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Boxed In: Hinge Closing Performance of Ornate Box Turtles (Terrapene ornata)

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BOXED IN: HINGE CLOSING PERFORMANCE OF ORNATE BOX TURTLES (*TERRAPENE ORNATA*)

A Master's Thesis

Presented to

The Graduate College of

Missouri State University

In Partial Fulfillment

Of the Requirements for the Degree

Master of Science, Biology

By

Gina L. Buelow

December 2021

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Biology

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ABSTRACT

Turtles are perhaps best known for the bony shells that encase them, a unique morphological trait that provides protection against predators. Many taxa have even evolved the ability to enclose themselves using hinges that can be used to create a seal between the carapace and plastron. I measured the hinge closing force of Ornate Box Turtles (*Terrapene ornata*) to assess the performance of this unusual yet ecologically important trait. I sampled head-started turtles from Thomson Sand Prairie in the Upper Mississippi River National Wildlife and Fish Refuge and wild turtles collected in northern Oklahoma. To assess the effects of head-starting on predator defense, I compared hinge closure force, behaviors when threatened, and shell morphometrics between the two populations. Wild turtles typically closed immediately and with greater force than head-started turtles. The head-started turtles exhibited bolder behaviors and often were hesitant to seal themselves completely into their shells. Those that were head-started also had disproportionately long plastrons relative to wild turtles, a characteristic that tended to prevent them from creating a tight seal between the plastron and carapace. These results suggest that future head-start efforts should take steps to meliorate maladaptive morphological and behavioral consequences of captivity to maximize anti-predator measures following release.

KEYWORDS: Conservation, head-start, reintroduction, animal behavior, turtle morphology

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INTRODUCTION

The turtle's shell is arguably the most easily recognizable of its shared derived traits and has been identified as being of great importance in several aspects of its biology, including defining—and constraining—the architecture of the body, providing protection from traumatic injuries, and aiding osmoregulation and calcium regulation (Minckley, 1966; Cordero and Quinteros, 2015). The shells of turtles have been studied for over a century (Agassiz, 1857), and its morphology and evolution have been investigated using advanced genetic analyses, geometric modeling, and phylogenetic simulations (Bramble, 1974; Feldman and Parham, 2002; Claude et al., 2004; Claude, 2006; Angielczyk et al., 2011; Cordero et al., 2018). These studies have helped to describe the evolution of morphological characters that are broadly relevant to most turtles, as well as traits that are peculiar to subsets of extant turtles.

Several lineages of turtles have evolved shell kinesis, in some cases as a means of relaxing the constraints imposed by a shell, and in others of enhancing its utility in excluding predators. Shell kinesis is broadly framed as any deviation from an entirely rigid shell, typically involving flexibility along loosely sutured joints or cartilaginous hinge structures of the plastron, and less commonly involving mobility of the carapace. Kinesis of the carapace is most highly derived in the genus *Kinixys* (Testudinidae), all members of which possess lateral hinges with flexible cartilaginous elements located posterior to the bridge and extending down to the anterior edge of the femoral fossae. These hinges are presumed to aid in both protecting the posterior appendages from predators (Coulson and Hailey, 2001) as well as allowing expansion of the space between the pygal and anal bones to permit passage of large, hard-shelled eggs. Semi-kinetic shells that result from reduced ossification of the shell and loosely sutured joints have also evolved to enhance some species' ability to wedge between rocks for protection, as occurs in the monotypic genera *Dogania* (*D. subplana*; Trionychidae) and *Malacochersus* (*M. tornieri*; Testudinidae) (Pritchard, 1978; Mautner et al., 2017).

Plastral kinesis is more widespread than carapacial kinesis or whole-shell pliability. It has evolved in several genera and is inferred to enhance fitness in a variety of ways (Feldman and Parham, 2002; Cordero et al., 2018). Among taxa, plastral kinesis ranges from slight flexibility between two loosely sutured plastral lobes (Rose and Judd, 1991) to a well-developed plastral hinge that allows for the turtle to completely seal itself in its shell (Bramble, 1974; Bramble et al., 1984). Although a logical advantage to a kinetic plastron is the defensive capability of a flexible shell protecting the body, it also serves as a mechanism for oviposition for turtles such as *Homopus signatus* and *Gopherus berlandieri* (Testudinidae), two species of tortoise that produce small clutches of large, hard-shelled eggs (Rose and Judd, 1991; Hofmeyr et al., 2005). Four out of five species in the genus *Testudo* (Testudines: Testudinidae) have also been observed to have a plastral lobe with some degree of kinesis, hypothesized to have evolved for both oviposition and other essential physiological functions (Rose and Judd, 1991).

Kinesis along hinges of the plastron has evolved independently in at least six extant turtle lineages (Bramble and Hutchison, 1981; Bramble et al., 1984; Ernst and Barbour, 1989; Claude, 2006; Angielczyk et al., 2011). Evolutionary reversals to akinesis have also likely occurred within Emydidae (Feldman and Parham, 2002). Turtles in the genera *Terrapene* (Emydidae), *Cuora* (Geoemydidae), and *Kinosternon* (Kinosternidae) exhibit highly derived plastral kinesis and have the ability to pull the anterior and posterior lobes of the plastron upwards to make close contact with the inferior edges of the carapace to form a sealed "box" (Angielczyk et al., 2011). Species within *Kinosternon* have both an anterior and posterior hinge that is connected to an inflexible central segment of their plastron, though the degree of kinesis displayed varies widely among species (Bramble et al., 1984).

Upon hatching, neonatal turtles of taxa that possess hinged plastrons do not yet have a fully developed and functional hinge. In the genus *Terrapene*, for example, the bone suture that separates the hinge from the posterior plastron typically forms when the turtle is around 3 years old and may not provide a tight seal between the plastron and carapace until the turtle is 3–5 years old (Cordero et al., 2018). Differences in musculo-skeletal phenotypes have been observed between reptiles raised in captivity and those found in the wild because of differing conditions during development (Frye, 1981; Arnold and Peterson, 1989; Erickson et al., 2004). Having a kinetic shell that creates a tight seal has been demonstrated to enhance survival of predation attempts, making the consequences to atypical development and function potentially severe (Minkley, 1966). Given the increasing application of head-starting and reintroduction as a tool for conservation, such effects of captivity are important to identify and meliorate to maximize survival and fitness potential of reintroduced animals.

I compared the plastron closure performance of wild and head-started Ornate Box Turtles (*Terrapene ornata*). I measured the hinge closing force and latency to close to determine the force individual turtles exert to close into their shell and compared their propensity to protect themselves against predation. I hypothesized that wild turtles would close their shells more readily and with greater force than turtles reared in captivity prior to release. Additionally, I predicted that the head-started turtles would differ in shell morphology from wild turtles due to different dietary and environmental conditions experienced during their first year of life.

MATERIAL AND METHODS

Field Sites and Measurements

Free-ranging head-started *Terrapene ornata* were equipped with VHS radio transmitters (164–165 MHz, ~12–13 g; Advanced Telemetry Systems, Isanti, Minnesota) as part of another study, so I used radio telemetry to locate and capture 17 head-started individuals at the Lost Mound Sand Prairie of the Upper Mississippi River National Wildlife and Fish Refuge in northern Illinois in mid-August 2020. The turtles were confined to a 7.3-ha soft-release enclosure surrounded by chain-link fencing and metal flashing to prevent terrestrial predators from entering or turtles from leaving. I measured mass, carapace length, carapace width, midline length of front and rear lobes of the plastron, and maximum shell height of each turtle, and released turtles within 6 h of capture. I also obtained sex and age data from records maintained by Upper Mississippi River National Wildlife and Fish Refuge.

I collected data from 32 wild *T. ornata* in Washington and Osage counties in northern Oklahoma in late May 2020. I captured the turtles by road-cruising, with most of my effort occurring between 07:00–11:00, though a handful of individuals were found serendipitously outside of this time range. I marked specimens with temporary paint markers to maintain the correct identity of individuals during testing.

During collection, I recorded precise geographical coordinates and returned to their point of capture. When practical, I estimated the age of turtles by counting growth annuli, a practice that has been shown to provide a reasonable estimate of age for *T. ornata* up to sexual maturity in at least some populations (Bernstein et al., 2019). I conducted all research with approval from the Missouri State University Animal Care and Use Committee (Approved:06/2019; IACUC ID:19-014) (Appendix).

Hinge Force

I measured hinge force by adopting similar methodology developed for measuring bite force (Herrel et al., 1999; Lappin and Jones, 2006; Herrel et al., 2010; Pfaller et al., 2011). I collected hinge force data using an isometric force transducer (model 9311B, range ± 5.000 N, Kistler, Switzerland) connected to a charge amplifier (model 5995A, Kistler, Switzerland). To trigger a defensive behavior, I placed contact plates between the hinge and the carapace and then tapped the feet of the turtle (**Figure 1**). The turtle was given one minute to close their hinge, and the maximum force exerted was recorded. I conducted three trials with a minimum of 30 min between each trial. To avoid damaging the shell, I affixed strips of leather to the contact plates (Lappin and Jones, 2014). The highest force read-out for each individual was considered their maximum hinge closing force.

I standardized closure angle by adjusting the distance between the contact plates, adding more distance for larger individuals (Herrel et al., 2009). The plate distance was standardized for different ranges of sizes based on carapace length: plates were spaced 1 mm apart for turtles with a straight midline carapace length (SCL) <75 mm, 1.5 mm for turtles with SCL = 75–100 mm, and 2.5 mm for turtles with SCL > 100 mm. To standardize hinge out-lever, I positioned the contact plates during the trials so the hinge and carapace closed on the bite plate at approximately the same angle (Lappin and Jones, 2014). By standardizing closure angle and bite out-lever for each individual and trial, the force measured represented the performance of similar groups of muscle fibers (Lappin and Jones, 2014).

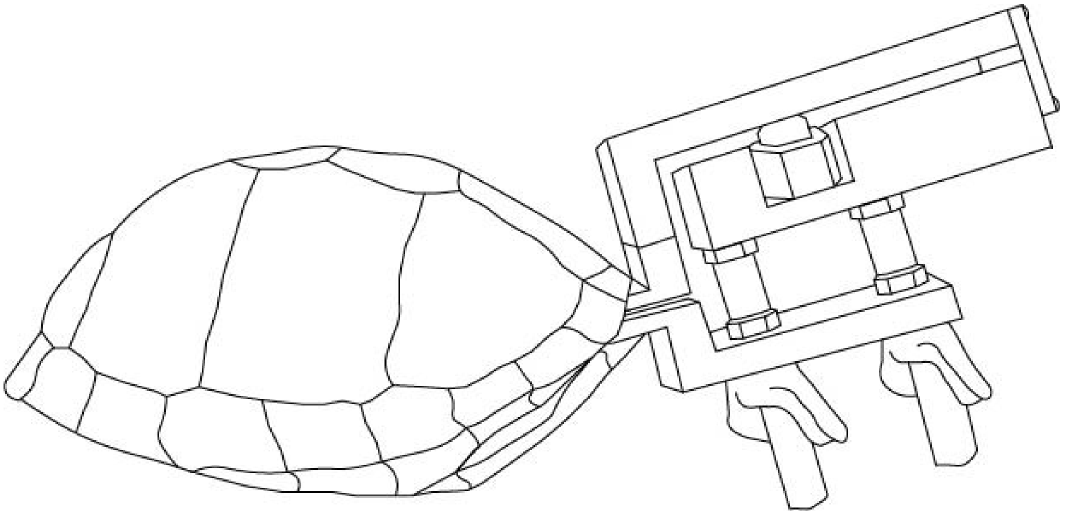

Figure 1. Diagram showing the insertion point of a force transducer used to measure the hinge closing performance of Ornate Box Turtles (*Terrapene ornata*). The contact plates of the meter were placed between the hinge and the carapace of the turtle to measure closing force applied in response to a perceived threat.

Analyses

To determine if the head-started and wild turtles had similar relationships between different body measurements, I used a standardized major axis (SMA) ANCOVA to examine the relationships between different body morphometrics for each population of turtles. This test was used to compare the relationship between shell height and carapace length, carapace length and plastron length, and total plastron length and hinge length. Data were $\log_{10}$ transformed to meet assumptions of normality and homogeneity of variance.

To test which morphometrics contributed to hinge force, I plotted the relationship between force and different measurements using a least-squares means regression. Hinge force was plotted with body mass and hinge length for both head-started and wild turtles. I then used ANCOVA tests to determine if hinge closing force different significantly between head-started and wild turtles when using body mass and hinge length as covariates.

I determined if turtles that closed for all three trials showed variability in force output between trials by conducting a Repeated Measures ANOVA test. It was necessary to $\log_{10}$ transform the hinge closing measurements to meet assumptions of normality. Because only turtles that closed on all three trials could be used in this analysis, a total of 11 head-started turtles and 30 wild turtles were included.

I quantified turtle behavior using an ordinal scoring system with values ranging 0–5, with 0 being the most willing to close and 5 the least willing to close. I tested the hypothesis that head-started turtles behaved significantly differently than wild turtles using a Mann-Whitney U Test. The Mann-Whitney U Test is appropriate to examine behavioral data, which does not often meet the assumption of normality.

I used Principal Component Analysis to determine which variables explain variation in hinge closing force in *T. ornata*. All measures of linear dimensions and body mass were included as variables in this analysis. I used an ANCOVA test to test the difference in hinge closing force between head-started and wild turtles after adjusting for the Principal Component with the highest explanatory value.

RESULTS

Head-started turtles all fell within a narrow size and age range relative to wild-caught turtles. While the wild turtles surpassed head-started turtles in almost every body measurement taken, head-started turtles exhibited greater average mass than wild turtles (**Table 1**). All head-starts were scored as sexually mature adults based upon size and presence of discernible secondary sex characteristics among males. In comparison, three juveniles were included among wild turtles. On average, wild turtles were older and larger than head-starts and, importantly, age

Table 1. Sex, age, morphometrics, and performance of wild and head-started Ornate Box Turtles *(Terrapene ornata).* Summary statistics for raw morphometric and maximum bite force data for wild and head-started Ornate Box Turtles. M = male; F = female; and J = juvenile. With the exception of Sex, values for all variables are expressed as mean ± 1 SE.

Variable	Wild Turtles	Head-Started Turtles
Sex	19 M, 8 F, 3 J	10 M, 6 F, 0 J
Estimated Age	8.3 ± 2.8	6.6 ± 1.8
Straight carapace length (mm)	100.0 ± 15.1	89.8 ± 7.8
Carapace width (mm)	81.9 ± 11.3	81.4 ± 5.7
Front plastral lobe length (mm)	41.1 ± 6.5	38. 0 ± 3.6
Posterior plastral lobe length (mm)	61.4 ± 8.7	57.7 ± 5.9
Total plastron length (mm)	102. 5 ± 14.5	95.6 ± 8.8
Dome height (mm)	50.6 ± 8.5	45.9 ± 3.2
Mass (g)	252. 3 ± 96.5	292.6 ± 47.1
Maximum Bite Force (N)	31.9 ± 13.0	15.4 ± 7.1

estimates in this group represent minima because box turtles typically stop adding discernible annuli upon reaching sexual maturity.

Head-started and wild turtles exhibited a significant interaction between shell height and carapace length (LR $\text{test}_1 = 5.6$, $p < 0.02$) **(Figure 2A)**. The shells of head-started turtles were more domed that those of wild turtles; however, as head-started turtles increased in size, their dome height increased at a slower rate than their wild counterparts. There was no significant interaction between length of the front lobe of the plastron and total plastron length of head-started and wild turtles (LR $\text{test}_1 = 0.91$, $p > 0.33$) **(Figure 2B)**; furthermore, there was no difference in the elevation of the regression lines when the interaction term was removed ($\text{Wald}_1 = 0.84$, $p > 0.35$) **(Figure 2B).** There was also no significant interaction between the plastron length and carapace length of head-started and wild turtles (LR $\text{test}_1 = 1.9$, $p > 0.16$), but there was a significant difference between the elevations of the two lines ($\text{Wald}_1 = 5.8$, $p < 0.02$) indicating that for any given carapace length, head-started turtles had proportionally longer plastrons than wild turtles **(Figure 2C).**

Both wild and head-started *T. ornata* exhibited similar repeatability of hinge closure force among trials (wild: $F_{2,58} = 0.97$, $p > 0.38$; head-started $F_{2,20} = 1.25$, $p > 0.31$) **(Figure 3)**. However, in a comparison of maximum hinge closure force between wild and head-started individuals, wild turtles consistently closed with greater force than head-started individuals (ANCOVA $F_{2,46} = 29.1$, $p < 0.0001$). Homogeneity of slopes ($p > 0.63$) (**Figure 4**). Principle Component 1 was used to adjust for variation in hinge force related to linear body dimensions and body mass, which explained 91.7% of variation.

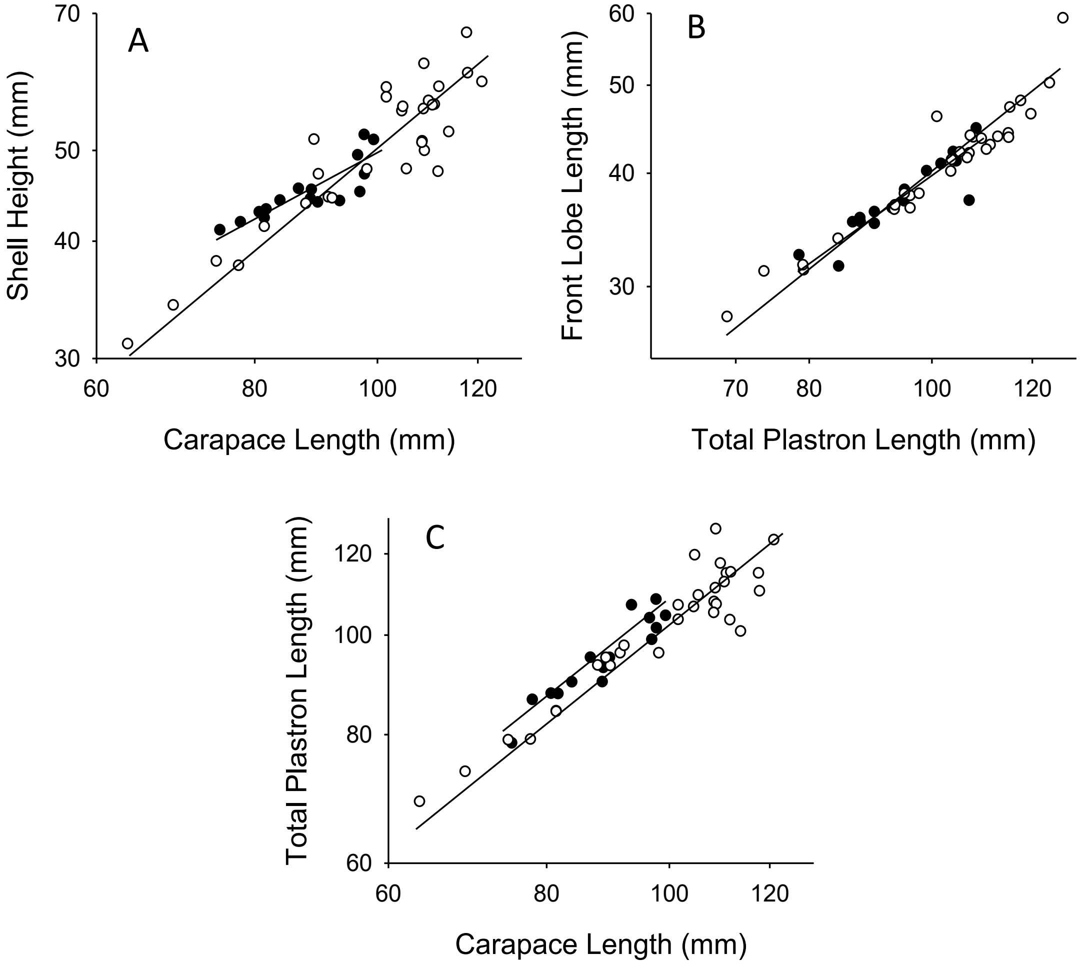

Figure 2. Standard Major Axis ANCOVA tests illustrate the relationship between A) shell height and carapace length and carapace length B) front lobe length and total plastron length, and C) total plastron length and carapace length of head-started and wild Ornate Box Turtles (*Terrapene ornata*). There was a significant interaction between shell height and carapace length related to wild (filled symbols) and head-started (open symbols) status with smaller turtles having initially higher domed shells compared to wild counterparts, but ultimately a slower dome height growth rate as carapace length increases. Head-started or wild status was not a significant predictor for the relationship between front hinge lobe and total plastron length. There was not a significant interaction between plastron length and carapace length of wild and head-started turtles, though there was a significant difference in the elevation of the two lines, indicating for any given carapace length, head-started turtles have longer plastrons than their wild counterparts.

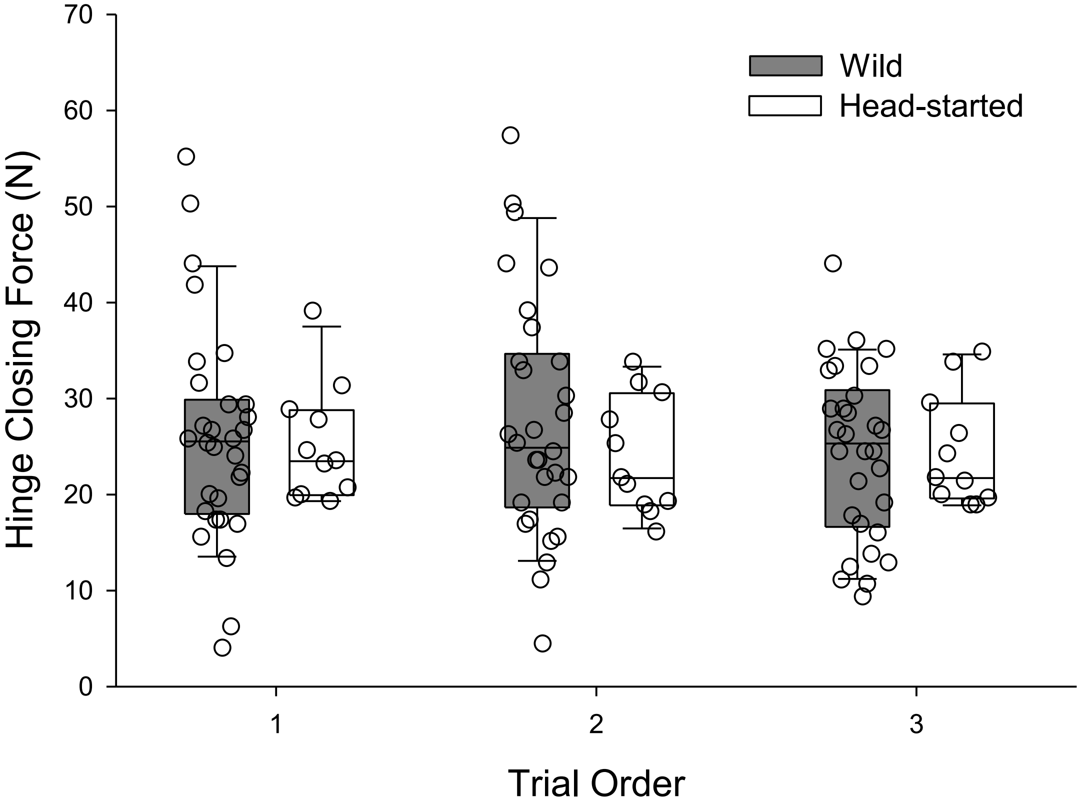

Figure 3. Box plots of hinge closing force trials of Ornate Box Turtles (*Terrapene ornata*). Maximum closing force did not differ significantly among trials in either the wild or head-started turtles. Open circles represent raw values from which box plots were calculated.

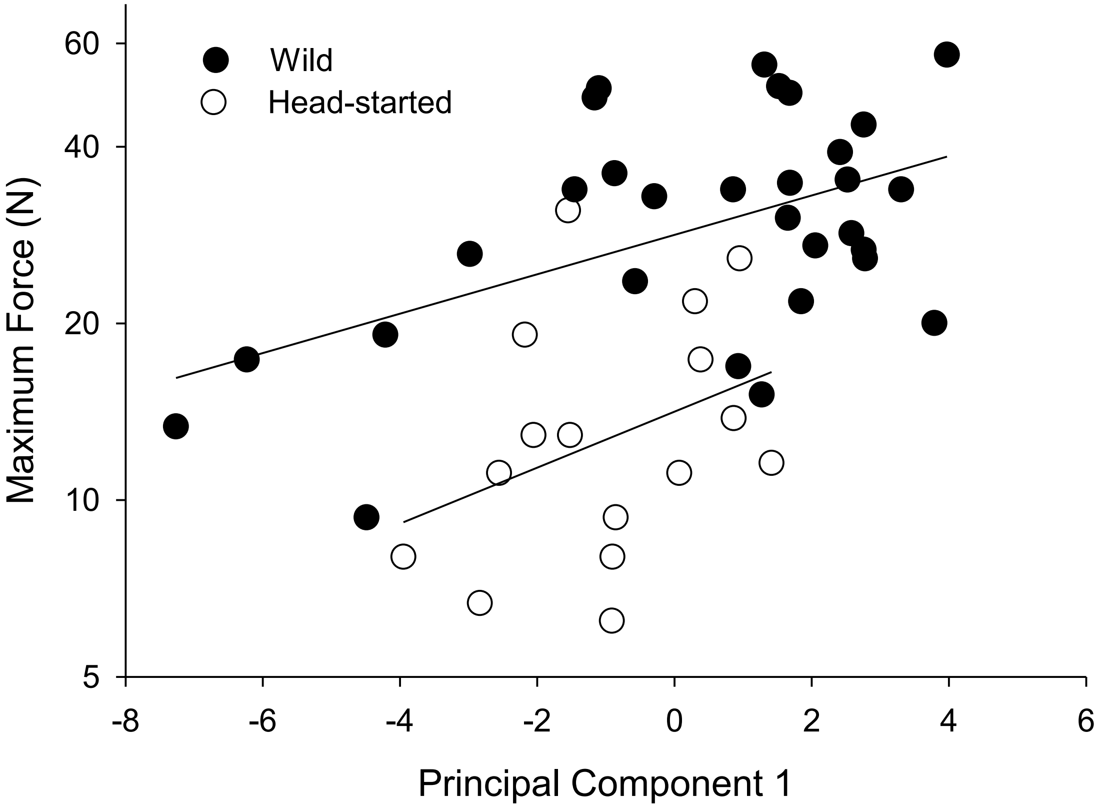

Figure 4. Scatter plot illustrating the relationship between Principal Component 1 (incorporating linear shell dimensions and body mass) and hinge closing force exerted by Ornate Box Turtles (*Terrapene ornata*). The two groups had similar slopes but wild *T. ornata* exerted significantly more force while closing compared to the group that was reared in captivity prior to release. Note that all y-axes are $\log_{10}$-transformed.

Head-started turtles received significantly higher behavior scores than wild turtles, indicating they exhibited greater boldness and aggression (Mann-Whitney U = 29.5, $p < 0.001$). While the most common response by wild turtles to being disturbed was to immediately retreat into their shell, I observed just one instance of an individual attempting to bite during the trial. In contrast, 11 of the 17 head-started turtles attempted to bite during one or more trial, often accompanied by a pushing motion using their front feet to attempt to push my hands away.

DISCUSSION

The force with which head-started and wild Ornate Box Turtles closed their shells was similarly explained by measures of body size. However, wild turtles exhibited dramatically higher hinge closing force than free-ranging head-started turtles did. Furthermore, defensive behaviors, including biting and withdrawing into the shell quickly, were muted among head-started turtles. Together, my results indicate that there is a substantial–and likely deleterious—effect of captive rearing on important predation avoidance strategies.

I was unable to discriminate between effects of morphology versus behavior on hinge force output because the groups differed significantly in both regards. Head-started turtles had longer plastrons than their wild counterparts, which may have adversely affected the closing geometry in which the plastron is pulled upward to make a tight seal with the carapace (Angielczyk et al., 2011). During development, the anterior lobe of the plastron grows at a slower rate than other portions of the shell to accommodate the disproportionately large head of hatchlings in the "box" (Cordero et al., 2019). The captive rearing environment that the group of head-started turtles experienced may have influenced growth due to differences in daily nutrient intake or to the artificially long active season that they experienced by skipping winter hibernation. Alternatively, it is possible that frequent closure of the plastron may place a constraint on excessive growth as the marginal edges of the carapace serve as a physical barrier against excessive lengthening. If true, this would suggest a direct effect of lax antipredator behavior on growth and subsequent morphology.

Animals reared in captivity often exhibit behaviors that deviate from those of their wild counterparts, and for many species naivety to predators reduces survival rates (Jule et al., 2008).

Among wild turtles, the most common response to a simulated threat was to close into their shells. Often, they would immediately pull their hinge toward their carapace but required light tapping to feel threatened enough to make a tight seal. I noted that the turtles often made a hissing noise, expelling air from their lungs when tapped, ostensibly to allow more room within the shell cavity for their limbs and head to fit comfortably. In contrast, head-started turtles did not typically react to the simulated threat by immediately closing into their shell, but rather attempted to offensively bite. When the head-started turtles did withdraw into their shells, it was often not with a tight seal, and I less frequently heard the audible expulsion of air. The head-started turtles tended to flail their limbs in an attempt to escape rather than withdrawing into the safety of their shell.

The head-start/reintroduction program from which I obtained study animals will eventually remove the barriers of the soft-release pen and release the turtles into the wild (Sievers, 2010), and head-starting is playing an increasing role in turtle conservation efforts worldwide (Haskell et al., 1996, Platt et al., 2017, Starking-Szymanski et al., 2018). To maximize the success of this and similar programs, the results of this study should be used to adjust husbandry protocols and reduce deviations in behavior and morphology from the wild type. Adjustments that warrant testing include introducing a period of hibernation consistent with that experienced by wild turtles at the same latitude, adjusting diet to more closely resemble that of wild turtles in both nutritional content and foraging phenology, minimize familiarity with human caregivers, and engage animals in predator recognition training (Mirza and Chivers, 2000; Shier and Owings, 2007; Crane and Mathis, 2011). For *T. ornata* and other species with highly developed shell kinesis, hinge closing performance may serve as a useful bioassay for assessing individual turtles' antipredator response. Finally, it may be instructive to quantify the effectiveness of shell closure as a means of avoiding predation to establish a baseline level of hinge performance required to increase survival.

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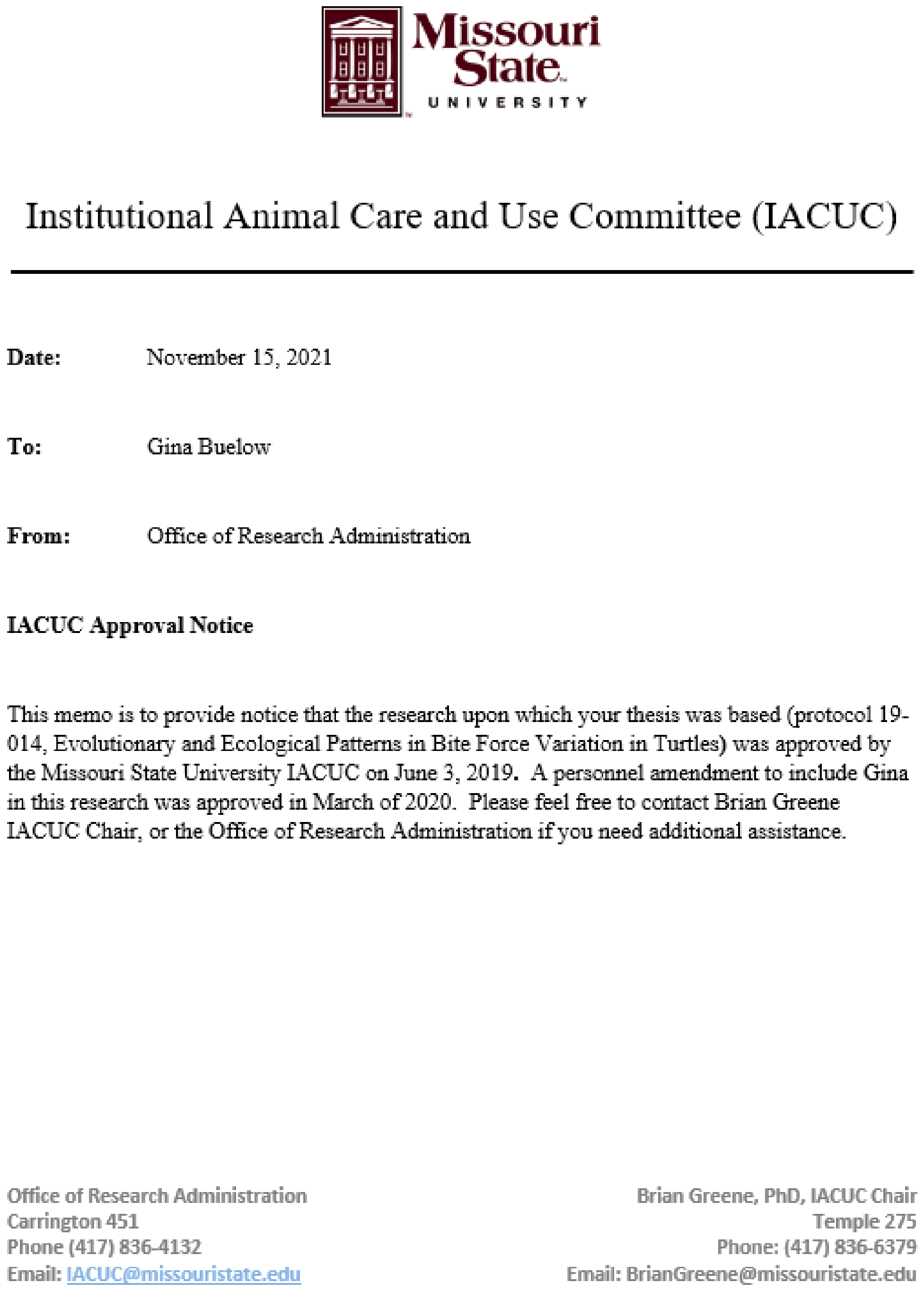
APPENDIX

Missouri State University Institutional Animal Care and Use Committee (IACUC) approval notice for research methods used for this study (protocol 19-014) approved on 3 June 2019.



Missouri State UNIVERSITY

Institutional Animal Care and Use Committee (IACUC)

Date: November 15, 2021

To: Gina Buelow

From: Office of Research Administration

IACUC Approval Notice

This memo is to provide notice that the research upon which your thesis was based (protocol 19-014, Evolutionary and Ecological Patterns in Bite Force Variation in Turtles) was approved by the Missouri State University IACUC on June 3, 2019. A personnel amendment to include Gina in this research was approved in March of 2020. Please feel free to contact Brian Greene IACUC Chair, or the Office of Research Administration if you need additional assistance.

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