutions, is the most accurate (Simkin and Robin 1973). If the bone is not tested within a short time from the animal’s death, it must be stored at a cold temperature. Turner and Burr (1993) stated that for long term storage, bones should be kept at -20°C or colder in a 0.9% saline-soaked gauze. They also found that there were no differences in bone stored at -20°C compared to -70°C (1993). The long-term storage of bone was found to have little effect on its stiffness. Linde and Sorensen (1993) found that after 100 days of storing human trabecular bone samples at -20°C, no changes in stiffness were noted. The study does not mention the bones being frozen with any liquid to keep the bone hydrated. Van Haaren et al. (2008) stored goat femora and humeri injected with 10% buffered formaldehyde solution and stored at -20°C for 12 months. They also found that “even after 1 year, no statistically significant differences could be found in stiffness, strength, and energy absorption”.

With this scenario, a pronghorn jumping a fence and fracturing its leg bone would need a test similar to the loading event. Fracture risk can depend on the event causing it and how frequently the event occurs, as in fatigue fractures that occur from repeated impacts (Nielsen et al. 2014). The fracture of a pronghorn’s limb from jumping would be the result from the impact of landing so a single-load event to failure would be needed for
testing. “One of the most widely used tests of the mechanical properties of bone has been the bending test of a simply supported, centrally loaded bar ("three point bending") (Simkin and Robin 1973). While the test is simpler than the similar tension or compression tests, “deflections are larger and the method is relatively insensitive to inaccuracies in the centricity of the load” (Simkin and Robin 1973). They also showed that bending strength and stiffness of bones cannot be estimated from its tensile properties alone.

Three-Point Bending Test

The American Society of Agricultural and Biological Engineers (1992) devised a standard for testing bone with three-point bending tests. The standard describes in detail on the instrument’s settings as well as variables that should be measured. The three-point bending test works by placing the bone on two supporting bars, while a third bar comes down from the top (halfway between the two bars below) to introduce an increasing amount of force until failure (Fig 6).

![Three-Point Bending Test Diagram](image)

Fig 6: The three-point bending test apparatus shows the locations of the supporting pins and the force as applied to the specimen.

The amount the bone was deflected from its natural plane can be plotted against the amount of force used to produce that deflection. A linear slope can be plotted from the amount of stress the bone withstood and the deflection or strain resulting from that stress.
This slope is also called the modulus of elasticity or Young’s modulus and is a useful material property when determining the resistance to force and thus overall strength.

The ultimate strength of a bone is a bit more complicated, because of the interactive nature of all the bone’s material properties as described by Cointry et al. (2014).

"The ultimate strength of a bone under a given load depends: a. upon the structure’s resistance against deformation, and thus its prevention of crack generation by avoiding excessive stretching (structural stiffness), and b. upon its ability to prevent crack propagation (structural toughness). A bone’s structural stiffness and toughness are thus determined by its material's stiffness and toughness (material properties) and by the spatial distribution of that tissue (geometric properties, or bone design), obviously in relation to the origin and direction of applied forces”.

While the three-point bending test is robust due to its simplicity, it may be generalizing complex dynamics throughout the bone’s structure (Mather 1967). The load is not distributed about the bone but rather where the central loading bar is in contact. Any failure of the bone will be due to the structural differences at the center of the bone and not from areas more distal (Martin and Boardman 1993). As stated before, different locations along the same bone can have different mechanical properties. This predictable location of fracture can also be seen as an advantage to the test. The ratio between the thickness of the bone and the distance between the two support columns underneath can change shear stresses during the test. Shear stresses from shear forces arise when equal and opposite forces are acting on opposite sides of an object. Significant amounts of shear stress, usually coming from supporting beams that are too close together compared to the thickness of the bone, can change the overall modulus of elasticity (Martin and Pramanik 1990). Having a consistent ratio will normalize these shear stresses across multiple bones tested.
No study has reported conducting a three-point bending test on pronghorn bones, however other related animas have been studied using the test. Bjora et al. (2001) used the test on Norwegian moose (*Alces alces*) metacarpal bones as a measure of bone strength. Three-point bending tests have also been performed on the femora (Olguin et al. 2013) and antlers (Landete-Castillejos et al. 2013) of Iberian red deer (*Cervus elaphus hispanicus*) when examining changes in nutrition (femora) and differences in public and private management (antlers) of the deer.

Due to the lack of data on the mechanical properties of pronghorn metacarpals and the potential value that knowledge of these properties could bring to the broader question of why pronghorn rarely choose to jump fences, the purpose of this study was to contribute information to this unexplored aspect. I hypothesize that some important structural difference in strength exists between the pronghorn and mule deer metacarpals leading to the jumping block observed in the pronghorn.
CHAPTER II

METHODS AND MATERIALS

Sample Collection

In October of 2016, I collected pronghorn and mule deer legs during hunting season from a meat processing facility near Peyton, Colorado. Hunters had killed the animals earlier that day and transported them to the facility. The legs were cut from the rest of the carcass between the cannon bone and the carpus or tarsus, respectively. For pronghorn, 20 left metacarpals, 19 right metacarpals, 36 left metatarsals, and 34 right metatarsals were collected. For mule deer, 20 left metacarpals and 19 right metacarpals were collected. Mule deer metatarsals were not obtained. Age and sex were not recorded.

Later, on the day of collection, each leg was stripped of flesh so that only the bone of interest was isolated. Each bone was wrapped in gauze soaked in 0.9% saline, placed in a plastic bag, and frozen at -20°C. Each bone was in contact with the air for less than 10 minutes before freezing.

Three-Point Bending Test

Bones were tested in batches from October to December of 2017. By this time, each bone had been frozen at -20°C for up to one year and two months (minimum of one year). Twenty-four hours before testing, the bones were placed in a container filled with 0.9% saline solution at room temperature to avoid any potential brittleness of testing while frozen (Fig 7).
I tested each bone using an MTS 858 Mini Bionix II Table Top System (Fig 8). The instrument applied pressure hydraulically from above the specimen and recorded outputs to sensors which were then displayed in a computer program (MTS software accompanied instrument). A custom testing apparatus made of aluminum was built and fitted to the instrument to hold the bones in the correct position (Fig 9 and 10). The two supporting bars as well as the loading pin were rounded to distribute force more evenly.
Fig 8. The MTS 858 Mini Bionix II Table Top System used. The custom testing apparatus can also be seen fitted in the machine’s middle.

Fig 9: The custom testing apparatus shown from an angled view.
Bones were tested one at a time. The bone was unwrapped and the following data were recorded: animal number, metacarpal or metatarsal, left or right, bone length, major diameter (coronal), and minor diameter (sagittal) (Fig 11). I measured diameters using digital calipers (Tresna Instruments, accurate within 0.01 mm) in the center of the bone at the intended break site. The supports were adjusted on the test apparatus so that the span length was greater than 10X the length of the minor diameter. The specimen was placed across the support bars with the anterior side facing up and the distal end pointed to the left. The loading bar was lowered until it touched the bone.
Fig 11: Typical cross section of elliptical bone. Diameters are indicated: major diameter (B), minor diameter (D), major inside diameter (b), and minor inside diameter (d) (American Society of Agricultural and Biological Engineers, 1992).

The loading bar was set to lower at 10 mm/min and the outputs to record force exerted onto the loading bar as well as the distance the loading bar had moved down (also known as the displacement of the bone). The outputs were measured from sensors every 0.01 second (100 Hz), with the loading bar being continuously lowered until failure of the specimen. Each bone’s time from being taken out of the saline bath to completion of the break was less than 10 minutes to avoid air exposure and thus drying of the bone. After the break, the inside major and minor diameters (Fig 11) were measured as well as the wall thickness from four sides using digital calipers.

Data Analysis

Force-deformation graphs from each bone tested were generated (Fig 12). These graphs show the resistance of a material to increasing force until failure. The highest force applied by the MTS machine while bending the bone (Ultimate Force, N) and the distance
the loading bar had moved at that point (Ultimate Deformation, m) were recorded from the graph.

Fig 12: The force-deformation curve for most materials. The initial toe region shows the material’s first resistance to the force. The elastic region (if the force is removed while in this region, the material will return to its original shape) displays a consistent slope until the yield point. The plastic region (if the force is removed while in this region, the material will not return to its original shape but will retain some degree of permanent angulation) displays a declining slope just before the failure point or break.

Several bones were excluded from the data set due to a compounding error when taring the instrument. Also, some bones did not break before the machine reached the end of its timed movement of lowering the loading bar. These tests could not reliably be continued because the machine was no longer steadily increasing the applied force. Bones from this small subset were excluded from the analysis. One bone featured a callus in the middle and was tested per normal procedure, but the results were excluded due to the thickened wall that was not representative of typical measurements. The final sample set included 29 pronghorn metacarpals (16 left and 13 right), 48 pronghorn metatarsals (25 left and 23 right), and 13 mule deer metacarpals (7 left and 6 right).
Variable Calculation

Variable calculations followed recommended procedures outlined by the American Society of Agricultural and Biological Engineers (1992). The moment of inertia (I, m$^4$) for a hollow ellipse was found using the outside major diameter (B, m), the outside minor diameter (D, m), the inside major diameter (B, m), and the inside minor diameter (b, m).

$$I = 0.049 \cdot [(B \cdot D^3) - (b \cdot d^3)]$$

The ultimate bending strength (stress) ($\sigma$, Pa, pascals) was found using the ultimate force (F, N), the distance between supports (L, m), the outside minor diameter (D, m), and the moment of inertia (I, m$^4$).

$$\sigma = \frac{F \cdot L \cdot \frac{D}{2}}{4 \cdot I}$$

The apparent modulus of elasticity or Young’s Modulus was found using the ultimate force (F, N), the distance between supports (L, m), the moment of inertia (I, m$^4$), and the ultimate deformation ($\delta$, m).

$$E = \frac{F \cdot L^3}{48 \cdot I \cdot \delta}$$

Statistical Testing

Bone measurements (length, inside and outside diameters, and thickness) were compared between both species using a two-tailed t-test on Excel ($\alpha = 0.05$) providing p-values. Physical properties of the bones (moment of inertia, ultimate force, ultimate deformation, work, ultimate bending stress, and apparent modulus of elasticity) were also
compared against each other using a two-tailed t-test on Excel ($\alpha = 0.05$), providing p-values.
CHAPTER III

RESULTS

Force-Deformation Curves

Data collected characterized the force exerted by the testing device on the diaphysis of each bone in the course of bending to failure. Data were collected every 0.01 s, and force deflection characteristic were then plotted (using R-studio with the ggplot package). The plots were organized to highlight each bone group (Fig 13), as well as all three bone groups (Fig 14) for comparison. Each force-deflection plot includes a colored line indicating the mean stiffness for that bone group. The mean stiffness was calculated by measuring the mean slope of the linear region for each curve.

The mule deer metacarpal group showed the most uniform force-deformation response, compared to both pronghorn groups, and these responses were narrower in their distribution. This finding could be a result of the small sample size, with only 13 mule deer metacarpals measured compared to 28 pronghorn metacarpals and 48 pronghorn metatarsals.

Best fit lines depicting mean stiffness values were nearly identical for the mule deer and pronghorn metacarpals, however the pronghorn metatarsals showed a steeper line indicative of a stiffer material.
Fig 13: Force-deformation curves for the three bone groups. The mean stiffness for each group is shown with a colored line.
Fig 14: Force-deformation curves of all three bone groups as well as their mean stiffness line (colored).
**Ultimate Force-Deformation**

Within each bone group, the maximum force measured on each curve (ultimate force, or strength) was plotted against the deformation (ultimate deformation) at that point. For the mule deer metacarpals (Fig 15), the greatest force measured was 4330.71 N and the smallest force measured was 2182.18 N. In the same group, the highest deformation measured was 10.24 mm and the smallest deformation measured was 6.47 mm.

![Mule deer metacarpal](image)

**Fig 15:** Ultimate force and deformation scatter plot for the Mule Deer metacarpal group (n = 13).

For the pronghorn metacarpals (Fig 16), the greatest force measured was 3017.41 N and the smallest force measured was 1022.18 N. In the same group, the highest deformation measured was 10.65 mm and the lowest deformation measured was 4.11 mm.
Fig 16: Ultimate force and deformation scatter plot for the pronghorn metacarpal group (n = 28).

For the pronghorn metatarsals (Fig 17), the greatest force measured was 3199.53 N and the smallest force measured was 1147.73 N. In the same group, the highest deformation measured was 9.40 mm and the lowest deformation measured was 3.44 mm.

Fig 17: Ultimate force and deformation scatter plot for the pronghorn metatarsal group (n = 48).

The ultimate force versus deflection plots for each bone group were combined into a single plot for comparison (Fig 18). As indicated, the observed the mule deer metacarpal group exhibited the greatest ultimate force, and the pronghorn metatarsal group exhibited
the greatest ultimate deformation. The pronghorn metacarpal group exhibited the smallest ultimate force, and the pronghorn metatarsal group exhibited the lowest deformation.

![Combined ultimate force and deformation scatter plot](image)

**Fig 18:** Combined ultimate force and deformation scatter plot for all three groups: mule deer metacarpal, pronghorn metacarpal, and pronghorn metatarsal.

**Dimensions**

Means and standard deviations were calculated for six dimensions along each bone (Table 1). These dimensions included bone length, outside major diameter, outside minor diameter, inside major diameter, inside minor diameter, and thickness.
Table 1: Mean and standard deviation for six dimensions for the three bone groups.

<table>
<thead>
<tr>
<th>Bone</th>
<th>Length (mm)</th>
<th>Outside major diameter (mm)</th>
<th>Outside minor diameter (mm)</th>
<th>Inside major diameter (mm)</th>
<th>Inside minor diameter (mm)</th>
<th>Thickness (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mule Deer</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Metacarpal</td>
<td>221.92 ± 8.03</td>
<td>17.93 ± 1.35</td>
<td>18.26 ± 2.06</td>
<td>8.79 ± 2.22</td>
<td>6.72 ± 1.48</td>
<td>4.29 ± 0.53</td>
</tr>
<tr>
<td>Metatarsal</td>
<td>215.63 ± 13.78</td>
<td>14.78 ± 1.40</td>
<td>16.21 ± 1.84</td>
<td>6.07 ± 1.30</td>
<td>7.00 ± 1.38</td>
<td>4.31 ± 0.39</td>
</tr>
<tr>
<td><strong>Pronghorn</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Metacarpal</td>
<td>208.61 ± 10.64</td>
<td>15.01 ± 1.15</td>
<td>14.64 ± 1.12</td>
<td>6.86 ± 1.26</td>
<td>6.00 ± 0.99</td>
<td>4.17 ± 0.47</td>
</tr>
<tr>
<td>Metatarsal</td>
<td>215.63 ± 13.78</td>
<td>14.78 ± 1.40</td>
<td>16.21 ± 1.84</td>
<td>6.07 ± 1.30</td>
<td>7.00 ± 1.38</td>
<td>4.31 ± 0.39</td>
</tr>
</tbody>
</table>

T-tests ($\alpha = 0.05$) were used to analyze pairwise comparisons between species for the six measured bone dimensions (Table 2). These tests showed significant differences between the mule deer metacarpal group and the pronghorn metacarpal groups for bone length, both outside diameters, and the inside major diameter. No significant differences were found among the groups for mean thickness of cortical bone.

Table 2: P-values from t-test for six dimensions comparing each bone group to another. MC = metacarpal. MT = metatarsal. Values with an asterisk denote significance.

<table>
<thead>
<tr>
<th>Comparison (p-value)</th>
<th>Mule Deer MC – Pronghorn MC</th>
<th>Mule Deer MC – Pronghorn MT</th>
<th>Pronghorn MC – Pronghorn MT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bone length</td>
<td>&lt; 0.001*</td>
<td>0.042*</td>
<td>0.016*</td>
</tr>
<tr>
<td>Outside major diameter</td>
<td>&lt; 0.001*</td>
<td>&lt; 0.001*</td>
<td>0.431</td>
</tr>
<tr>
<td>Outside minor diameter</td>
<td>&lt; 0.001*</td>
<td>0.005*</td>
<td>&lt; 0.001*</td>
</tr>
<tr>
<td>Inside major diameter</td>
<td>0.010*</td>
<td>&lt; 0.001*</td>
<td>0.012*</td>
</tr>
<tr>
<td>Inside minor diameter</td>
<td>0.130</td>
<td>0.548</td>
<td>&lt; 0.001*</td>
</tr>
<tr>
<td>Mean thickness</td>
<td>0.520</td>
<td>0.891</td>
<td>0.206</td>
</tr>
</tbody>
</table>
**Physical Properties**

Means (+/- 1 standard deviation) for six biomechanical properties of each bone were also calculated from the MTS, three-point bending tests (Table 3). These properties included ultimate force, ultimate deformation, mechanical work, stiffness, ultimate bending stress, and apparent modulus of elasticity.

Table 3: Means and standard deviations for six physical properties for the three bone groups.

<table>
<thead>
<tr>
<th>Bone</th>
<th>Ultimate force (N)</th>
<th>Ultimate deformation (mm)</th>
<th>Work (J)</th>
<th>Stiffness (N/mm)</th>
<th>Ultimate bending stress (GPa)</th>
<th>Apparent modulus of elasticity (GPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mule Deer</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Metacarpal</td>
<td>3083.76 ± 725.76</td>
<td>8.57 ± 1.18</td>
<td>15.55 ± 4.70</td>
<td>0.47 ± 0.11</td>
<td>0.26 ± 0.3</td>
<td>9.92 ± 1.68</td>
</tr>
<tr>
<td><strong>Pronghorn</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Metacarpal</td>
<td>2156.26 ± 476.66</td>
<td>6.52 ± 1.54</td>
<td>8.36 ± 2.51</td>
<td>0.47 ± 0.15</td>
<td>0.27 ± 0.3</td>
<td>11.25 ± 2.62</td>
</tr>
<tr>
<td>Metatarsal</td>
<td>2355.08 ± 563.10</td>
<td>5.15 ± 1.24</td>
<td>7.57 ± 1.91</td>
<td>0.60 ± 0.20</td>
<td>0.25 ± 0.5</td>
<td>12.71 ± 3.88</td>
</tr>
</tbody>
</table>

T-tests (α = 0.05) were used to analyze pairwise comparisons between species for each of the six measured physical properties (Table 4). The tests showed significant differences between the mule deer metacarpal group and the pronghorn metacarpal groups for ultimate force, ultimate deformation, work, and apparent modulus of elasticity. No significant differences were found between the groups for ultimate bending stress.
Table 4: P-values from t-test for six physical properties comparing each bone group to another. MC = metacarpal. MT = metatarsal. Values with an asterisk denote significance.

<table>
<thead>
<tr>
<th>Comparison (p-value)</th>
<th>Mule Deer MC – Pronghorn MC</th>
<th>Mule Deer MC – Pronghorn MT</th>
<th>Pronghorn MC – Pronghorn MT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ultimate force</td>
<td>&lt; 0.001*</td>
<td>0.004*</td>
<td>0.106</td>
</tr>
<tr>
<td>Ultimate deformation</td>
<td>&lt; 0.001*</td>
<td>&lt; 0.001*</td>
<td>&lt; 0.001*</td>
</tr>
<tr>
<td>Work</td>
<td>&lt; 0.001*</td>
<td>&lt; 0.001*</td>
<td>0.156</td>
</tr>
<tr>
<td>Stiffness</td>
<td>0.943</td>
<td>0.006*</td>
<td>0.002*</td>
</tr>
<tr>
<td>Ultimate bending stress</td>
<td>0.264</td>
<td>0.625</td>
<td>0.068</td>
</tr>
<tr>
<td>Apparent modulus of elasticity</td>
<td>0.044*</td>
<td>&lt; 0.001*</td>
<td>0.071</td>
</tr>
</tbody>
</table>
CHAPTER IV

DISCUSSION

My study explored a morphological approach of pronghorn and their reluctance or inability to jump over fences which larger ungulates, such as mule deer, do not display. While some biologists have suggested a behavioral block (Popowski and Pyle 1982), in this study I looked at another explanation: risk of injury. Since the pronghorn’s primary habitat is that of flat grasslands, any leg injury arising after landing improperly from jumping a fence could seriously impact the quality of the animal’s life. To test this hypothesis, I measured the strength of pronghorn metacarpal bones using a three-point bending test. I compared the results to the metacarpal strength of mule deer, a larger ungulate that has some habitat overlap with the pronghorn. The mule deer, however, displays no restriction to its jumping ability. While other anatomical structures assist in the landing, such as the joints, tendons, and other leg bones, I chose the metacarpal as a testable proxy as that bone has been shown to bend during landing in horses (Bienwener et al. 1983). I hypothesized that the mule deer would exhibit stronger metacarpal bones compared to the pronghorn’s.

When comparing the mean ultimate force between the mule deer and pronghorn metacarpals, I found a significant difference (Table 4). This ultimate force value is based on the individual bones tested with no standardization that included bone size or species mass. The mule deer metacarpal, with its larger bone size and diameters, predictably handled a greater mean ultimate force (3083.76 ± 725.76 N) compared to the mean ultimate force for the pronghorn metacarpal (2156.26 ± 476.66 N). I saw similar results when comparing the ultimate deformation between the mule deer and pronghorn metacarpals.
(Table 4). Although the larger bone could withstand more force before failure, the mule deer metacarpal’s mean ultimate deformation (8.57 ± 1.18 mm) was also about 2 mm greater than the pronghorn’s metacarpal (6.52 ± 1.54 mm) showing again its increased flexibility.

It might be expected that due to the larger body size of the mule deer, these animal’s leg bone strength would be greater than pronghorn’s to support their greater body weight. Thus, I used a normalized measure to address this issue. Determination of equalized bone dimensions (the larger mule deer bone comparable to the same pronghorn bone) in combination with the force required to bend the bone to failure is one such method.

The elastic modulus (also known as Young’s Modulus) for a material is a measure of deformation, technically strain, against added stress. The equation for the elastic modulus as given by the American Society of Agricultural and Biological Engineers (1992) combines the maximum force the bone experiences during the bending test, the area moment of inertia (distribution of a load perpendicular to the axis of interest), the length of the bone, and the span between the two support points during the test. The resulting elastic modulus, which includes dimensional properties of the bone, can then be compared to other materials. Due to a bone’s nonhomogeneous composition consisting of multiple layers of differing density and material composition, the term “apparent modulus of elasticity” is used to signify its complex nature. When comparing the mean apparent moduli of elasticity for mule deer metacarpals and pronghorn metacarpals, I found a significant difference (Table 4) in the values. This seems to indicate that at the material level for each species’ metacarpal, a comparable force introduced to each will result in different levels of resistance. The mule deer metacarpal is more flexible (mean apparent
modulus of elasticity = 9.92 ± 1.68 GPa, gigapascals) compared to the more rigid pronghorn metacarpal (mean apparent modulus of elasticity = 11.25 ± 2.62 GPa) or the even more rigid pronghorn metatarsal (mean apparent modulus of elasticity = 12.71 ± 3.88 GPa). The flexibility of the mule deer’s metacarpal, an important bone used in the landing of a jump, may allow it to disperse the force of the landing more effectively than a pronghorn’s metacarpal.

While the elastic modulus is a measure of flexibility based on the bone’s material properties, the stiffness is a measure of flexibility based on the structural properties of the bone. This measure of stiffness accounts for both bone composition and the shape and distribution of the bone material, derived from the amount the bone deflects in response to an applied force. This stiffness characteristic was calculated for each bone from the slope, in the linear region, of the force-deformation curves. When comparing the mean stiffness of the mule deer metacarpal (0.47 ± 0.11 N/mm) to the pronghorn metacarpal (0.47 ± 0.15 N/mm), I found nearly identical means (p = 0.943, α = 0.05) indicating that both bones deflect at the same rate with the application of a continuous bending force. This result could mean that pronghorn metacarpals are able to sustain the forces of landing just as well as those of mule deer metacarpals. It should be noted however, that in this experiment the three-point bending test was carried out with a slow, continuously increasing load applied to the bones, rather than a rapid and intense force as the bone probably experiences in jump landings.

Follow-up studies should look at differences in age or sex as specimens used in this work could not be fully identified for that comparison. Weak assumptions could be made that the hunters who brought these leg bones to the collection site were not targeting very
young animals as their intention was the harvesting of meat or trophy animals. This assumption might also extend to a female dominance in the samples tested, as meat-hunters frequently aim for females while trophy-hunters aim to take males with larger horns and skulls.

Specific to the mechanical testing protocol, while the three-point bending testing method used in this study is common and preferred for testing bone strength (Simkin and Robin 1973, Martin and Boardman 1993) it focuses on a single loading mode, generating a central (at the loading site) breaking point. If any small microfractures or other weaknesses exist at this central location before testing, the load-deformation response will indicate an overall weaker bone.

In conclusion, it appears mule deer leg bones, while larger and able to withstand greater forces, are also more flexible from a materials level perspective (modulus of elasticity). This finding could explain why deer easily jump over fences, because their bones absorb more energy than a stiffer bone (a materials level effect) than the pronghorn bones. However, at a structural level, which I would argue is more relevant to the consideration of jumping, mule deer and pronghorn have nearly equivalent flexibility (stiffness) in their metacarpal bones. A few pronghorn metacarpal bones even showed similar force limits (ultimate force) to mule deer metacarpals despite the mule deer’s larger body size. This seems to suggest that pronghorns can jump over fences without a high risk of a broken metacarpal.

As there is no doubt pronghorn can jump very high barriers (Spillett, Low, and Sill 1967), there must be another reason for their reluctance to jump. Some (Caton 1881, Buechner 1950) suggest that the jumping block is more behavioral in nature, describing
the pronghorn as “unaware of their ability to jump” (Buechner 1950) and thus not considering it as an option. This could be related to the fact that pronghorn have inhabited the plains of North America for thousands of years (Byers 1997), and have never had a need to overcome fences or other vertical obstacles, especially when they have the option to go around. Mule deer however, live in varied environments including a range of elevation changes and rough topography. Such environments logically present to them numerous situations requiring jumping.

Other studies (Spillett, Low, and Sill 1967, Popowski and Pyle 1982) focused on a different anatomical reason for the jumping block. These researchers suggest that pronghorn’s powerful, long-distance eyesight may not be suited to seeing the strands of typical fences clearly, motivating them to choose to avoid jumping, fearing failure. Future studies could focus on analyzing pronghorn jumping decisions from these other perspectives.

Regardless of the reason for the pronghorn jumping block, the fragmentation of the pronghorn’s habitat due to fencing is obvious. Without specialized fences for the pronghorn to crawl under (no barbs on the bottom wire and high enough [0.5 m] for them to pass under) they could be extremely limited in the resources they can access as well as limiting gene flow between populations. Studies such as this can increase our understanding as to how human movements and construction on a landscape can conflict with the natural history and continued success of this iconic species of the North American West.
LITERATURE CITED


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PHOTO CREDITS

