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Turtle Girdles: Comparing the Relationships Between Environment and Behavior on Forelimb Function in Loggerhead Sea Turtles (*Caretta caretta*) and River Cooters (*Pseudemys concinna*)

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ABSTRACT

Locomotion in water and on land impose dramatically different demands, yet many animals successfully move in both environments. Most turtle species perform both aquatic and terrestrial locomotion but vary in how they use their limbs. Freshwater turtles use anteroposterior movements of the limbs during walking and swimming with contralateral fore- and hindlimbs moving in synchrony. In contrast, sea turtles swim primarily with "powerstroke" movements, characterized by synchronous forelimb motions while the hindlimbs act as rudders. High-speed video has been used to study powerstroking, but pectoral girdle movements and long-axis rotation (LAR) of the humerus are likely both key components to turtle locomotor function and cannot be quantified from external video. Here, we used XROMM to measure pectoral girdle and humeral movements in a sea turtle (loggerhead, *Caretta caretta*) compared to the freshwater river cooter (*Pseudemys concinna*) during terrestrial and aquatic locomotion. The largest difference among species was in yaw of the pectoral girdle during swimming, with loggerheads showing almost no yaw during powerstroking whereas pectoral girdle yaw in the cooter during rowing was over 30°. The magnitude of humeral LAR was greatest during loggerhead powerstroking and the temporal pattern of supination and pronation was opposite from that of cooters. We hypothesize that these kinematic differences are driven by differences in how the limbs are used to power propulsion. Rotations at the glenoid drive the overall patterns of movement in freshwater turtles, whereas glenohumeral LAR in loggerheads is used to direct the position and orientation of the elbow, which is the joint that determines the orientation of the thrust-generating structure (the flipper) in loggerheads.

Christopher J. Mayerl and John G. Capano contributed equally to this article.

1 | Introduction

Many animals move through multiple environments that impose distinct physical demands (Gillis and Blob 2001). Among such species, it is common for one set of structures to power locomotion in one habitat, but a different set of structures to be used in others. For example, birds power flight with the forelimbs but use the hindlimbs to walk over land (Carrier and Leon 1990; Gatesy et al. 1996; Heers 2016), whereas salamanders, lizards, and crocodilians use movements of their limbs to propel themselves on land, but switch to axial undulations when swimming in water (Ashley-Ross and Bechtel 2004; Baier et al. 2018; Delvolvé, Bem, and Cabelguen 1997; Fish 1984; Seebacher, Elsworth, and Franklin 2003). Yet, many species that move in multiple environments use the same structures to do so. For example, a wide range of aquatic birds use the hindlimbs for propulsion during both walking and swimming, and many frogs power both jumping and swimming through movements of the hindlimbs (Clifton and Biewener 2018; Johansson and Norberg 2001; Nauwelaerts, Stamhuis, and Aerts 2005; Robovska-Havelkova et al. 2014). Species that use the same structures to move through multiple habitats can serve as useful models for understanding the extent to which the performance of specific structures can be modulated to accommodate novel demands in different physical environments.

Among species that use the same structures to produce locomotion in different habitats, turtles represent an intriguing model for several reasons. Integration of much of the vertebral column as part of the bony shell constrains axial movements and requires all turtles to use their limbs to power locomotion both in water and on land (Blob et al. 2016; Pace, Blob, and Westneat 2001; Rivera et al. 2006). However, different lineages of turtles use distinct patterns of limb movement. Most species of freshwater turtles use asynchronous movements of the limb pairs during both walking and swimming, with each of the two limbs in a pair (fore or hind) moving out of phase (Blob, Rivera, and Westneat 2008; Mayerl, Brainerd, and Blob 2016; Rivera and Blob 2010). Three feet are often on the ground simultaneously during walking (Walker 1971a; Zug 1972), and swimming entails primarily anteroposterior excursions, or rowing motions (Davenport, Munks, and Oxford 1984; Mayerl, Brainerd, and Blob 2016; Zug 1971). Sea turtles, in contrast, exhibit novel patterns of motion (Davenport, Munks, and Oxford 1984; Mazouchova, Umbanhowar, and Goldman 2013; Renous and Bels 1993; Wyneken 1997) and are capable of using rowing motions in water; young cheloniid sea turtles commonly retain the use of asynchronous, alternating forelimb movements during terrestrial locomotion. However, adult sea turtles typically rely on synchronous movements of the forelimbs to propel themselves during most swimming behavior (Wyneken 1997), in which the two forelimbs move in phase with each other. These in-water limb movements are frequently referred to as “flapping,” “underwater flight,” or “powerstroking” (Rivera, Wyneken, and Blob 2011; Wyneken 1997). Synchronous movements of the forelimbs during terrestrial locomotion, termed “crutching,” are also common and predominate as some species of sea turtles (*Chelonia mydas, Natator depressus*) grow in size and maturity (Mazouchova, Umbanhowar, and Goldman 2013). In cases where synchronous forelimb motions are used, they incorporate substantial dorsoventral excursions of the limb (Davenport, Munks, and Oxford 1984; Renous and Bels 1993; Rivera and Blob 2013; Rivera, Wyneken, and Blob 2011; van der Geest et al. 2022). This range of limb motion patterns exhibited by turtles across different environments provides an opportunity to evaluate the diversity of modulation strategies employed during appendage-based propulsion.

The general patterns of limb movement in both freshwater and marine turtles have been characterized through a variety of experimental techniques, including electromyography (EMG) and high-speed video (Blob, Rivera, and Westneat 2008; Rivera and Blob 2013; Rivera, Wyneken, and Blob 2011). Though these approaches generated important insights (including the patterns detailed above), potentially significant aspects of limb function can remain obscure when comparisons are restricted to external kinematic measurements (Kambic, Roberts, and Gatesy 2014; 2015). For turtles in particular, the presence of the bony shell may impede visualization of proximal limb joints as well as the limb girdles, which are located deep to the shell. The use of X-Ray Reconstruction of Moving Morphology (XROMM) has enabled measurements of both girdle and limb bone movements for a freshwater emydid turtle, the river cooter *Pseudemys concinna* (hereafter referred to as cooter), during locomotion both in water (rowing) and walking on land (Mayerl, Brainerd, and Blob 2016; Mayerl et al. 2019). These studies show that pectoral and pelvic girdle rotations, especially yaw, contribute to the magnitude of limb excursion and stride length during both aquatic rowing and terrestrial walking, particularly for the forelimb, and play a crucial role in locomotor function (Mayerl et al. 2019). However, these large yaw rotations could reflect the anteroposterior movements of the limbs (which would correspond with yaw of the girdle) more than any anatomical constraint of girdle movement. Moreover, humeral excursions for both abduction/adduction and protraction/retraction were greater during rowing in water, but long-axis rotation of the humerus was greater during walking on land (Mayerl et al. 2019).

Whether such patterns also hold for sea turtles, with their distinctive tendencies for extensive dorsoventral forelimb movements, is unknown. For example, the pectoral girdle of sea turtles might function similarly to that of freshwater turtles, acting to enhance stride length (Mayerl et al. 2019). In contrast to the river cooter, EMG data indicate that the sea turtle deltoideus muscle may act to stabilize the pectoral girdle during swimming (Rivera, Wyneken, and Blob 2011), allowing it to function as a brace or strut during locomotion. Sea turtle pectoral girdle and humeral movements together may vary depending on both locomotor mode and locomotor environment.

Here, we use XROMM to measure the forelimb and pectoral girdle rotations of the loggerhead sea turtle (*Caretta caretta*, suborder: Cryptodira; family: Cheloniidae) during aquatic and terrestrial locomotion, enabling comparisons with previous data from the river cooter (Mayerl et al. 2019, *P. concinna*, suborder: Cryptodira; family: Emydidae). These comparisons allow us to evaluate how the emergence of powerstroking in sea turtles may have influenced their limb function in other locomotor modes. We predict that the increased incorporation of synchronous dorsoventral forelimb movements in powerstroking by sea turtles will correspond with greater dorsoventral girdle rotations (i.e., pitch) compared to those of freshwater turtles such as river cooters. Correspondingly, we expect girdle rotations in other planes, particularly yaw, to be lower in loggerheads during powerstroking than in cooters during rowing and walking due to the asynchronous anteroposterior movements used in these turtles. Finally, we expect to see greater variation across environments and behavior in the humeral movements than in the girdles, as this element interacts directly with the environment during locomotor behaviors. More broadly, our comparisons seek to provide insight into how the evolution of novel behavior can impact the mechanisms used to perform functional tasks.

2 | Materials and Methods

2.1 | Animal Husbandry and Data Collection

To quantify three-dimensional skeletal rotations and translations during locomotion, we followed techniques for marker-based XROMM (Brainerd et al. 2010). Posthatchling (pelagic-stage juvenile) loggerhead sea turtles (*C. caretta*) ~500 g were obtained from Florida Atlantic University (FAU) with approval from the Florida Fish and Wildlife Conservation Commission (FWC Permit MTP-073 to JW). All surgical procedures were completed at FAU after FAU IACUC approval (A18-06). At least three radio-opaque markers were implanted into the carapace, plastron, humerus, and pectoral girdle of each individual, with effort to maximize intermarker distances and avoid collinearity to increase rigid-body accuracy (Brainerd et al. 2010).

Turtles ($n = 7$, mass = 431–456 g) were anesthetized with intravenous Alfaxalone at 5 mg/kg. As soon as the turtles were induced, the ventral axilla was cleaned with a standard alternating betadine and chlorhexidine scrub and a 1–1.5 cm medial to lateral incision through the skin was made to allow access to the acromion process. A second smaller incision into the ventral skin overlying the humerus was made to allow access to the brachium. Muscle bodies were separated by blunt dissection. The humeri and pectoral girdles were marked with tungsten carbide conical markers (Kambic, Roberts, and Gatesy 2014). Following marker placement, the incisions were closed with cruciate sutures using 4–0 glyconate monofilament absorbable suture material. The incision sites were infused with 1% lidocaine (2–4 mg/kg) and topical lidocaine was placed in each closed incision. Before recovery, Ketoprofen was administered intramuscularly (2 mg/kg) every 24 h for 5 days to assist with pain control. Verification radiographs were taken of each turtle to confirm marker placements immediately after the surgery. Dosages for all drugs used were based upon Norton et al. (2017), Phillips et al. (2017), and Wyneken et al. (2006). The turtles were returned to their individual tanks at 15–18 h after the surgery. All swam using both the unmarked and marked flippers. If any turtle was a hesitant to use its flipper's full range by the 3rd day after returning to the water, "cold laser" treatments were provided every 2–3 days for up to four treatments. Turtles resumed using the marked limb within 20–72 h following surgery.

After a minimum of 7 days recovery, loggerheads received computed tomography (CT) scans at FAU. The carapace and plastron of all individuals were marked with press-fitted 0.8 mm tantalum beads (Baltec) before CT scanning. The four turtles with the best marker placements were shipped from FAU to Brown University for x-ray video collection. Each turtle was housed in a large plastic container filled with seawater sufficiently deep for them to swim. Seawater was made with pH-balanced and dechlorinated water and Instant Ocean (Spectrum Brands) with water temperatures kept between 18°C and 26°C. Turtles were monitored twice a day and offered their normal in-house manufactured gel diet, made at FAU.

CT scans were collected at the FAU MRI Facility using a G.E. 64-slice Lightspeed VCT scanner (GE Healthcare Technologies) with a slice thickness of 0.625 mm. We generated 3D polygonal mesh surface models of the carapace, plastron, humerus, pectoral girdle, and associated radio-opaque markers with the open-source medical imaging software Horos (Purview). Any additional model cleaning was performed in GeoMagic Studio 2014 (3D Systems). To analyze the biplanar x-ray videos, we used XMALab to track the 3D coordinates of each radio-opaque marker and generate rigid-body transformations (Knörlein et al. 2016). Mean marker tracking precision was 0.13 mm (best pairwise standard deviation [SD] = 0.05 mm; worst pairwise SD = 0.37 mm).

For x-ray video data collection, individual turtles were temporarily moved from their housing containers and placed into a large acrylic tank filled with water. The tank was filled with approximately 10 cm of water to allow the turtles to swim without impediment. In some trials, individuals were temporarily outfitted with a monofilament loop around their carapace. This "tether," positioned over the centers of mass and buoyancy, enabled researchers to provide enough resistance to cause the turtles to locomote directly within the narrow x-ray field of the biplanar setup. After each trial, individuals were immediately removed from the large acrylic tank and placed back into their respective housing containers. X-ray videos were recorded with custom biplanar video radiography equipment at 200 frames per second with 110 kV and 200 mA (Miranda et al. 2011). Video data are deposited on the XMAPortal (www.xmaportal.org) under the study Loggerhead Sea Turtle Locomotion with permanent ID Brown75. Data are maintained according to best practices for video data management in organismal biology (Brainerd et al. 2017). We also recorded visible light video for each trial with a GoPro camera, which facilitated our ability to distinguish behaviors qualitatively (also available on XMAPortal). We collected 13 useable walking cycles and 13 useable swimming cycles from three individual cooters. The loggerheads provided 14 useable cycles of swimming and five cycles of walking across three individuals (Table 1). We acknowledge that these sample sizes are small, which was due to both the difficulty of collecting good XROMM data and limited numbers of individuals that our permits allowed for this study (*C. caretta* is a protected species). We consider issues related to small sample size in the Discussion.

All animal husbandry, transportation, surgical, and experimental procedures for each respective portion of these studies were approved by the Institutional Animal Care and Use Committees of FAU and Brown University, with all necessary permits regarding sea turtle species approved by the Florida FWC and United States Fish and Wildlife Services (USFWS).

TABLE 1 | Sample sizes (number of cycles) for statistical analyses.

Species	ID	Locomotor mode	Glenohumeral rotations (n)	Shoulder girdle rotations (n)
Cooter	1	Row	4	4
		Walk	4	4
	2	Row	5	5
		Walk	5	5
	3	Row	4	4
		Walk	4	4
Loggerhead	110	Powerstroke	6	6
		Walk	1	1
	409	Powerstroke	6	6
		Walk	3	3
	410	Powerstroke	2	2
		Walk	0	1

2.2 | Data Processing

We tracked data using XMALab and exported rigid body motions to be imported into Maya. Bone motions were animated in Autodesk Maya using the XROMM MayaTools (https://bitbucket.org/xromm/xromm_mayatools). Relative bone motions were measured with joint coordinate systems (JCSs) after Grood and Suntay (1983) to quantify six degree-of-freedom kinematics of both the pectoral girdle and humeri, relative to the plastron following standards in the turtle pectoral girdle established in Mayerl et al. (2019). Each JCS was based on two anatomical coordinate systems (ACSs) derived from combinations of inertial calculations of bone models calculated in MatLab (MathWorks) and geometric primitive fits produced in GeoMagic Studio 2014. We followed the methods and procedures similar to those used in previous studies (Baier, Gatesy, and Dial 2013; Bhullar et al. 2019; Heers et al. 2016; Kambic, Roberts, and Gatesy 2014; Miranda et al. 2010) and calculated all axes such that each axis followed the right-hand rule. All axis calculations were done with bone models in their CT coordinate positions (without moving bones in Maya or other software).

The body axes for all individuals were generated in relation to the plastron, about which all relative motions occurred. We constructed a reference scene for sea turtles to match the reference scene used previously for the cooter pectoral girdle to eliminate variation across individuals, and across species in evaluated movement (detailed in Mayerl et al. 2019 and in Supporting Information).

Data were exported from Maya, and individual limb cycles (hereafter termed cycles) were isolated. We defined a cycle as beginning at the frame of maximal humeral abduction and ending at the frame before the beginning of the next cycle. We interpolated all cycles to 101 points using a quintic spline to account for variation in total stride duration. We calculated the total kinematic excursion of each axis of rotation for each joint. As we were interested in the total excursion of the joints across species, rather than the position of those joints relative to the body, for evaluating differences in rotation throughout a cycle we set the beginning of the cycle as zero. Reported angular movements thus represent Euler angles relative to the joint rather than angles relative to the body axis, which have been previously described elsewhere (e.g., Rivera, Wyneken, and Blob 2011; Mayerl et al. 2019). Here, we describe movement of limb pairs (forelimbs are a pair, hindlimbs are a pair) as synchronous when the pair is protracted and retracted together, and asynchronous when the protraction and retraction are out of phase with each other.

2.3 | Statistical Analysis

Newly collected Sea turtle data were compared with previously reported data on cooter pectoral and humeral function (Mayerl et al. 2019). New statistical analyses were performed to compare rotations of the humerus and girdle between the species from these two data sets, as well as within species across locomotor environment, using linear mixed-effects models in R (Bates et al. 2015) with individual as a random effect. When interactions between species and environment were significant, we used planned contrast analyses in the R Package emmeans (Lenth 2018). We calculated effect sizes of all comparisons using Cohen's D (Cohen 1992).

3 | Results

3.1 | Qualitative Differences in Limb Movement Between Species

To provide context for our new comparisons, we first provide qualitative descriptions of the limb movements for each taxon. Cooters used asynchronous movements of the forelimbs during swimming (rowing) and walking (Mayerl et al. 2019), whereas the juvenile sea turtles used synchronous movements of the forelimbs during swimming (powerstroking), and asynchronous movements of the forelimbs during walking, which involved contralateral limbs being used to elevate the plastron from the ground, and then propel the animal forwards (verified by light video). Although the asynchronous patterns of forelimb movement in juvenile sea turtles roughly approximated the patterns

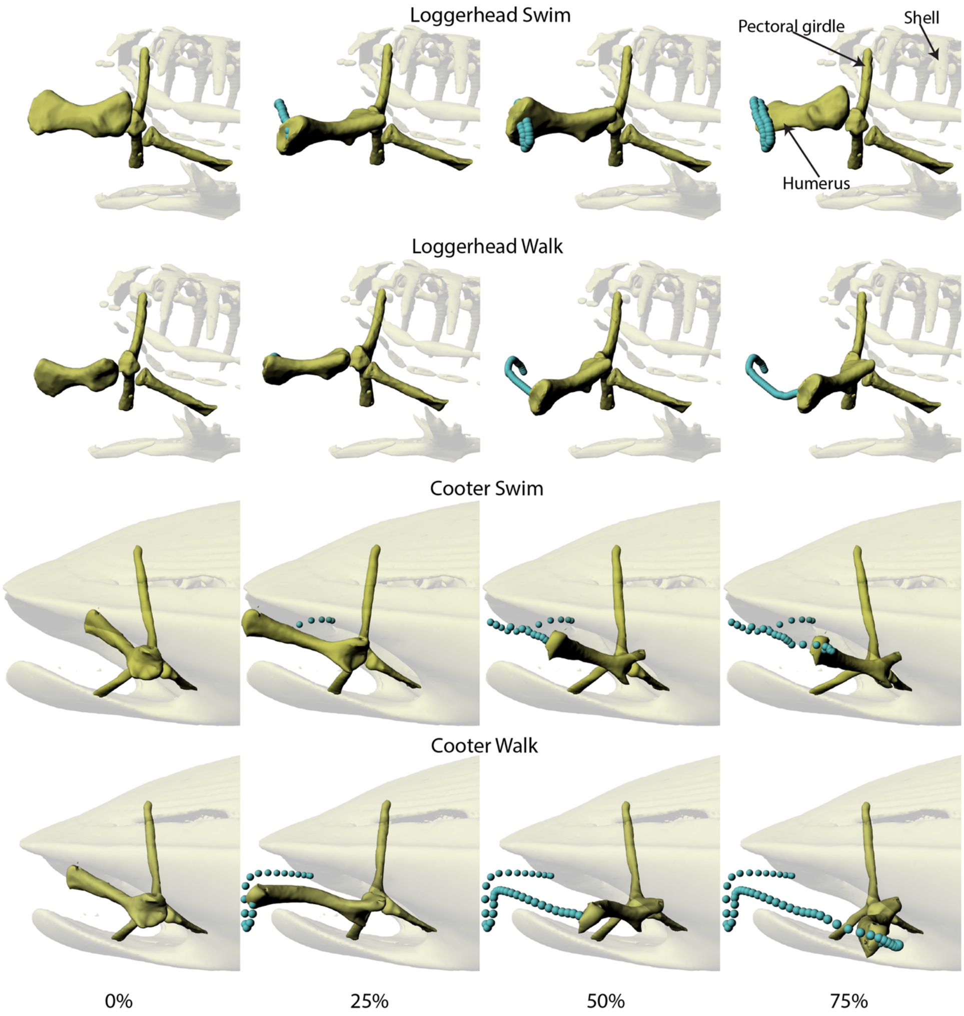

FIGURE 1 | Still frame images of XROMM animations of loggerhead sea turtles swimming (powerstroking) and walking, and cooter swimming (rowing) and walking. The left girdle and stylopodia are viewed in the context of cranial carapace and plastron, in lateral view. For visualization, the position of the distal humerus (blue dots) was traced through the beginning of the cycle (left), 25% of the cycle, 50% of the cycle, and 75% of the cycle. Note the pronounced changes in humeral movements in the loggerhead between environments and the differences between species in both environments.

observed in cooters, the magnitude of rotation was different between the species, likely due to variation in how the distal elements of the forelimb are used for propulsion across species (Figure 1). As we performed surgery on only one side of the body and are interested primarily in overall behavioral variation, we use asynchronous versus synchronous as holistic descriptions rather than quantitatively assessing synchrony, in addition to previous descriptions of locomotor function in these behaviors in the literature (Blob, Rivera, and Westneat 2008; Davenport, Munks, and Oxford 1984; Mayerl, Brainerd, and Blob 2016, Mayerl et al. 2017, 2019; Pace, Blob, and Westneat 2001; Renous and Bels 1993; Rivera, Wyneken, and Blob 2011; Wyneken 1997, Zug 1972).

3.2 | Pectoral Rotations

Pectoral girdle rotations are described as roll, pitch, and yaw with respect to the plastron, with roll defined as rotation about a craniocaudally oriented axis, pitch about a mediolaterally oriented axis and yaw about a dorsoventrally oriented axis (red, green, and blue, respectively, in Figure S1). The largest difference among species was in yaw of the pectoral girdle during swimming, with loggerheads showing almost no yaw (5 ± 1.5°) during synchronous powerstroking whereas pectoral girdle yaw in the cooter during asynchronous rowing was over 30° (Figure 2). Locomotor environment impacted girdle rotations in loggerheads, and locomotor environment had an impact on roll of the girdle in both cooters and loggerheads. Overall, roll and pitch rotations were smaller than yaw in both species and in both locomotor environments.

3.2.1 | Roll

Roll of the pectoral girdle was low for both species and across all conditions ($< 10°$), and we observed an interaction between species and environment ($\chi^2 = 5.6$, $p = 0.01$). Roll was higher during walking than during swimming in cooters ($t = 2.6$, $p = 0.01$, $D = 1.7$, walking mean $= 5.3° \pm 1.1°$, swimming mean $= 3.3° \pm 1.3°$, Figure 2D, Table 2), and higher during walking than during swimming in loggerheads ($t = 4.6$,

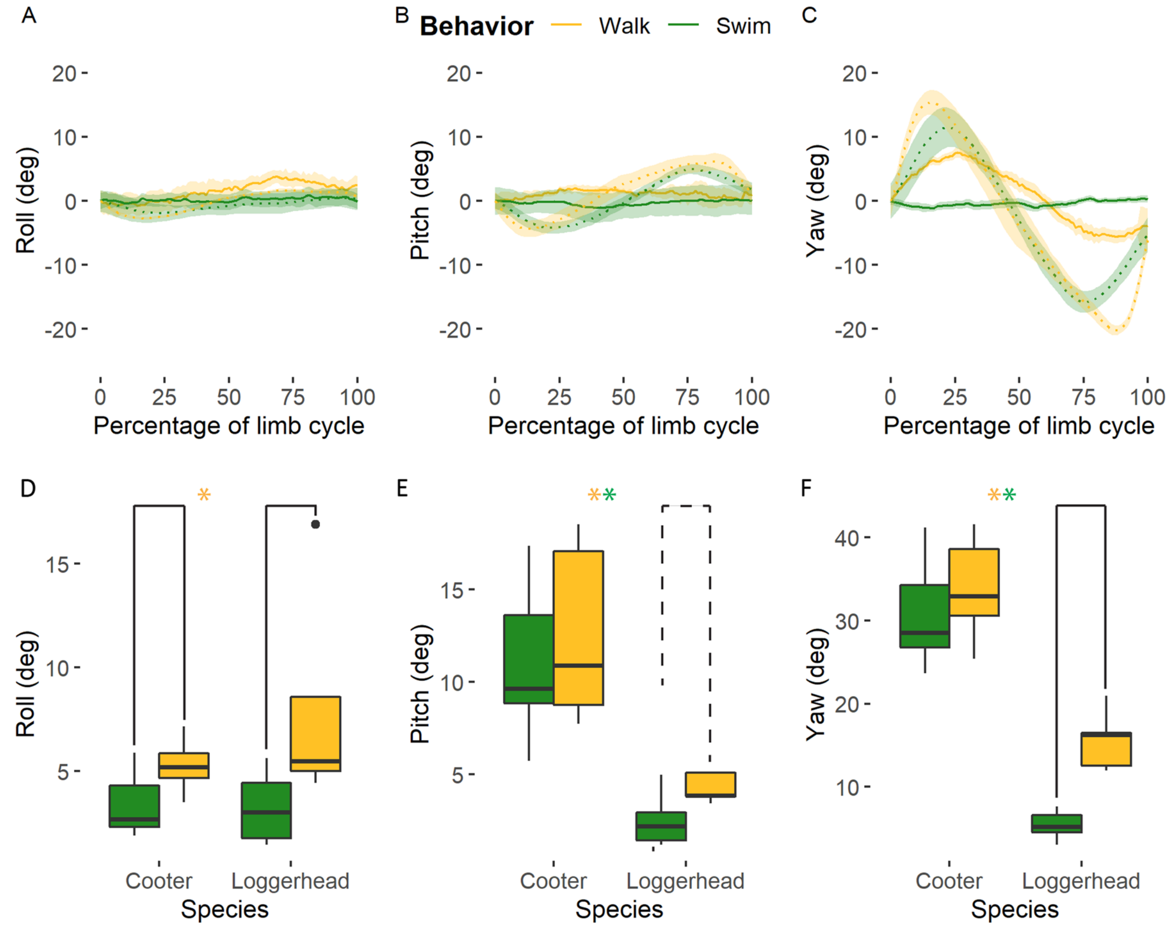

FIGURE 2 | Rotations of the pectoral girdle relative to the plastron in loggerhead sea turtles (solid lines) and cooters (dotted lines) throughout a limb cycle (A–C), and the total excursion of those cycles (D–F) during swimming (green) and walking (yellow). Shaded areas in (A–C) represent the mean (solid) ± SE for each group. Boxes in (D–F) represent the median and interquartile range, with dots outside the boxplots indicating outliers. Solid lines connecting plots represent statistically significant differences across locomotor modes within a species with large effect sizes, whereas dashed lines in (E) indicate nonsignificant differences with large effect sizes. Colored asterisks in (D–F) indicate a medium or large effect size within a locomotor mode between species. Excursions in (A, B, and C) appear to be less than those in statistical analyses (D, E, and F) due to variation in the timing of when the maximum and minimum occurs across cycles.

$p < 0.001$, $D = 1.8$, walk mean 8.1° ± 5.1°, swim mean = 3.2° ± 1.4°). Across species, the cooter pectoral girdle rolled less than the loggerhead girdle during walking (Figure 2A, Table 2).

3.2.2 | Pitch

We observed a significant effect of species ($\chi^2 = 9.7$, $p = 0.002$) and environment ($\chi^2 = 18.4$, $p < 0.001$) on girdle pitch. Pairwise comparisons indicated that pectoral girdle pitch did not differ by locomotor mode in cooters (swimming mean = 10.9° ± 3.6°, walking mean = 12.2° ± 4.0°). In contrast, pitch during swimming was lower than walking in loggerheads (swimming mean = 2.4° ± 1.2°, walking mean = 4.3° ± 0.8°, $t = -1.2$, $p = 0.24$, $D = -1.76$). Loggerheads' pectoral girdles pitched less during swimming and walking than those of cooters (Figure 2E, Table S1).

3.2.3 | Yaw

There was an interaction between species and environment in girdle yaw ($\chi^2 = 19.6$, $p < 0.001$) In cooters, yaw was similar during walking and rowing (Tables 2 and S1), but in loggerheads, yaw was higher during walking than swimming, with a large effect size ($t = 4.4$, $p < 0.001$, $D = 4.7$, Tables 2 and S1; Figure 2F). Cooters exhibited more than double the yaw seen in loggerheads during walking and six times the yaw during swimming (Figure 2F, Table 2).

3.3 | Humeral Motions

We found substantial differences in humeral motions across species and across conditions.

3.3.1 | LAR

There was a significant interaction between species and environment in humeral LAR ($\chi^2 = 47.6$, $p < 0.001$). In cooters, LAR excursion was greater during walking than during swimming (Figure 3D, $t = -3.1$, $p = 0.004$; $D = 0.99$). In contrast, LAR was higher during swimming than during walking in loggerheads ($t = 4.1$, $p = 0.001$, $D = 2.19$). During walking, the total excursion of

TABLE 2 | Planned contrasts results (*t* statistic, *p* value; Cohen's D) across species and within species between locomotor modes (walking [walk], swimming [swim]).

	C Swim vs. C Walk	C Swim vs. L Swim	C Walk vs. L Walk	L Swim vs. L Walk
Hum-Pec-Rx-LAR	**2.5, 0.02; 0.99**	**5.7, < 0.001; 2.4**	**1.9, 0.07; 0.95**	**4.1, < 0.001; 2.2**
Hum-Pec-Ry-AbAdd	**2.9, 0.005; 1.4**	**8.0, < 0.001; 3.2**	0.79, 0.44; 0.43	**2.7, 0.01; 1.2**
Hum-Pec-Rz-ProRet	0.8, 0.42; 0.27	**8.5, < 0.001; 4.6**	**5.6, < 0.001; 2.4**	0.46, 0.65; 0.4
Pec-Shell-Rx-Roll	**2.6, 0.01; 1.7**	0.14, 0.89; 0.08	**2.6, 0.01; 1.0**	**4.6, < 0.001; 1.8**
Pec-Shell-Ry-Pitch	1.1, 0.28; 0.33	**7.3, < 0.001; 3.2**	**5.0, < 0.001; 2.3**	*1.2, 0.24; −1.7*
Pec-Shell-Rz-Yaw	1.8, 0.08; −0.56	**14.7, < 0.001; 6.1**	**7.7, < 0.001; 3.7**	**4.4, < 0.001; 4.7**

Note: Bolded values indicate statistically significant differences with large effect sizes. Italicized values indicate values with nonsignificant differences, but with large effect sizes.

Abbreviations: C, river cooter; Hum-Pec, humeral rotations relative to the pectoral girdle; L, loggerhead; Pec-Shell, pectoral girdle rotations relative to the plastron; Rx-LAR, long axis rotation; Ry-AbAdd, abduction adduction rotation; Rz-ProRet, protraction retraction rotation.

LAR was also higher in cooters than in loggerheads ($t = 1.8$, $p = 0.07$, $D = 0.95$), whereas the opposite was true during swimming ($t = 5.7$, $p < 0.001$, $D = 2.4$). The pattern of LAR within a cycle was similar during walking and swimming in cooters (Figure 3A). Strikingly, loggerheads used different patterns of humeral rotation than cooters during both swimming and walking. During loggerhead walking, the humerus remained in a supinated posture until approximately 90% of the limb cycle was complete, whereas during cooter walking the humerus remained in a supinated posture until only 50% of the cycle was complete. The pattern of LAR also differed between the two species during swimming (Figure 3A).

3.3.2 | Abduction/Adduction

We observed a significant interaction between species and environment in abduction/adduction ($\chi^2 = 15.7$, $p < 0.001$). The two species exhibited different patterns of abduction/adduction of the limb depending on locomotor mode. In cooters, abduction/adduction excursion was higher when swimming than when walking (swimming mean = 75.8° ± 9.9°, walking mean = 63.5° ± 7.6°, $t = 3.25$, $p = 0.002$, $D = 1.38$, Figure 3E). In loggerheads, humeral abduction/adduction during swimming was less than abduction/adduction during walking. The two species used similar amounts of abduction/adduction during terrestrial locomotion, but during swimming abduction/adduction was greater in cooters (Figure 3E, Table 2).

3.3.3 | Protraction/Retraction

The humeri in cooters had much greater protraction-retraction excursions compared to those of loggerheads in both environments. Cooters used more than double the protraction/retraction during both aquatic and terrestrial locomotion than loggerheads ($\chi^2 = 20.7$, $p < 0.001$), Figure 3F, Table 2). Within species, the amount of protraction/retraction the humerus underwent during locomotion did not vary by locomotor environment (Figure 3F).

4 | Discussion

Loggerhead sea turtles and river cooters used different movements of the pectoral girdle and humerus during locomotion, and the two structures exhibited different responses with changes in locomotor mode. As predicted, pectoral girdle rotations were minimal in sea turtles, potentially due to the action of stabilizing muscles like deltoideus during powerstroking (Rivera, Wyneken, and Blob 2011). In this context, the most substantive differences in girdle movements occurred between species rather than between habitats, especially in yaw due to the large rotations exhibited by cooters. Humeral movements also differed as predicted between species and among locomotor modes.

4.1 | Girdle Function

Rotations of the pectoral girdle are critical for enhancing locomotor performance across many vertebrates (Fischer, Krause, and Lilje 2010; Jenkins and Goslow 1983; Jenkins and Weijs 1979; Nyakatura and Fischer 2010; Peters and Goslow, Jr. 1983; Veeger and van der Helm 2007). In addition to enhancing locomotor performance, the girdles of tetrapods also play the key role of supporting the weight of the body during locomotion (Carrier, Deban, and Fischbein 2006). Buoyancy supports much of the body weight in water, whereas during terrestrial locomotion substantial body weight support is functionally integrated, and girdle function and movements are expected to differ between habitats.

We found that the pectoral girdle rotations in both species exhibited generally similar patterns of change between aquatic and terrestrial locomotion. The pectoral girdle rotated less during aquatic locomotion than during terrestrial locomotion in both species, especially in roll and yaw, although these differences were proportionally more substantial in loggerheads. Our results support the hypothesis that patterns of pectoral girdle rotation likely were driven by the environment in which locomotion occurs. The need for body support against gravity on land generates greater forces on the pectoral girdle, and is associated with increased rotations in both species during terrestrial locomotion. How these rotations are reflected by bone strain, body support, and locomotor performance could provide key insights into how tetrapods made the transition from water to land and, in the case of sea turtles and some other lineages (i.e., mosasaurs, plesiosaurs, and pinnipeds), how the secondary evolution from land back to water was accomplished (Blob et al. 2016; Kawano and Blob 2013; Young et al. 2017).

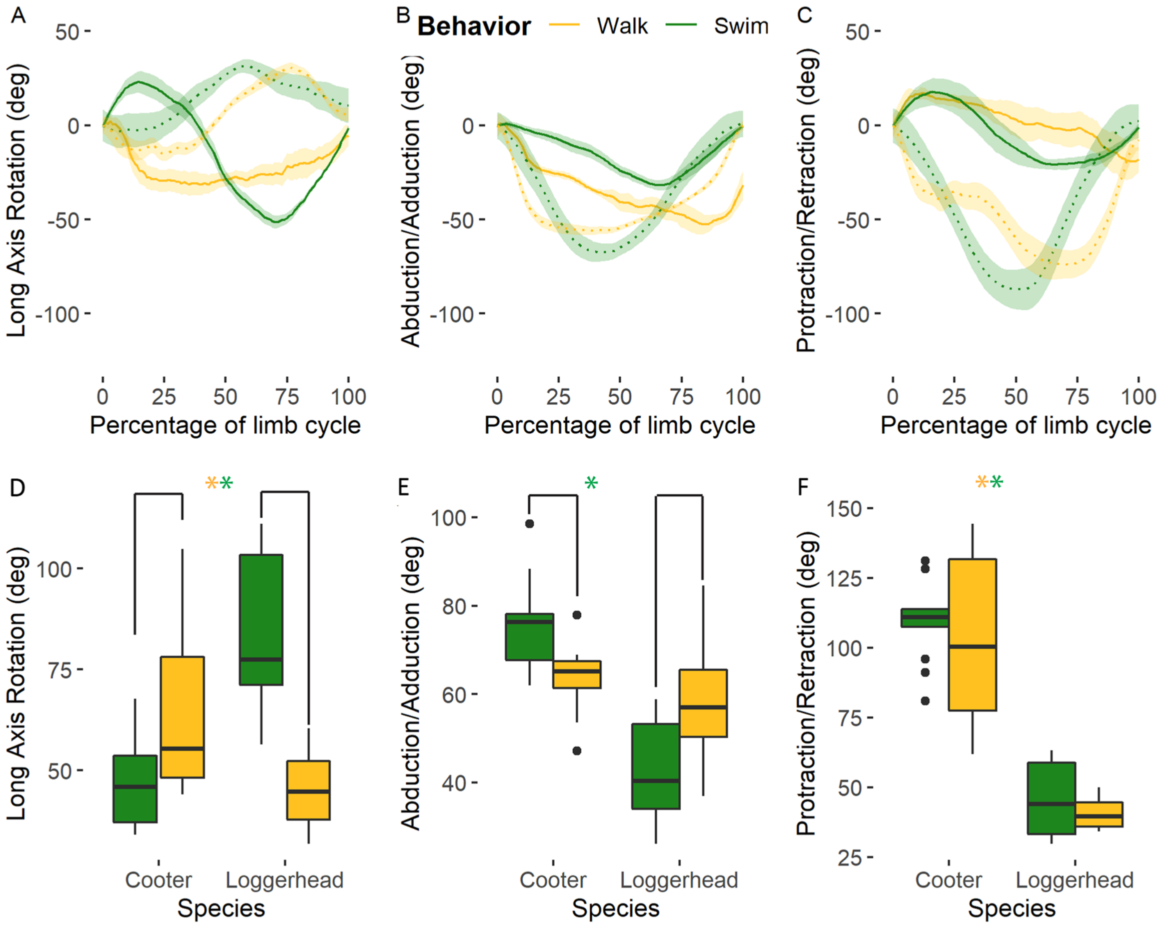

FIGURE 3 | Rotations of the humerus relative to the pectoral girdle in sea turtles (solid lines) and cooters (dotted lines) throughout a limb cycle (A–C), and the total excursion of those cycles (D–F) during swimming (green) and walking (yellow). Shaded areas in (A–C) represent the mean (solid) ± SE for each group. Boxes in (D–F) represent the median and interquartile range, with dots outside the boxplots indicating outliers. Solid lines connecting plots represent statistically significant differences with large effect sizes across locomotor modes within a species. Colored asterisks in (D–F) indicate statistically significant differences within a locomotor mode between species. Excursions in (A, B, and C) appear to be less than those in statistical analyses and (D, E, and F) due to variation in the timing of when the maximum and minimum occurs across cycles.

Although the general patterns of girdle rotation were mostly similar for both species, their magnitudes were very different. Cooter pectoral girdles yawed more than 30° in both environments, which is six times greater than the yaw observed during swimming in loggerheads, and more than twice as much yaw compared with walking in loggerheads. However, we also predicted that pitch would be larger in loggerheads than in cooters due to the synchronous movements occurring during powerstroking but found the opposite to be true. The additional stride length contributed by pectoral yaw in cooters (Mayerl et al. 2019) with their limb movements in the horizontal plane. The lack of pitch mobility observed in the loggerhead pectoral girdle initially may seem surprising, especially during aquatic powerstroking ($< 3°$), in which synchronous movements of the forelimbs are primarily dorsoventral. We hypothesize that the extensive humeral rotations driving the elongated autopod (flipper blade) require a relatively stable girdle skeleton during powerstroking. Thus, the musculature associated with the sea turtle pectoral girdle likely evolved to function more as a stabilizer rather than as a means of enhancing stride length (Rivera, Wyneken, and Blob 2011).

Stabilization of the pectoral girdle during powerstroking in loggerheads could occur either through passive skeletal, active muscular, or combined passive and active means. For comparison, during flapping flight in birds the coracosternal joint is fairly immobile, with rotations in any dimension being $< 6°$, in contrast to the glenohumeral joint, which undergoes excursions of over 100° (Baier, Gatesy, and Dial 2013). While differing in magnitude, these trends are similar to what we observed in loggerheads between the pectoral girdle-shell joint and the glenohumeral joint. In loggerheads, the lack of girdle rotations could arise from an anatomical constraint associated with how it attaches via ligaments and locomotor muscles to the shell. This possibility seems likely as at least a partial explanation for the patterns we observed; the loggerhead girdle rotations never reached the yaw magnitudes observed in the semiaquatic cooter. An additional muscular factor may be that some muscles associated with the pectoral girdle appear to be active as stabilizers during powerstroking and may have insufficient neuromotor plasticity to facilitate large-amplitude girdle movements during other locomotor modes. This possibility is supported by the observation that the deltoideus muscle in freshwater turtles acts as a limb protractor/elevator, whereas in sea turtles this muscle acts primarily as a joint stabilizer during powerstroking (Rivera, Wyneken, and Blob 2011). It is likely that a combination of these passive and active factors could contribute to the lack of girdle rotations in loggerheads. Future work could explore these contributions explicitly, in conjunction with the foundation of anatomy, EMG activity and limb kinematics highlighted in Rivera, Wyneken, and Blob (2010, 2011).

4.2 | Limb Function

As the direct interface between an animal and the environment through which it moves, the limbs may exhibit diverse kinematic patterns depending on locomotor mode and the nature of the environments being traversed. For example, many tetrapods use a range of distinct gaits within the same environmental medium (e.g., land, water) in which the limbs are moved in different sequences or combinations (Farley and Taylor 1991; Hildebrand 1989; Mayerl and Blob 2017; Renous et al. 2002). Similarly, fishes, mammals, amphibians, and reptiles have all been observed to exhibit different patterns of appendicular movements in different media (Biewener and Gillis 1999; Gillis and Blob 2001; Mayerl et al. 2017; Nauwelaerts and Aerts 2003). In this context, the highly variable humeral kinematics we observed in both cooters and loggerhead sea turtles across different locomotor modes generally followed expectations.

The most striking differences in how the humerus moved in river cooters and loggerheads during different propulsive modes occurred in the relative use of long-axis rotation and protraction/retraction. Long-axis rotation can serve multiple functions and often plays a role in orienting the more distal elements of the limb to maximize propulsive force generation and working range (Ashley-Ross and Bechtel, 2004; Kambic, Roberts, and Gatesy 2014; 2015; Reilly and Delancey, 1997; Rewcastle, 1983). In river cooters, the humerus is generally pronated during the propulsive phase, likely maximizing thrust during paddling, and orienting the limb so the foot plants against the ground during walking. Such patterns are similar between swimming and walking. In contrast, the loggerhead humerus undergoes distinctly different patterns of long-axis rotation depending on locomotor mode. During walking, humeral rotations increase supination during stance and remain supinated until the end of the cycle. However, during powerstroking, the humerus undergoes substantial LAR, with high pronation occurring at the beginning of the cycle (the downstroke) before switching to supination during the middle half of the cycle (Figure 2A). This temporal difference in LAR during powerstroking contrasts with what is observed during walking in loggerheads and during swimming and walking in cooters. This pattern in loggerheads also differs from those observed in birds during ascending flight (Baier, Gatesy, and Dial 2013), and likely relates to differences in the elbow joint as well as how the limbs are used to generate thrust. In birds, the humerus acts in concert with the distal elements of the wing to move the entire limb (Baier, Gatesy, and Dial 2013; Tobalske, Hedrick, and Biewener 2003; Tobalske et al. 2007). In contrast, our work suggests that the sea turtle humerus acts as a separate unit controlling the lift-generating component of the limb. Additionally, the humeral head in loggerheads is offset less than in many birds and the loggerhead glenoid cavity is roughly oval, producing different restrictions of angles of humeral rotation than in birds (Walker 1971b).

River cooter humeri undergo more than twice the amount of rotation in protraction and retraction of the humerus during aquatic and terrestrial locomotion than loggerheads. These interspecific differences in the magnitudes of rotation likely are due to differences in how the limbs are used during terrestrial locomotion. Cooters walk by protracting the stylopodia (humeri) and zeugopodia (radii and ulnae), and then plant the autopodial elements (distal end of the limb) and move the body forward by retracting and depressing the zeugopodia while supporting the body. During this behavior, the opposite hindlimb mirrors the movements of the forelimb. Loggerheads walk by alternating left and right forelimbs with the elbow flexed, which qualitatively results in similar stylopodial excursions to that of cooters, albeit with different structures. There is little elevation of the plastron and walking is accomplished by protracting the stylopodia (humeri) and planting the zeugopodia and autopodial elements (distal end of the limb and the preaxial edge of the flipper blade) into the ground. These elements then contribute anchoring as the stylopodia (rather than zeugopodia, as in cooters) are retracted and rotated. The opposite hindlimbs are protracted and retracted asynchronously yet contribute little to propulsive force (Mazouchova, Umbanhowar, and Goldman 2013; Renous and Bels 1993).

The asynchronous rowing patterns of limb motion in river cooters correspond with an oar-like manus used for creating drag-based thrust during swimming (Vogel 2013). In contrast, the forelimb of sea turtles is specialized as a lift-generating structure (Wyneken 1997). We suggest that the differences we observe between species in humeral movements likely relate to how these propulsive units are used during swimming. In cooters, movement of the humerus drives the primary movement of the limb, such that overall limb movement generally follows patterns of humeral movements (i.e., during retraction of the humerus, the entire forelimb is retracted). However, in loggerheads, the effect that humeral movements have on the rest of the limb (the flipper blade) is more often mediated by the position of the elbow joint, and long axis rotation of the humerus drives the orientation of the elbow joint during retraction and depression of the distal elements of the limb. Future work investigating the interplay between movements of the humerus and the distal elements of the limb will be informative. Such studies have implications both for the development of bioinspired amphibious robotics (Baines et al. 2022; Mazouchova, Umbanhowar, and Goldman 2013), as well as for understanding the evolution and plasticity of neural control in the locomotor system of vertebrates (Gillis and Blob 2001; Gruner and Altman 1980; Mayerl et al. 2017; Rivera, Wyneken, and Blob 2011).

4.3 | Sample Size Caveats

XROMM remains a challenging method due to the many steps in the process and many things that can go wrong at every step. For example, our study of loggerhead locomotion included five turtles and 50 saved locomotor trials (and many more attempts that were not saved). The marker sets of two sea turtles turned out not to be useable due to challenges associated with surgically placing markers blindly and only a small fraction of the locomotor trials of the remaining three turtles' data contained full cycles in which all of the markers were visible in both x-ray cameras. Small sample sizes limit the ability to quantify differences among individuals and may limit future interspecific comparisons. However, despite small sample sizes the consistency of the data give us confidence that the available data support our most substantial conclusions: (1) the pectoral girdle in loggerheads is stabilized during power stroking; (2) the environment has a substantial effect on pectoral girdle kinematics in both cooters and loggerheads; and (3) the patterns and function of humeral long-axis rotation differ between cooters and loggerheads.

4.4 | Conclusions and Future Directions

The evolution of powerstroking in sea turtles has bearing on humeral and pectoral girdle function in different ways and to different degrees. Movements of the humerus appear highly adaptable depending on both environmental and behavioral contexts. In contrast, while the magnitude of pectoral girdle movements varies substantially between species, with loggerhead girdle motions being much smaller than those of cooters, the patterns of girdle movements are similar between locomotor modes in that girdle motions in swimming are larger than those during walking. To further disentangle interactions between evolutionary history, limb movements, and locomotor medium, future work could focus on how the limbs and girdles function in animals that transition between environments, and which use variable movements within an environment. Moreover, although this study has focused only on proximal components of the locomotor system, much of the propulsive thrust generated by turtles comes from the distal limb elements. Functional studies of these components of the limb are much more limited (hind limb: Schoenfuss et al. 2010; forelimb: Davenport, Munks, and Oxford 1984, van der Geest et al. 2022, Walker 1971b), but understanding the role of the limbs and their flexibility to adjust their motor output could provide further insight into changes in overall limb function through the evolution of new behavioral and functional specializations.

Author Contributions

Christopher J. Mayerl: conceptualization, formal analysis, data curation, writing original draft, visualization, methodology, investigation, editing. **John G. Capano:** data curation, methodology, investigation, editing. **Noraly MME van Meer:** methodology, investigation, editing. **Hannah I Weller:** methodology, investigation, editing. **Elska B Kaczmarek:** methodology, investigation, editing. **Maria Chadam:** methodology, investigation, editing. **Richard W. Blob:** conceptualization, supervision, methodology, investigation, editing. **Elizabeth L. Brainerd:** conceptualization, visualization, supervision, methodology, investigation, editing. **Jeanette Wyneken:** conceptualization, visualization, supervision, methodology, investigation, editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data used in statistical analyses are available at 10.6084/m9.figshare.26528008.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.