

SHORT COMMUNICATION

A novel, bounding gait in swimming turtles: implications for aquatic locomotor diversity

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ABSTRACT

Turtles are an iconic lineage in studies of animal locomotion, typifying the use of slow, alternating footfalls during walking. Alternating movements of contralateral limbs are also typical during swimming gaits for most freshwater turtles. Here, we report a novel gait in turtles, in which the pleurodire *Emydura subglobosa* swims using a bounding gait that coordinates bilateral protraction of both forelimbs with bilateral retraction of both hindlimbs. Use of this bounding gait is correlated with increased limb excursion and decreased stride frequency, but not increased velocity when compared with standard swimming strokes. Bounding by *E. subglobosa* provides a second example of a non-mammalian lineage that can use bounding gaits, and may give insight into the evolution of aquatic flapping. Parallels in limb muscle fascicle properties between bounding turtles and crocodylids suggest a possible musculoskeletal mechanism underlying the use of bounding gaits in particular lineages.

KEY WORDS: Locomotion, Biomechanics, Reptile, Fascicle length, Limb muscle

INTRODUCTION

Comparative studies of animal locomotion rely on several parameters to characterize patterns of movement. One of the most fundamental of these is the gait, or the sequence in which propulsive structures interface with the substrate (Goiffon and Vincent, 1779). Early photographic studies set the stage for systematically distinguishing different gaits based on quantifiable criteria (Muybridge, 1887), such as the order of footfalls and their temporal overlap (Hildebrand, 1976). Animals may transition between gaits to minimize energy consumption across changes in speed (Hoyt and Taylor, 1981), or to reduce peak forces on the musculoskeletal system (Farley and Taylor, 1991). Anatomical factors, such as muscle structure, may also help determine what gaits an animal can use (Taylor, 1978; Allen et al., 2014). Investigating how these factors govern gait usage has facilitated understanding of the basic patterns underlying gait preferences and speed changes in vertebrates (Reilly and Biknevičius, 2003).

A primary distinction among categories of gaits in tetrapods is between those that are symmetrical (such as the walk), versus those that are asymmetrical (such as the gallop) (Hildebrand, 1976). Symmetrical gaits can be identified as those with footfalls of the left–right limb pairs evenly spaced in time, whereas in asymmetrical gaits, footfalls are unevenly spaced in time (Hildebrand, 1976, 1980; Reilly and Biknevičius, 2003). Though mammals were long

thought to be the only lineage capable of using asymmetrical gaits (Reilly and Biknevičius, 2003), several species of crocodylians have also been observed to gallop (Webb and Gans, 1982), including bounding gallops in which the left and right forelimbs are extended together, followed by simultaneous extension of the left and right hindlimbs (Renous et al., 2002). Within crocodylians, galloping has been observed in crocodylids as well as gharials (Whitaker and Andrews, 1988), but not in alligatorids (Allen et al., 2014). One factor that has been proposed to contribute to the distribution of this trait among crocodylians is that crocodylids have longer limb muscle fascicles than alligatorids, potentially facilitating rapid limb excursions that would enable galloping (Allen et al., 2014).

Characterization of gaits has also been extended to aquatic locomotion (Webb, 1994; Drucker, 1996; Hove et al., 2001; Liao et al., 2003). Moreover, species that use appendages to power swimming can be categorized along a continuum from rowing to flapping (Davenport et al., 1984; Walker and Westneat, 2000; Rivera et al., 2013). Among tetrapod swimmers, rowing species typically use anteroposterior movements of all four limbs with simultaneous retraction and protraction of the contralateral forelimbs and hindlimbs; in contrast, flapping involves synchronous, dorsoventral movements of the forelimbs, with the hindlimbs contributing primarily to steering (Davenport et al., 1984). Rowing is regarded as the primitive pattern of limb movements in swimming tetrapods, in part because of its resemblance to the patterns of limb motion during symmetrical walking gaits on land (Fish, 1996; Blob et al., 2016).

Turtles are an iconic group for the characterization of both terrestrial and aquatic patterns of limb movements. On land, they exemplify the use of slow, alternating footfalls (Walker, 1971; Zug, 1971; Zani et al., 2005), and in water they include rowing and flapping species (Davenport et al., 1984; Wyneken, 1997; Rivera et al., 2013; Blob et al., 2016). Rowing species are characterized by using the equivalent of a diagonal sequence walk, where contralateral limbs operate together (Zug, 1971; Renous et al., 2008). However, during measurements of swimming performance by the pleurodire turtle *Emydura subglobosa*, which we collected during studies of their limb muscle function (Mayerl et al., 2017), we observed a novel pattern of limb movements that closely resembles the patterns of limb motion exhibited by bounding crocodylians and mammals (Movie 1). Our first goal in this study was to characterize this behavior and test for its impact on performance. We predicted that bounding limb cycles would be used at faster locomotor speeds. Our second goal was to evaluate potential anatomical features that might contribute to the ability of *E. subglobosa* to perform a behavior not previously reported for other turtles. Because previous work has shown that crocodylians capable of bounding gaits have longer fascicle lengths in their limb muscles (Allen et al., 2014), we hypothesized that *E. subglobosa* will have longer limb muscle fascicles than species of turtles that do not exhibit a bounding gait. Finally, we discuss potential

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implications of the presence of this gait in turtles for their locomotor evolution.

MATERIALS AND METHODS

Four pink-bellied sideneck turtles, *E. subglobosa* (Krefft 1876) (carapace length, 181.5±5.17 mm) were purchased from a commercial vendor (Turtles and Tortoises, Inc., Brooksville, FL, USA). Turtles were housed in stock tanks in a temperature-controlled greenhouse and fed turtle pellets *ab libitum*. Kinematic data were collected in a flow tank using biplanar high-speed (100 Hz) video with high-contrast joint markers (see Rivera et al., 2011, for details on points tracked). The speed of the flow tank was adjusted per trial to match turtle-selected velocities [approximately 2 body lengths (BL) s⁻¹] so that multiple kinematic sequences could be recorded per trial. Landmarks were tracked using DLTDDataViewer5 (Hedrick, 2008), and the resulting 2D coordinate data were processed using custom-written MATLAB routines to determine kinematic excursions (protraction and retraction) of the forelimbs and hindlimbs during swimming (Rivera and Blob, 2010). For both limbs, an angle of 0 deg represents a limb directed anteriorly, parallel with the midline of the body, and an angle of 90 deg indicates a limb perpendicular to the midline. These variables were then processed through a quintic spline to interpolate the data to values representing 0–100% of the limb cycle so that kinematic profiles for locomotor cycles of different absolute durations could be compared (Rivera et al., 2013; Mayerl et al., 2016). All animal care and experimental procedures were approved by the Institutional Animal Care and Use Committee (IACUC) at Clemson University (2013-051).

Locomotor velocity, limb excursions, cycle durations and limb angular velocity were compared between gaits using linear mixed effects models (Bates et al., 2015). A representative limb angular velocity was calculated for each trial by dividing the excursion of the left forelimb by the duration of its cycle. We used gait as a fixed effect, and individual and trial (intercept varying within trial) as random effects [$X \sim \text{species} + (1|\text{individual}/\text{trial})$]. For all statistical analyses, effect sizes were calculated using the R package *effsize* (<https://CRAN.R-project.org/package=effsize>). *P*-values were obtained by likelihood ratio tests of the full model with the effect in question against the model without the effect in question, and were considered significant at $P < 0.05$. Statistical analyses were performed in R (v 3.2.1, www.r-project.org), and variation within the data is reported as standard error of the mean (s.e.m.).

To compare muscle fascicle lengths, we collected fascicle length measurements for the hip muscles of six previously euthanized *E. subglobosa* and six *Trachemys scripta*, a representative semiaquatic cryptodire turtle in which bounding has never been reported (Pace et al., 2001; Blob et al., 2008; Mayerl et al., 2017). To collect these data, we dissected out the hip muscles with the femur at 90 deg and the knee extended, and used digital calipers to measure the length of fascicles at the center of the muscle when it was laid flat on a dissecting tray (Butcher and Blob, 2008). Fascicle lengths were standardized to body size by dividing fascicle length by femur length. Muscles measured include caudi-iliofemoralis (CIF), flexor tibialis internus (FTI), puboischiofemoralis internus (PIFI) and iliofemoralis (ILF), which are the muscles primarily responsible for hip retraction (FTI, CIF) and protraction (PIFI, ILF) (Mayerl et al., 2017). We were unable to collect fascicle data from forelimb muscles as these were, unfortunately, no longer available for the specimens we were able to dissect. Fascicle lengths were compared using linear mixed effects models (Bates et al., 2015), with species as a fixed effect and individual as a random effect [$X \sim \text{species} + (1|\text{individual})$].

RESULTS AND DISCUSSION

Emydura subglobosa used standard rowing for most swimming strokes (Mayerl et al., 2017), in which the left forelimb and right hindlimb were retracted for the first half of the cycle, while the right forelimb and left hindlimb were protracted (Fig. 1B). This is similar to the limb coordination of aquatic freshwater cryptodire turtles, and is characterized as a diagonal sequence gait (Zug, 1971; Renous et al., 2008). However, all four *E. subglobosa* also exhibited the novel swimming gait, which occurred in 10% of trials ($n=11$ of 110). In contrast to both rowing and flapping observed previously in turtles, during the novel gait the forelimbs were retracted while the hindlimbs were protracted (Fig. 1A), resembling the two-step gallop, or bound, reported for juvenile freshwater crocodiles (Renous et al., 2002). Among the four turtles, we observed four bounds from one individual, two from another two, and three from the last turtle. Two instances of bounding were single limb cycles, with the other nine consisting of two to three consecutive cycles before returning to standard rowing swimming. These gaits occurred as the turtles swam without external perturbation. Both the duration and excursion of limb movements also differed between rowing and the novel, bounding gait. During rowing, retraction occurred for 41% of the limb cycle in the hindlimbs and 45% in the forelimbs, whereas during bounding, retraction in the hindlimbs still occurred over 41% of the cycle, but the forelimbs were retracted for 68% of the cycle (Fig. 1). Limb protraction/retraction excursion for both the forelimbs and hindlimbs was also ~20 deg (and ~20%) greater during bounding than during rowing (Fig. 2, Table 1).

Use of bounding gaits was not correlated with velocity, as turtles swam slightly faster than the flow at equivalent speeds during both bounding (2.59±0.05 BL s⁻¹) and rowing (2.66±0.06 BL s⁻¹; Cohen's $d=-0.18$, $P=0.58$). Similarly, yaw excursion was similar between bounding (10.51±2.13 deg) and rowing (11.40±1.92 deg; Cohen's $d=-0.05$, $P=0.88$). However, bounding cycles took nearly two times longer to complete (0.55±0.03 s) than rowing cycles (0.26±0.02 s; Cohen's $d=4.99$, $P<0.001$). Because of the increased duration of bounding strokes, the limb moved more slowly during bounding (227.42±11.26 deg s⁻¹) than during rowing (390.80±5.30 deg s⁻¹, $P<0.001$, Cohen's $d=-1.54$), even though limb excursion was also greater during bounding than during swimming (Fig. 2, Table 1). Fascicle lengths were substantially greater in *E. subglobosa* than in *T. scripta* for all four muscles compared (Cohen's $d>0.8$; Table S1).

Emydura subglobosa can use a pattern of propulsive limb movements during swimming that is novel among turtles, coordinating simultaneous protraction of the two forelimbs with simultaneous retraction of the two hindlimbs to produce a gait that resembles the bound exhibited by terrestrial mammals and crocodylids. The scope of such similarities, however, should be qualified. For example, unlike crocodylids and mammals, turtles cannot incorporate axial flexion into bounding gaits, because of the fusion of their dorsal vertebrae to the shell; moreover, crocodylids do not use bounding gaits in water, and turtles have not been observed to use them on land. Nonetheless, our study builds upon a growing body of work indicating that a dichotomous classification of appendicular propulsion in water as either 'rowing' or 'flapping' likely oversimplifies the complex range of behaviors that animals use to generate aquatic thrust (Feldkamp, 1987; Walker and Westneat, 2000; Rivera et al., 2013; Davenport et al., 2016; Mayerl et al., 2017; Young et al., 2017). The identification of a bounding gait in turtles also demonstrates flexibility in motor control of the limbs in turtles

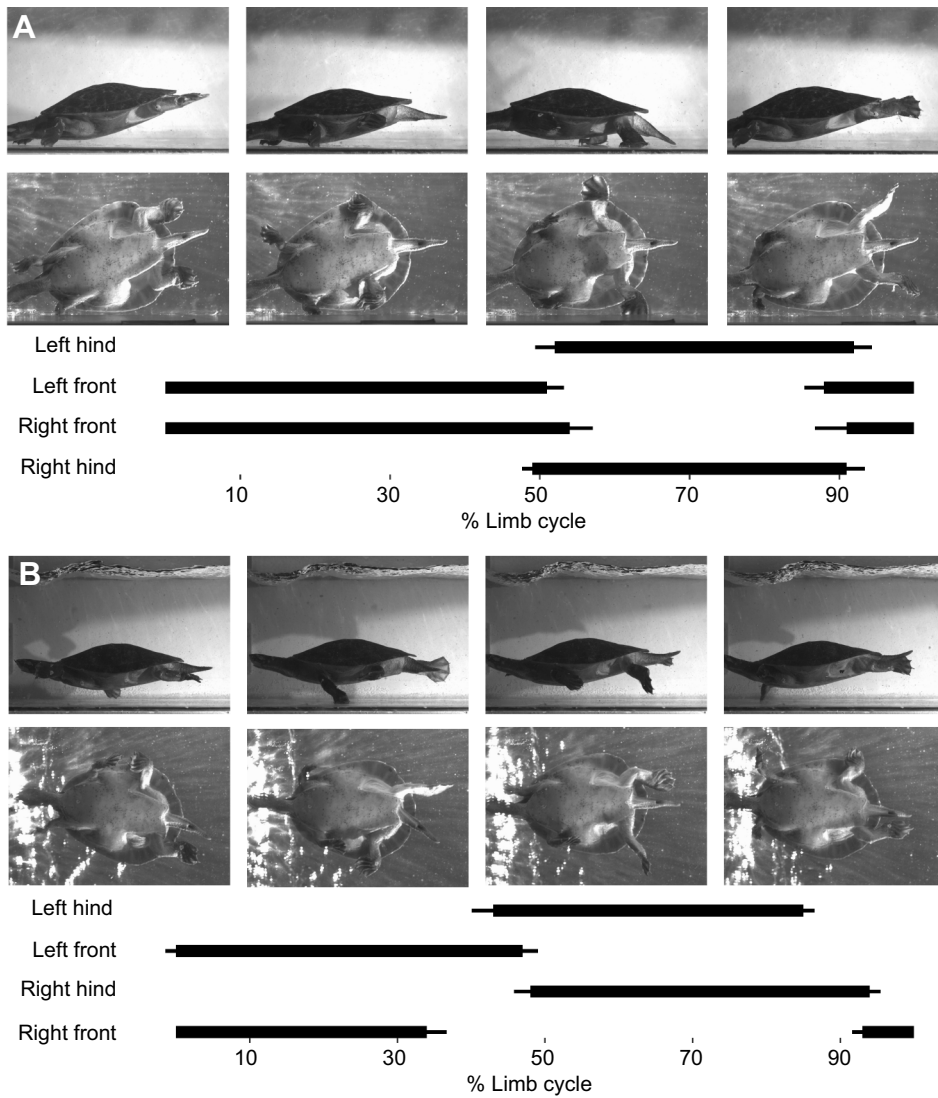


Fig. 1. Mean duration of retraction for each limb throughout a swimming cycle in *Emydura subglobosa*. (A) Bounding ($N=11$). (B) Rowing ($N=99$). Images represent kinematic patterns at 0%, 25%, 50% and 75% of a cycle.

(Blob et al., 2008; Rivera and Blob, 2010; Mayerl et al., 2017). This pattern of limb movement might have been coopted from other behaviors, such as diving from basking surfaces into the water when startled.

Although bounding involved slower limb movements and longer cycle durations than rowing strokes, whole-body velocity was similar for the two locomotor patterns. To produce a similar speed with slower movements, greater forward thrust should be generated during limb retraction in bounding than in rowing. This context also

provides a framework for considering potential factors in the evolution of flapping propulsion from rowing, as flapping turtles are characterized by simultaneous movement of the forelimbs (Renous et al., 2008; Blob et al., 2016). Bilateral forelimb flapping is typically regarded as advantageous for sustaining high-speed swimming already in progress (Walker and Westneat, 2000). The occurrence of bounding gaits in *E. subglobosa* suggests the possibility that evolutionarily early uses of bilateral forelimb stroking could have related primarily to producing high force

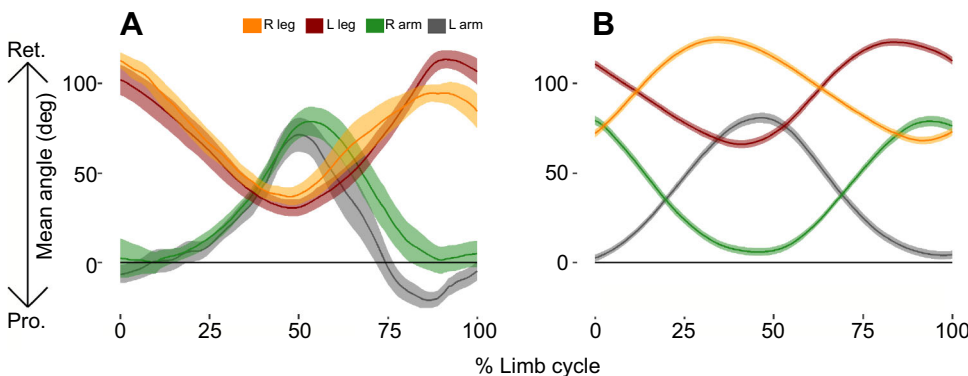


Fig. 2. Mean protraction/retraction excursion of limbs throughout the swimming cycle in *E. subglobosa*. (A) Bounding ($N=11$). (B) Typical rowing ($N=99$). Lines are mean values, with shaded areas indicating s.e.m. Forelimb and hindlimb kinematics are synchronized in A, whereas contralateral forelimbs and hindlimbs are synchronized in B. Ret., retraction; Pro., protraction.

Table 1. Mean±s.e.m. protraction/retraction excursion during bounding and rowing in *Emydura subglobosa*

Limb	Bounding (deg)	Rowing (deg)	Cohen's <i>d</i>	<i>P</i>
Left fore	123.63±6.04	97.98±1.96	1.26	<0.001
Right fore	113.99±5.98	97.78±1.74	0.89	0.009
Left hind	98.66±6.32	75.20±1.43	1.51	<0.001
Right hind	90.45±5.05	77.21±1.17	1.05	0.002

Turtles exhibit significantly greater excursion for all limbs during bounding ($N=11$) than during rowing ($N=99$).

swimming strokes, rather than sustained swimming (Walker and Westneat, 2000).

The novel recognition of aquatic bounding in *E. subglobosa* may relate to previous biases in available kinematic data for swimming turtles: whereas *E. subglobosa* belongs to the pleurodire lineage, all previous locomotor data from turtles have been collected from the other major turtle lineage, the cryptodires (Davenport et al., 1984; Rivera et al., 2013; Young et al., 2017). Structural differences in the musculoskeletal system of these lineages may provide an explanation for why no cryptodire has been observed to gallop. Pleurodire turtles possess a novel fusion of the pelvic girdle to the shell that has resulted in the hip muscles shifting in their origin from the pelvis to the shell (Walker, 1973; Mayerl et al., 2017). This change in muscle leverage is correlated with the greater fascicle lengths of hindlimb muscles that power femoral movements in a bounding pleurodire than in a non-bounding cryptodire (Table S1). As pelvic girdle fusion and the subsequent change in muscle architecture is a synapomorphy of pleurodire turtles, we expect that longer muscle fascicle lengths relative to cryptodires may be a common feature in the clade, at least within the hindlimb.

Muscle fascicle length determines the distance over which a muscle may contract and underlies several biomechanical principles of muscle function, with longer fascicles enabling the use of a larger range of contraction (Allen et al., 2014). Large arcs of limb motion are thought to be a key feature of asymmetrical gaits in crocodylids (Renous et al., 2002), which are the only other non-mammalian lineage that has been documented to use asymmetrical gaits. Within crocodylians, those species that use these gaits (crocodylids) have longer muscle fascicles than those that do not (alligatorids) (Allen et al., 2014). As with crocodylians, we found that the use of an asymmetrical gait in turtles coincided with greater limb excursion. Although our data are only from a single species within each lineage, the similarities in kinematics (having larger limb excursions) and muscle architecture (having longer hindlimb muscle fascicle lengths) observed between bounding turtles and crocodylians is consistent with the conclusion of Allen et al. (2014) that longer muscle fascicle lengths may provide an anatomical mechanism that can facilitate the use of bounding gaits in reptiles.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: C.J.M.; Methodology: C.J.M.; Software: C.J.M.; Formal analysis: C.J.M.; Investigation: C.J.M.; Data curation: C.J.M.; Writing - original draft: C.J.M.; Writing - review & editing: C.J.M., R.W.B.; Visualization: C.J.M.; Supervision: R.W.B.; Funding acquisition: C.J.M., R.W.B.

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Data availability

Data are available from the Dryad Digital Repository (Mayerl and Blob, 2017): <http://dx.doi.org/10.5061/dryad.r5v8d>

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.164103.supplemental>

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Table S1. Hip muscle fascicle lengths standardized by femur length for *E. subglobosa* (N = 6) and *T. scripta* (N = 6).

Muscle	<i>E. subglobosa</i>	<i>T. scripta</i>	P	D
CIF	1.034 ± 0.059	0.847 ± 0.066	0.035	1.215
FTI	1.468 ± 0.114	1 ± 0.062	<0.001	2.079
ILF	0.999 ± 0.114	0.818 ± 0.059	0.16	0.81
PIFI	1.103 ± 0.059	0.786 ± 0.072	<0.001	1.949

CIF: Caudi-iliofemoralis; FTI: Flexor tibialis internus; ILF: Iliofemoralis; PIFI: Puboischiofemoralis internus.

Bolded values are those which show a large effects size.



Movie S1. Example of two bounds played at 50% speed.