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“On the Fence” versus “All in”: Insights from Turtles for the Evolution of Aquatic Locomotor Specializations and Habitat Transitions in Tetrapod Vertebrates

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Synopsis Though ultimately descended from terrestrial amniotes, turtles have deep roots as an aquatic lineage and are quite diverse in the extent of their aquatic specializations. Many taxa can be viewed as “on the fence” between aquatic and terrestrial realms, whereas others have independently hyperspecialized and moved “all in” to aquatic habitats. Such differences in specialization are reflected strongly in the locomotor system. We have conducted several studies to evaluate the performance consequences of such variation in design, as well as the mechanisms through which specialization for aquatic locomotion is facilitated in turtles. One path to aquatic hyperspecialization has involved the evolutionary transformation of the forelimbs from rowing, tubular limbs with distal paddles into flapping, flattened flippers, as in sea turtles. Prior to the advent of any hydrodynamic advantages, the evolution of such flippers may have been enabled by a reduction in twisting loads on proximal limb bones that accompanied swimming in rowing ancestors, facilitating a shift from tubular to flattened limbs. Moreover, the control of flapping movements appears related primarily to shifts in the activity of a single forelimb muscle, the deltoid. Despite some performance advantages, flapping may entail a locomotor cost in terms of decreased locomotor stability. However, other morphological specializations among rowing species may enhance swimming stability. For example, among highly aquatic pleurodiran turtles, fusion of the pelvis to the shell appears to dramatically reduce motions of the pelvis compared to freshwater cryptodiran species. This could contribute to advantageous increases in aquatic stability among predominantly aquatic pleurodires. Thus, even within the potential constraints of a body plan in which the body is encased by a shell, turtles exhibit diverse locomotor capacities that have enabled diversification into a wide range of aquatic habitats.

Introduction

Some of the strongest functional demands that animals face are posed by the physical habitats in which they live (Denny 1993; Gillis and Blob 2001; Ashley-Ross et al. 2013; Blob and Higham 2014). Among vertebrates, one of the most fundamental distinctions in habitat is between aquatic and terrestrial environments. Animals that are surrounded by water face a very different world than animals that contact solid ground and are surrounded by air. The physical disparities between these worlds include features ranging from the oxygen content and thermal capacity of

the surrounding medium, to the viscosity of the surrounding medium and its capacity for supporting gravitational loads (Denny 1993; Vogel 1994). Such disparities can have important consequences for a variety of important functions, from respiration and reproduction to feeding and locomotion (Ashley-Ross et al. 2013). Given these impacts, the potential for evolutionary transitions between aquatic and terrestrial habitats would seem likely to be limited by significant functional challenges. Nonetheless, since the initial invasion of land by tetrapods, multiple tetrapod lineages have reinvaded the water with

varying degrees of completeness (Fish 1996; Motani 2005; Renous et al. 2008; Smith and Clarke 2014).

Among the tetrapod lineages that have reinvaded water, turtles possess a suite of features that make them well suited for gaining insight into these evolutionary transitions, particularly with regard to the locomotor system. The oldest, fully-shelled turtles were likely terrestrial (Joyce and Gauthier 2004; Scheyer and Sander 2007; Schoch and Sues 2015). However, extensive use of aquatic habitats became pervasive soon thereafter, to the extent that, among living turtles, all terrestrial lineages are nested within primarily aquatic clades (Gosnell et al. 2009). Yet, different turtle lineages have become specialized for aquatic habitats to differing degrees (Davenport et al. 1984; Pace et al. 2001; Blob et al. 2008). Many turtle clades make frequent use of both aquatic and terrestrial habitats, spending considerable time in water but still making extended forays over land (Cagle 1944; Bennett et al. 1970; Gibbons 1970; Blob et al. 2008). These taxa are sometimes referred to as “semiaquatic,” but this description from the aquatic perspective may not fully capture the conditions that such species experience. Living “on the fence” between two habitats can pose distinct functional challenges, particularly when the demands of those habitats differ (Gillis and Blob 2001). But among such taxa, lineages more exclusively specialized for aquatic lifestyles have also evolved (Renous et al. 2008). This range of habits among living species of turtles means that comparisons of locomotor function can be performed between taxa that live “on the fence” between aquatic and terrestrial habitats, and hyperspecialized species that have gone “all in” and moved essentially completely into aquatic habitats. Such comparisons can clarify the changes necessary to facilitate evolutionary transitions in locomotor function, and the mechanisms through which they were achieved.

In addition to the range of habitat specialization found among turtles, distinctive anatomical features of the lineage also facilitate efforts to understand locomotor evolution through the course of secondary aquatic invasions. The fusion of the trunk vertebrae to a bony shell in turtles makes most of the body axis inflexible, except for the neck and tail. Thus, given the limited role of the tail in locomotion for most turtle species (Willey and Blob 2004), tests of how locomotor function changes across habitats can be simplified in turtles by focusing on the limbs as the primary propulsive structures (Gillis and Blob 2001; Pace et al. 2001; Rivera et al. 2006). Given the significance of limb usage during the early stages of aquatic invasion for many groups of

vertebrates (Fish 1996; Smith and Clarke 2014), insights generated from studies of turtles should have broad relevance, even among non-shelled lineages.

Among vertebrates that use their appendages to swim, a major source of functional diversity arises from differences in the ways that taxa move their appendages. Taxa that have recently invaded aquatic habitats, or that still make frequent use of terrestrial habitats, typically move their limbs with predominantly anteroposterior (i.e., fore-aft) oscillations that include distinct recovery and power strokes, producing a rowing motion that broadly resembles patterns retained from terrestrial kinematics (Davenport et al. 1984; Fish 1996; Walker and Westneat 2000; Rivera and Blob 2010). However, taxa that have become highly specialized for life in water often show predominantly dorsoventral (i.e., up-down) oscillations of the limbs, producing flapping motions through which propulsive forces may be generated during both the up- and downstrokes (Vogel 1994; Walker and Westneat 2000; Rivera et al. 2013). Whereas rowing strokes have been shown to be advantageous for swimming that requires frequent turns and maneuvers, flapping has been found to be more energetically efficient than rowing regardless of swimming speed, providing an advantage for species that may need to conserve energy while swimming long distances (Walker and Westneat 2000).

Species that are specialized as flapping swimmers typically show a specialized morphology, in which the appendages taper distally to produce a wing-shaped structure (Walker 2002; Walker and Westneat 2002a, 2002b). Among tetrapods, such shapes are usually accompanied by elongation and flattening to produce a flipper shape that is often accentuated in the forelimbs (Rivera et al. 2013; Smith and Clarke 2014; Young and Blob 2015a). Whereas several advantages of flipper morphology and flapping kinematics among hyperspecialized swimmers have been identified (Walker and Westneat 2000, 2002a, 2002b; Walker 2002), the mechanisms that may have facilitated such transitions have remained less clear. Moreover, though impacts of swimming style on locomotor maneuverability have been proposed (Walker and Westneat 2000), less perspective is available on the complementary locomotor component of stability. Hydrodynamic stability is the ability to correct for external and self-generated disturbances during aquatic motion that can cause deviations from a given trajectory and, thereby, decrease locomotor efficiency (Webb 2002; Weihs 2002; Bartol et al. 2003). Since performance tradeoffs are often found between stability and maneuverability (Weihs 2002), it is

possible that the reduced maneuverability projected for flapping swimmers might correspond to increased stability.

In this article, we will review the studies we have conducted on the aquatic locomotion of turtles in our effort to understand (1) the mechanisms that facilitated evolutionary transitions in function from species “on the fence” between water and land to species that moved “all in” to aquatic habitats, and (2) the performance consequences of such functional changes. We will conclude with suggestions for future avenues along which insight might be gained into functional diversification in secondarily aquatic vertebrates.

Moving off the fence: mechanisms facilitating evolutionary change in limb structure and control during aquatic hyperspecialization in turtles

During aquatic locomotion, the use of flattened appendages as dorsoventrally flapping propulsors can facilitate continuous, energetically efficient thrust production that is advantageous for sustained, long-distance swimming (Vogel 1994; Walker and Westneat 2000, 2002a, 2002b; Walker 2002). The potential for such hydrodynamic advantages is clear once flipper-like morphology and flapping motions are present; however, species that secondarily invade aquatic habitats typically begin that process with very different patterns of limb structure and control (Fish 1996). Land-dwelling tetrapods generally have tubular, rather than flattened, limb bones; moreover, they also tend to move the limbs with predominantly anteroposterior, rather than dorsoventral, oscillations (Fish 1996). Thus, among turtle lineages that became hyperspecialized for aquatic propulsion, what factors may have promoted the evolution of flattened flippers from plesiomorphic, tubular limbs, and how was limb control reorganized to shift from anteroposterior to dorsoventral oscillations?

Limb bone loading and shape

Among terrestrial tetrapods, the shapes of bones often have a strong relationship with the patterns of loads to which they are exposed, responding to changes in loading environment over intervals ranging from within the life span of an individual, to the course of evolutionary time (Lanyon et al. 1982; Bertram and Biewener 1990; Blob et al. 2014). Given that the forces to which animals are exposed during locomotion differ substantially between water and land (Gillis and Blob 2001; Blob et al. 2003; Butcher and Blob 2008), we sought to test whether

changes in skeletal loading environment between swimming and walking might have facilitated an evolutionary transition from tubular to flattened limb bones (Young and Blob 2015a). To perform these tests, we compared *in vivo* strains on the femora of slider turtles (*Trachemys scripta*) between swimming in a flow tank and walking on a treadmill (Young and Blob 2015a). Following published protocols (Biewener 1992; Blob and Biewener 1999; Butcher et al. 2008; Aiello et al. 2013), strains were measured by surgically attaching strain gauges to the femur. These included single-element gauges, capable of measuring longitudinal strains aligned with the long axis of the bone (reflecting axial compression and bending), and rosette gauges, capable of measuring shear strains (reflecting torsional, or twisting, loads).

Our measurements showed that, overall, strains on the femur were much lower (by nearly 68%) during swimming than during walking (Young and Blob 2015a). This result was not surprising, because the buoyancy of turtles in water (Zug 1971) provides support for the weight of the body that the limb bones must provide on land (Butcher and Blob 2008; Butcher et al. 2008). However, specific comparisons of how torsional loads differed between habitats provided deeper insight into the potential mechanisms facilitating morphological change in the limb skeleton. Femoral shear strains for turtles are quite high during terrestrial walking (Butcher et al. 2008), but shear strain magnitudes during swimming were only approximately 10% of those during walking (Young and Blob 2015a) (Fig. 1A). This decrease was, in part, due to an overall reduction in loads between water and land, but it also related substantially to a change in load orientation. During swimming, peak principal strains showed an average orientation to the long axis of the femur (Φ_T) that was just over -6° , essentially in line with the shaft of the bone; however, during walking, Φ_T averaged nearly -20° , considerably closer to an absolute value of 45° that would indicate maximal torsion (Fig. 1B). *Trachemys scripta* swims using a rowing pattern of hind limb motion, in which the foot is rotated between a low-drag, feathered orientation during limb protraction, and a high-drag orientation perpendicular to flow that is used to generate thrust during retraction (Blob et al. 2008). Though it might have been expected that the femur would rotate about its long axis to contribute to this rotation of the foot during swimming strokes, our strain measurements indicate that, instead, axial rotation must be concentrated in the distal limb, because femoral twisting is drastically reduced in water

Fig. 1 Comparison of femoral shear strain (**A**) magnitudes and (**B**) orientation (Φ_T) between swimming and walking for *T. scripta* ($n=2$ individuals, 101 swimming limb cycles, 56 walking limb cycles). Shear is significantly lower during swimming, due at least in part to lower Φ_T that reflects a decrease in femoral twisting in water. Adapted from Young and Blob (2015a).

(Young and Blob 2015a). Our subsequent studies have, in fact, confirmed this inference through X-ray based analyses of femoral kinematics (Mayerl et al. 2016). Such reduction of twisting in the proximal limb bones of rowing swimmers could have facilitated the evolution of hydrodynamically advantageous limb bone flattening (Young and Blob 2015a). Tubular limb bones are advantageous for resisting torsional loads from twisting; however, the reduction of torsional loads would have released the limbs from a mechanical environment favoring tubular bones, potentially opening opportunities for the limb skeleton to diversify into hydrodynamically specialized morphologies. Thus, morphological change could only proceed after the invasion of a new habitat exposed turtles to a new mechanical environment.

Novelty and conservation of motor control for limb muscles

Among turtles, hyperspecialization for aquatic locomotion entailed not only changes in the structure of the limbs, but also changes in how the limbs were moved. The rowing strokes of species living “on the fence” between aquatic and terrestrial habitats are

broadly similar in kinematics to the steps they take on land, in that both involve predominantly antero-posterior movements of the limbs (Davenport et al. 1984; Fish 1996; Gillis and Blob 2001; Pace et al. 2001; Blob et al. 2008; Rivera and Blob 2010). However, flapping strokes of hyperspecialized taxa that have moved “all in” to aquatic habitats are reoriented from this plesiomorphic pattern, such that motion is predominantly dorsoventral (Davenport et al. 1984; Renous and Bels 1993; Wyneken 1997; Walker and Westneat 2000; Rivera et al. 2011a). How can such dramatic changes in patterns of limb motion arise?

In general, new locomotor modes might evolve through changes in morphology, changes in the activation patterns of controlling muscles, or a combination of these factors (Lauder and Reilly 1996; Rivera et al. 2011a; Rivera and Blob 2013). Though changes in muscle activation patterns might be expected to accompany dramatic changes in behavior, remarkably similar motor patterns have been found across taxa executing diverse ranges of feeding and locomotor behaviors in several cases (Jenkins and Weijs 1979; Jenkins and Goslow 1983; Peters and Goslow 1983; Goslow et al. 1989, 2000; Westneat and Wainwright 1989; Dial et al. 1991). These results contributed to the formalization of the “neuromotor conservation hypothesis,” which proposed that new behaviors might arise through evolutionary changes in structure, without accompanying changes in motor control patterns (Smith 1994). However, studies of neuromotor conservation in the locomotor system have focused primarily across different modes of terrestrial locomotion, and across transitions from walking to flight (Jenkins and Weijs 1979; Jenkins and Goslow 1983; Peters and Goslow 1983; Goslow et al. 1989, 2000; Dial et al. 1991).

To better understand the evolution of locomotor hyperspecialization among secondarily aquatic swimmers, we used electromyography to compare the activation patterns of major limb muscles across species of turtles using different patterns of limb motion during swimming (Rivera et al. 2011a; Rivera and Blob 2013). Following published protocols (Loeb and Gans 1986; Blob et al. 2008; Rivera and Blob 2010; Schoenfuss et al. 2010), we inserted bipolar, fine-wire electrodes to test the actions of five target muscles that, based on their anatomical positions (Walker 1973), were predicted to control all major planes of forelimb motion during swimming. These muscles included coracobrachialis (predicted humeral retractor), pectoralis (predicted humeral retractor and depressor), latissimus dorsi and deltoideus (predicted humeral protractors and elevators)

and the triceps complex (predicted elbow extensor). All muscle recordings were synchronized with high-speed video, allowing us to test how the activity of muscles contributed to specific limb motions (Rivera et al. 2011a; Rivera and Blob 2013). Our focal species included two rowing taxa (the slider *T. scripta* and the Florida softshell, *Apalone ferox*), one flapping taxon (the loggerhead sea turtle, *Caretta caretta*), and the pig-nosed turtle, *Carettochelys insculpta*. The pig-nosed turtle is the single living species remaining from a freshwater lineage related to softshells that, independent from sea turtles, evolved hypertrophied, superficially flipper-shaped forelimbs and which swims using a unique, hybrid pattern of forelimb movements intermediate between classically defined rowing and flapping (Rivera et al. 2013). Comparisons of forelimb muscle activity and kinematics across these taxa, therefore, allowed us to test the extent of neuromotor conservation across transitions from rowing to flapping by testing which, if any, forelimb muscles showed different patterns of activity across these locomotor modes, and whether such differences might be parallel across independent evolutions of aquatic hyperspecialization.

Our measurements showed that, for many forelimb muscles, activation patterns were highly conserved between flapping and rowing turtle taxa, with two major exceptions (Rivera et al. 2011a; Rivera and Blob 2013). First, although the primary bursts of activity for the pectoralis and triceps were concordant across all four taxa, the most terrestrial of our focal species (the slider, *T. scripta*) showed variable, secondary bursts for the triceps and pectoralis (Fig. 2). These differences cannot be attributed strictly to differences in the swimming modes of these taxa because they are present in only one of the two rowing species. Instead, they may reflect constraints on motor patterns associated with the retention of frequent terrestrial locomotion, as walking motor patterns in *T. scripta* (at least for triceps) also show two bursts of activity (Rivera and Blob 2010). The second major exception to the conservation of forelimb motor patterns across species of swimming turtles occurred in the activity patterns of the deltoideus. In both classically rowing taxa (*T. scripta* and *A. ferox*) the deltoideus is active during forelimb protraction, supporting its predicted role (Walker 1973) as a humeral protractor and elevator (Fig. 2). However, in flapping sea turtles (*C. caretta*), deltoideus activity has shifted to occur during forelimb retraction and depression (Fig. 2), potentially reflecting a shift in its functional role to one as a stabilizer against the simultaneous activity of the enlarged pectoralis of this taxon (Rivera et al.

2011a). Strikingly, the activity of deltoideus in the hybrid rower/flapper *C. insculpta* is intermediate in timing between that of flapping *C. caretta* and rowing *T. scripta* and *A. ferox* (Fig. 2). Thus, a shift in the activity pattern of the same muscle may be largely responsible for both independent shifts away from rowing kinematics among turtle lineages that are hyperspecialized for swimming locomotion in aquatic habitats (Rivera and Blob 2013). More broadly, these comparisons illustrate how novel locomotor modes can evolve through simple shifts in activation timing among a small subset of major muscles (Gillis and Blob 2001, Rivera and Blob 2013).

Performance consequences of specialization for aquatic locomotion in turtles

Morphological specializations and kinematic shifts to flapping propulsion in aquatic vertebrates have a number of documented and predicted impacts on locomotor performance, including improvements to top locomotor speed and energetic efficiency, but a reduction in locomotor maneuverability (Walker and Westneat 2000, 2002a, 2002b; Walker 2002). Such considerations of multiple axes of performance are crucial for understanding the emergence of functional transitions (Biewener 2002; Blob and Higham 2014) because, in many cases, improvements in one aspect of performance come at the detriment of others, leading to tradeoffs between performance components (Ghalambor et al. 2003, 2004; Walker 2007; Langerhans 2009; Blob et al. 2010). One such tradeoff that has received considerable attention in studies of aquatic locomotion is that between maneuverability and stability (Walker 2000; Fish 2002; Weihs 2002). Maneuverability is the ability to minimize the space required to execute a change in orientation (i.e., minimize the radius of a turning path: Howland 1974; Rivera et al. 2006), whereas stability is the capacity to resist forces that can generate changes from a path of movement (Webb 2002; Weihs 2002; Bartol et al. 2003). With one of these components entailing a change in locomotor direction, but the other resisting it, the potential for a tradeoff between the two is intuitive. Thus, flapping turtles, predicted to suffer low maneuverability, might be expected to benefit from enhanced stability (Dougherty et al. 2010; Rivera et al. 2011b). However, aquatic habitats are three-dimensional environments in which motion is possible in multiple directions. Could particular patterns of propulsor movement affect some directions of motion more than others? Moreover, are there structural

Fig. 2 Bar plot showing mean ($\pm$ S.E.M.) patterns of forelimb muscle activation during swimming in *C. insculpta* (black), *A. ferox* (white), *T. scripta* (gray, hatched = variable), and *C. caretta* (diagonals). Vertical lines demarcate switch from protraction/elevation to retraction/depression (solid = *Apalone/Trachemys*, dashed = *Carettochelys/Caretta*) based on maxima/minima of kinematics; a limb cycle is defined by the major plane of forelimb motion (start of protraction to end of retraction for *Apalone*, *Trachemys*, and *Carettochelys* and elevation followed by depression for *Caretta*). Adapted from Rivera and Blob (2013).

mechanisms that might help to enhance stability in turtles that do not use flapping propulsion?

Hydrodynamic stability in flapping versus rowing turtles

In aquatic environments, both external forces (e.g., turbulent flows) and internal forces (e.g., movements of the appendages or other propulsive structures) can destabilize animals and cause motion that is extraneous to their direction of travel (Hove et al. 2001; Bartol et al. 2002; Webb 2002). These motions include rotations such as pitch (rotation about the transverse axis of the body), yaw (rotation about the dorsoventral axis of the body), and roll (rotation about the longitudinal axis of the body), as well as translations such as heave (vertical displacement), sideslip (lateral displacement), and surge (anteroposterior displacement). Such extraneous motions can have a variety of detrimental consequences, from decreasing locomotor efficiency to inhibiting sensory perception (Fish 2002; Webb 2002; Weihs 2002). Selection for features that enhance locomotor

stability might, therefore, be expected in many aquatic species, particularly taxa such as sea turtles that commonly engage in long-distance migrations (Musick and Limpus 1997; Plotkin 2003). Some inferences about the hydrodynamic stability of swimming sea turtles have been proposed (Walker 1971a; Davenport et al. 1984; Avens et al. 2003), but it is unclear whether flapping sea turtles might show improved or reduced stability in comparison to other species of turtle that use the plesiomorphic pattern of rowing limb motions. Such comparisons are key to understanding the consequences of locomotor hyper-specialization. Given that the primary planes of limb motion differ between flapping (dorsoventral) versus rowing (anteroposterior), sea turtles might not show enhanced stability in all directions, compared to rowing species.

To test for potential differences in hydrodynamic stability between flapping and rowing turtles, we collected high-speed video from posthatchlings of two species of sea turtle (loggerheads, *C. caretta*, and green turtles, *Chelonia mydas*), as well as juveniles

from one species of emydid turtle that swims using rowing motions of the limbs (painted turtles, *Chrysemys picta*) (Dougherty et al. 2010; Rivera et al. 2011b). Turtles (all similar in size) were trained to chase a prey stimulus, which was attached to a vertical sting that could be manually slid along a track suspended over a water-filled tank. As we slid the stimulus along a straight path, we recorded and measured deviations of turtles from a straight swimming path in lateral and ventral views (Dougherty et al. 2010; Rivera et al. 2011b).

We found that, in contrast to simple expectations based on a potential tradeoff between maneuverability and stability, rowing painted turtles were actually more stable than either species of flapping sea turtle for six out of eight parameters that we compared (Fig. 3). Several factors may contribute to these results, relating primarily to the different patterns of limb movements that power these two modes of propulsion. With primarily anteroposterior limb movements, rowing turtles experience limited heave (dorsoventral translation) compared to dorsoventrally flapping turtles. In addition, because hyperspecialized flapping turtles only use the forelimbs (at the front of the body) to propel swimming, they experience greater pitch rotations than rowing turtles that swim using all four limbs. Moreover, rowing turtles also appear to be able to limit sideslip (lateral translations) by coordinated phasing of contralateral forelimb and hind limb movements. Such lateral stability may be difficult to achieve in sea turtles, in which it would require precise synchronization of both the speed and orientation of the bilaterally flapping forelimbs (Dougherty et al. 2010; Rivera et al. 2011b). It is important to acknowledge that our comparisons are based on a small number of species, and that taxa with different foraging strategies, or individuals of different sizes (e.g., adult sea turtles), could show different patterns of stability. Nonetheless, tradeoffs between stability and maneuverability may not be simple to predict across species of swimming turtles, and some performance advantages of locomotor hyperspecialization in flapping turtles may be balanced by costs in other aspects of performance.

Impacts of pelvic-shell fusion on the locomotion of pleurodiran turtles

Across turtle clades, sea turtles show some of the most dramatic specializations for living primarily in water. However, many freshwater lineages also have moved “off the fence,” showing varying degrees of preference for living in aquatic habitats, and exhibiting a range of associated specializations of the

locomotor system (Blob et al. 2008). For example, in highly aquatic trionychid (softshell) turtles, webbing is elaborated in the forefeet as well as in the hindfeet, and the rowing motions of the forelimbs nearly match those of the hind limbs in efficiency (Pace et al. 2001; Blob et al. 2008). In another example (Rivera and Blob 2013; Rivera et al. 2013), the pig-nosed turtle (*C. insculpta*) exhibits forelimb hypertrophy and distinct patterns of limb kinematics and muscle activity during swimming that relate to its aquatic specialization (as noted earlier in this article).

In such a context, other specializations of the limbs and associated structures of highly aquatic freshwater turtles also might be considered with regard to their potential impacts on locomotor function. We are currently pursuing such studies through comparisons of aquatic and terrestrial locomotion between cryptodiran and pleurodiran turtles (Mayerl et al. 2016). These clades represent the primary phylogenetic division among extant turtle lineages (Barley et al. 2010), and their species differ in their most common locomotor habitat. In addition to encompassing “all in” aquatic hyperspecialists such as sea turtles and *C. insculpta*, cryptodires also include multiple highly terrestrial lineages; in contrast, pleurodires are virtually all primarily aquatic (Bonin et al. 2006). Pleurodires also possess a number of derived anatomical traits in comparison to cryptodires. With respect to the locomotor system, in pleurodires the pelvis is fused to both the carapace (dorsal portion of the shell) and plastron (ventral portion of the shell); in contrast, in cryptodires the pelvis connects to the shell via a sliding joint between the ilium and sacrum, and via a ligamentous connection between the pubis and ischium and the interior of the plastron (Walker 1973). The consequences of these structural differences for locomotion are not clear. Reducing pelvic mobility might enhance locomotor stability in pleurodires, which could be advantageous for swimming performance in a lineage that is primarily aquatic. However, with the pelvis housed inside a bony shell in all turtles, pelvic mobility might be limited for all turtle species (Walker 1971b), providing little support for an association between this trait and locomotor performance.

To begin assessing how structural differences between cryptodires and pleurodires might relate to their differing degrees of specialization for aquatic locomotion, we used marker-based X-ray Reconstruction of Moving Morphology (XROMM; Brainerd et al. 2010) to compare pelvic mobility and femoral motion during walking and swimming

Fig. 3 Box-plots comparing values of body stability for eight focal parameters with results of pair-wise nested ANOVAs. (A) Maximum heave magnitude. (B) Heave excursion. (C) Maximum pitch magnitude. (D) Pitch excursion. (E) Maximum sideslip magnitude. (F) Sideslip excursion. (G) Maximum yaw magnitude. (H) Yaw excursion. Species compared are: painted turtles (CP; $n=96$), logger-head turtles (CC; $n=120$), and green turtles (CM; $n=72$). Boxes enclose the median (centerline) and the 25th and 75th percentiles (bottom and top of boxes, respectively). Whiskers indicate the 10th and 90th percentiles; circles indicate the 5th and 95th percentiles. Light gray lines indicate the mean. Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; NS, not significant. Endpoints of horizontal lines indicate species used in each test. Sequential Bonferroni correction did not alter significance of pair-wise comparisons. Adapted from Rivera et al. (2011b).

between representative species of cryptodire (*Pseudemys concinna*) and pleurodire (*Emydura subglobossa*) turtles that both regularly inhabit aquatic environments (Mayerl et al. 2016). The pelvis, femur, and shell of each individual were implanted with radio-opaque beads, and animals were filmed during swimming and walking using biplanar X-ray video. Markers were tracked from videos using XMALab software (open source; bitbucket.org/xromm/xmalab). These data were coordinated with computed tomography (CT)-derived models of the bones in Maya (Autodesk Inc., San Rafael, CA, USA), allowing the calculation of three-dimensional movements of the pelvis and femur with respect to the shell, and of the femur with respect to the pelvis.

In contrast to earlier X-ray observations that suggested little movement of the pelvis in walking cryptodires (Walker 1971b), our XROMM data indicated substantial pelvic movement in cryptodires during both walking and swimming (Fig. 4). This was particularly evident for lateral (yaw) rotations, which showed values of nearly 20° for walking and 10° for swimming per cycle, comparable to pelvic motions in many non-shelled taxa (Jenkins 1971; Gatesy 1991; Pridmore 1992; Reilly and Delancey 1997; Russell and Bels 2001; Nyakatura et al. 2014). In contrast, the pleurodire pelvis was essentially immobile in both locomotor environments (Fig. 4). These differences in pelvic movement also contributed to cryptodires having greater femoral protraction in both walking and swimming when compared to pleurodires (Mayerl et al. 2016). In light of these results, we are now pursuing comparisons of hydrodynamic stability and maneuverability between these taxa, to evaluate if the functional consequences of this structural feature might enhance an aspect of pleurodire locomotor performance that facilitated their specialization for aquatic habitats (Mayerl et al. 2015).

Perspectives and directions for future research

Even within the constraints imposed by a body design encased by a shell, turtles exhibit diverse locomotor capacities that have enabled diversification into a wide range of aquatic habitats. The studies we have conducted point the way toward further work that can help to clarify both the mechanisms through which secondary aquatic locomotor specializations evolve, and the consequences of variations in design for aquatic locomotor performance.

Some direct extensions of our previous work could facilitate deeper insight into secondary

specialization for aquatic locomotion. For example, our measurements of skeletal loading during swimming have focused (thus far) on the hind limb (Young and Blob 2015a), but nearly all tetrapods that are hyperspecialized for flapping propulsion in water exhibit hypertrophy of the forelimbs. Measurements of forelimb loading during swimming could provide useful perspective for understanding how loading influences the skeletal design of swimming tetrapods (Young and Blob 2015b). In addition, our XROMM data comparing pelvic mobility between cryptodiran and pleurodiran turtles (Mayerl et al. 2016) sets the stage for direct comparisons of aquatic stability and maneuverability between these lineages (Mayerl et al. 2015).

Beyond these direct extensions of our work, many other lines of research on turtle locomotion hold promise for generating novel insights into the evolution and diversification of secondary locomotor specializations for aquatic habitats. For example, turtles are unusual among secondarily aquatic lineages in that multiple clades (e.g., tortoises, box turtles) have returned to primarily terrestrial habits (Gosnell et al. 2009). Comparisons of how different terrestrial lineages swim could provide insight into the extent to which primitive functions are retained through evolutionary transformations. In addition, whereas most studies of aquatic locomotor function in vertebrates focus on swimming, multiple lineages of turtles that have moved primarily into aquatic habitats (e.g., kinosternids, chelydrids) largely eschew swimming and, instead, mainly walk along the bottoms of lakes and rivers (Zug 1971; Willey and Blob 2004). The performance and control of underwater walking, as well as the factors that contribute to such behavioral preferences, have received little attention in studies of secondary aquatic specialization. Furthermore, though considerable research has focused on aquatic hyperspecialization, living ‘on the fence’ between water and land has its own specialized demands that have received limited attention (Fish 1996; Gillis and Blob 2001; Blob et al. 2008). Species with only moderate levels of aquatic specialization might retain terrestrial capacities without a significant decline in performance, but that performance could incur greater costs. For example, softshell turtles have moved further off the fence, into aquatic habitats, than sliders, but are able to move over land equally (or more) quickly. However, comparisons of limb kinematics show that to achieve such performance, softshells must extend their legs to positions that may place their limb muscles at lengths that are longer than optimal for efficiently generating force (Blob et al. 2008).

Fig. 4 (A, B) X-ray images of turtles during locomotion. (A) Cryptodire (*P. concinna*) walking, lateral view. (B) Pleurodire (*E. subglobossa*) swimming, ventral view. Blue dots indicate markers on the pelvis, red dots indicate markers on the femur, and green dots are markers located on the shell (carapace and plastron). (C–F) Pelvic girdle rotations in cryptodire (*P. concinna*) and pleurodire (*E. subglobossa*) turtles during walking and swimming. Solid lines represent mean traces for each motion, shading represents standard errors for each motion, and colors indicate different axes of rotation (black = roll; blue = pitch; red = yaw). Traces were normalized to the same duration. Vertical dashed lines represent the transition from stance to swing (walking) or from stroke to recovery (swimming). (C) Cryptodire pelvic rotations while walking ($n=3$ individuals, 54 cycles). (D) Pleurodire pelvic rotations while walking ($n=2$ individuals, 35 cycles). (E) Cryptodire pelvic rotations while swimming ($n=3$ individuals, 30 cycles). (F) Pleurodire pelvic rotations while swimming ($n=2$ individuals, 18 cycles). Adapted from Mayerl et al. (2016).

Through future studies of such topics and others, studies of turtle locomotion have strong potential to provide deeper understanding of the patterns and processes of adaptive functional diversification through evolutionary transitions in habitat.

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