Biomechanical Factors Influencing Successful Self-Righting in the Pleurodire Turtle, *Emydura subglobosa*

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Summary statement – Success in self-righting freshwater turtles is determined primarily by the velocity of the attempt and the moment exerted by the head during self-righting efforts.

Abstract

Self-righting performance is a key ability for most terrestrial animals, and has been used as a metric of fitness, exhaustion, and thermal limits in a variety of taxa. However, there is little understanding of the underlying mechanisms that drive variation in self-righting performance. To evaluate the mechanical factors that contribute to success versus failure when animals attempt to self-right, we compared force production and kinematic behavior in the rigid-bodied, pleurodire turtle *Emydura subglobosa* between successful and unsuccessful self-righting efforts. We found that the moment exerted during efforts to roll the body and the velocity of that roll are the primary drivers behind self-righting success. Specifically, turtles that self-righted successfully produced both larger moments and faster rolls than turtles that failed. In contrast, the angle at which the head was directed to lever the body and the extent of yaw that was incorporated in addition to roll had little impact on the likelihood of success. These results show that specific performance metrics can predict the ability of animals to self-right, providing a framework for biomimetic applications as well future comparisons to test for differences in self-righting performance across animals from different environments, sexes, populations, and species.

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Introduction

Self-righting, or the ability of an animal to recover from an inverted position, is a critical function for many animals. In terrestrial settings, inverted animals may risk stranding, exposure, or increased predation if they cannot right themselves in a timely fashion. In this context, performance during self-righting has been considered as a factor related to fitness in several invertebrate and vertebrate taxa (e.g. Penn and Brockman, 1995; Delmas et al., 2007; Jusufi et al., 2008; Jusufi et al., 2011; Porter et al., 2011; Kaspari et al., 2016; Mitchell et al., 2016). For example, better self-righting performance has been linked to greater rates of survival in horseshoe crabs (Penn and Brockman, 1995) and higher fitness in turtles (Steyermark et al., 2001; Delmas et al., 2007).

Self-righting performance depends on both the shape and flexibility of the body. Animals with flexible bodies can twist and bend their anterio-posterior body axis to self-right (Jusufi et al., 2011; Evangelista et al., 2014; Singleton and Garland, 2018); however, animals with rigid bodies (e.g. beetles, crabs, turtles) cannot execute such movements. Self-righting can be particularly important for many rigid-bodied animals because they are often forced into procumbent positions through competition, predation attempts, or falls during the navigation of complex environments (Penn and Brockman, 1995; Mann et al., 2006; Golubović et al., 2013).

With their limited axial mobility, rigid animals employ a variety of alternative strategies to flip over. For example, beetles exhibit approximately 20 different, stereotyped self-righting behaviors, depending on the species (Frantsevich, 2004), and locusts rely on their large hindlegs to self-right (Faisal and Matheson, 2001). Turtles use a variety of strategies that are thought to

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be primarily dependent on shell morphology, which itself is strongly correlated with the habitat in which species live. In terrestrial taxa such as tortoises, the carapace (top of the shell) is typically domed, and turtles use a strategy primarily involving movements of the limbs to shift the center of mass and induce rolling of the body (Ashe, 1970; Chiari et al., 2017). However, in aquatic species with a flatter, more streamlined carapace, structures such as the limbs and head (though typically not the tail, which is reduced in most turtles) may be able to reach the ground and act as levers to flip the body (Ashe, 1970).

Previous studies have evaluated how various morphological factors influence self-righting in turtles, often through comparisons of how long it takes until an attempt is made (latency), or how long it takes until an attempt is successful (duration) (Mann et al., 2006; Delmas et al., 2007; Domokos and Varkonyi, 2008; Golubović et al., 2013; Mitchell et al., 2016; Chiari et al., 2017). However, this approach only provides insight into the correlation between morphological variation and the end-product of the self-righting behavior. An understanding of the actual mechanics that drive success *versus* failure during a righting attempt is still lacking. Such an understanding could establish a predictive framework of which factors, among many possible movements and exerted forces, are most likely to contribute to righting success and its critical consequences. To evaluate such factors, we used force-platform recordings synchronized with high-speed video to compare the magnitude and orientation of forces produced between successful and unsuccessful righting attempts by the pink-bellied side-neck turtle *Emydura subglobosa*, a pleurodire that primarily uses its head to flip. We predicted that during successful attempts the head would limit antero-posteriorly directed forces and, instead, exert consistently greater moments to produce roll about the long axis of the body.

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Investigating these factors represents a promising avenue for bettering our understanding of self-righting in rigid-bodied animals and provides a framework for investigating the processes governing this behavior.

Materials and Methods

Four pink-bellied side-neck turtles, *Emydura subglobosa* (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 pellets *ab libitum*. All experiments were conducted under Clemson University IACUC guidelines (protocol 2017-034).

To facilitate measurement of flipping kinematics from videos, turtles were marked with high contrast points on the ventral midline at the anterior and posterior margin of the plastron, and at three points along the anterior plastron margin. To elicit self-righting attempts, turtles were inverted and placed on their carapace, such that the dorsal surface of the head contacted a custom-built force platform (K&N Scientific, Guilford, VT, USA). Specifications of the force platform and signal processing are reported by Butcher and Blob (2008) and Kawano et al. (2016). Three-dimensional forces were recorded at 5000 Hz using a custom LabVIEW (v.6.1, National Instruments, Austin, TX, USA) routine, while being filmed with digitally synchronized high-speed video in dorsal and frontal views at 100 Hz (Phantom v 5.1, Vision Research Inc., Wayne, NJ, USA). Video and force data were synchronized by a trigger that sent a light pulse to the video and a square wave pulse to the force recordings. Forces were only recorded from the head because it is the only mobile structure that contacts the ground during righting attempts

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by *E. subglobosa*. To avoid exhaustion, trials were conducted no more than 10 times per day over five non-consecutive days for each turtle. We recorded approximately eight successful flips (Movie 1) and eight failed attempts (Movie 2) from each individual, for a total of ~64 videos.

Force data were processed using the R package 'Kraken' (https://github.com/MorphoFun/kraken). Video data were tracked using DLTdataviewer software (Hedrick, 2008). Processed kinematic and force data were combined in custom MatLab routines to calculate net ground reaction force (GRF), and its anteroposterior (AP) and mediolateral (ML) inclination angles in the frame of reference of the turtle. We also calculated the angle of the head to the ground, total yaw (lateral rotation of the body), and roll velocity. We calculated the flipping moment as the vector product of GRF and the moment arm between the roll axis of the shell and the point where the head of the turtle contacted the ground.

Statistical analyses were conducted using mixed-effects models, with individual as a random effect (full model: Success/Failure ~ Mean anteroposterior-GRF angle + Mean mediolateral-GRF angle + Mean head angle + Mean roll velocity + Mean flip moment (the GRF standardized by turtle mass * moment arm of the head, (body-weight * meters, BWm)) + Total yaw + 1|Individual). We used Akaike's Information Criteria (AIC) to assess the importance of variables in determining success or failure, and model averaging to find the variables that best predicted success (Burnham et al., 2011). All statistical analyses were conducted in R v. 3.3.2 (www.r-project.org).

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Results and Discussion

We found that the best predictors of a successful flip were mean roll velocity, mean flipping moment, and mean anteroposterior-GRF angle (Table 1). Head angle, mean mediolateral-GRF angle, and total yaw of the body were not substantial predictors of flipping success (Table 1) Successful flips were characterized by a much higher roll velocity (Success = 175.39 ± 22.81 deg/sec; Failure = 26.31 ± 10.70 deg/sec), double the flipping moment (Success = 0.13 ± 0.03 BWm Failure = 0.07 ± 0.01 BWm), and a more vertically directed anteroposterior GRF angle (Success = 28.03 ± 6.79 deg; Failure = 41.23 ± 4.82 deg) (Fig. 1, Table S1).

For *E. subglobosa,* righting success was determined not only by the magnitude of the flipping moment exerted, but also by the speed of the attempt (Fig. 1 A, B). The role of speed in successful flipping suggests that success is probably determined very early in a self-righting attempt, with slow, continued straining likely proving to be fruitless. Among factors that might impact the effective production of a flipping moment, excess yaw (lateral rotation) might be expected to impede roll about the long axis of the shell. However, even though failed flips showed twice as much yaw as successful flips, yaw was limited in all attempts (averaging <20°) and had little influence on righting success (Table S1). The mediolateral angle of the GRF and the angle of the head relative to the body also played negligible roles in determining self-righting performance (Table 1). The small effect of head angle suggests that the primary driver of differences in flipping moment between successful and failed self-righting attempts is the magnitude of the force being applied, rather than the orientation and length of the moment arm between the head and the roll axis of the shell.

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By combining kinematic analyses of self-righting with data on force production, our analysis provides novel insight into the mechanisms through which successful self-righting is achieved. While most previous research has used patterns of flipping performance to measure exhaustion and other fitness-related traits (Penn and Brockman, 1995; Delmas et al., 2007; Kaspari et al., 2016; Mitchell et al., 2016), there has been little focus on the actual mechanisms governing flipping performance and success. Our data provide a foundation for further evaluations of how such mechanics might influence performance across morphologically diverse systems. For example, neck posture and shell morphology differ dramatically in turtles across species, between sexes, and throughout ontogeny (Ashe, 1970). Certain shell shapes are thought to facilitate self-righting and reduce the energy required to successfully flip (Ashe, 1970), but the ability to self-right is important for all species of turtle. By integrating biomechanical data with morphological comparisons, it may be possible to identify traits that enable turtles to self-right despite morphological constraints (Chiari et al., 2017).

In addition to anatomical factors, numerous environmental conditions (e.g. temperature, substrate) are known to influence terrestrial locomotion (Lailvaux, 2007; Kaspari et al., 2016) and could potentially influence self-righting performance for a range of taxa. Future studies could examine if and how differences in the environment influence self-righting mechanics and performance. Furthermore, these data help to establish a framework for evaluating self-righting in other rigid animals (e.g. beetles, crustaceans) as well as in additional taxa, providing new perspective for studies that use self-righting performance to estimate fitness. Such broader comparisons within and between species for a variety of conditions could

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also inform biomimetic applications in which rigid bodies with alternative constructions must self-right under variable conditions.

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Competing interests. We declare we have no competing interests.

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Data accessibility. All data will be deposited in Dryad upon acceptance Link:

Author's contributions. A.M.R. and C.J.M conceptualized the experiment and experimental design was done by A.M.R., R.W.B., and C.J.M. Data collection was done by A.M.R., R.W.B., and C.J.M and data processing was done by A.M.R. and C.J.M. A.M.R. drafted the manuscript and R.W.B. and C.J.M wrote analysis code and edited manuscript text. All authors gave final approval for publication and are accountable for the content it contains.

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Figures and tables

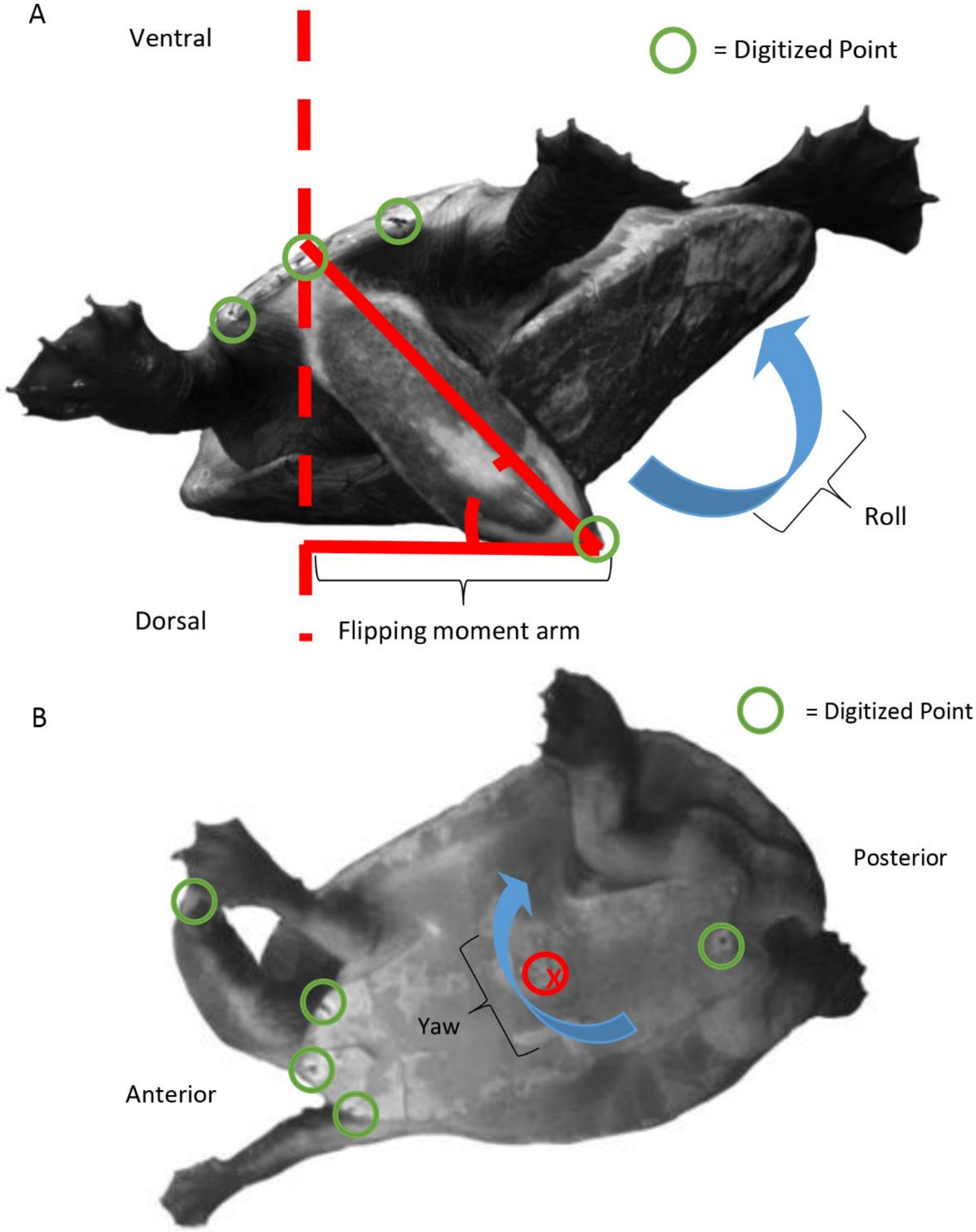

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Figure 1. Schematic of digitized points, and kinematic and force-production variables, from anterior (A) and ventral (B) views. Green circles represent points digitized using DLT Dataviewer (Hedrick, 2008). Blue arrows indicate rotational variables. Red symbols indicate angles (θ) and axes of rotation used to calculate moment arms and body axis rotations.

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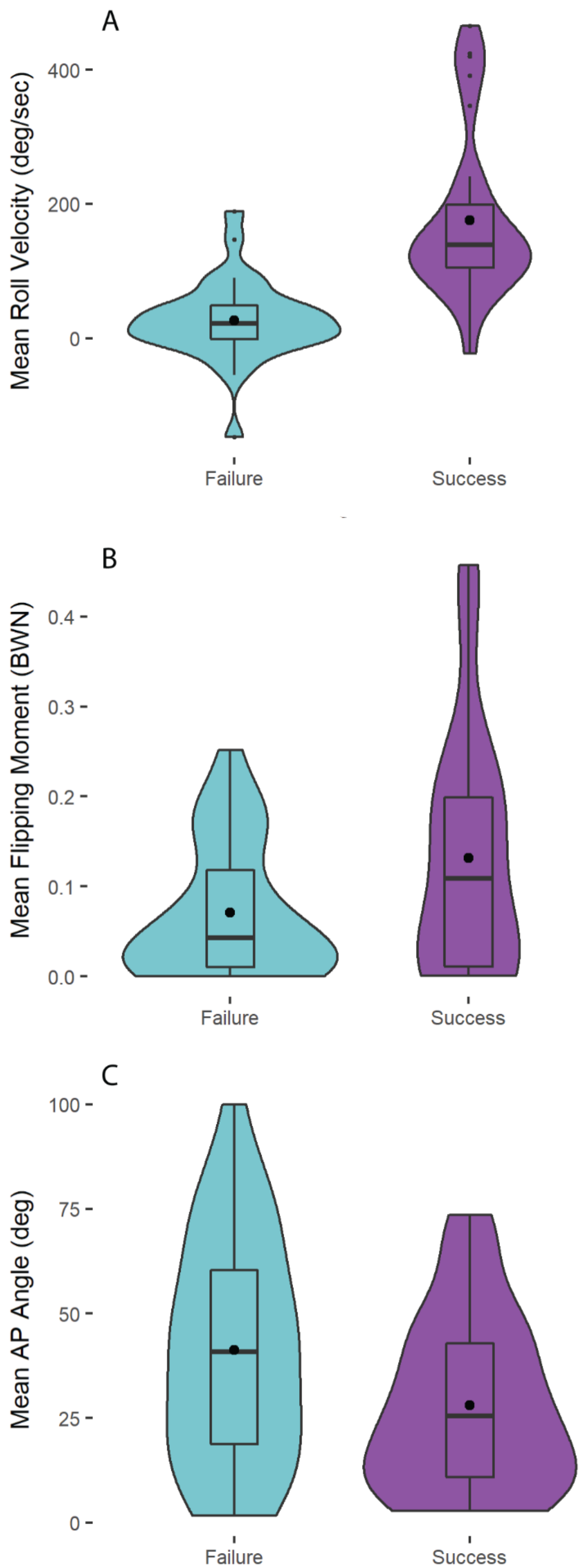
A
Mean Roll Velocity (deg/sec)
400
200
0
Failure
Success
B
Mean Flipping Moment (BWN)
0.4
0.3
0.2
0.1
0.0
Failure
Success
C
Mean AP Angle (deg)
100
75
50
25
0
Failure
Success

Figure 2. Violin plots showing the differences between failed and successful attempts at self-righting in the three most predictive variables (N = 29 Failures; N = 29 Successes). (A) Mean roll velocity; (B) Mean flipping moment, (C) Mean anterio-posterior ground reaction force (AP GRF) angle. Large black circles indicate mean; small black dots indicate outliers; width of graphs indicate the frequency of the data along the y-axis.

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Table 1. Top seven models (with ΔAIC <3) used in determining the variables that contribute most to self-righting success.

Δ AIC	Mean roll velocity	Mean flip moment	Mean AP angle	Total yaw degrees	Mean head angle	Mean ML angle
0	+	+				
1.44	+	+	+			
2.13	+	+		+		
2.37	+	+			+	
2.37	+	+				+
2.51	+					
2.53	+		+			
Importance	1.00	0.84	0.35	0.15	0.13	0.13

+ indicates that the variable was included in the model. All models included mean roll velocity, the top five included mean flip moment, two of seven included mean anterio-posterior (AP) angle, and the other variables were only included in one model each (ML angle: mediolateral angle).

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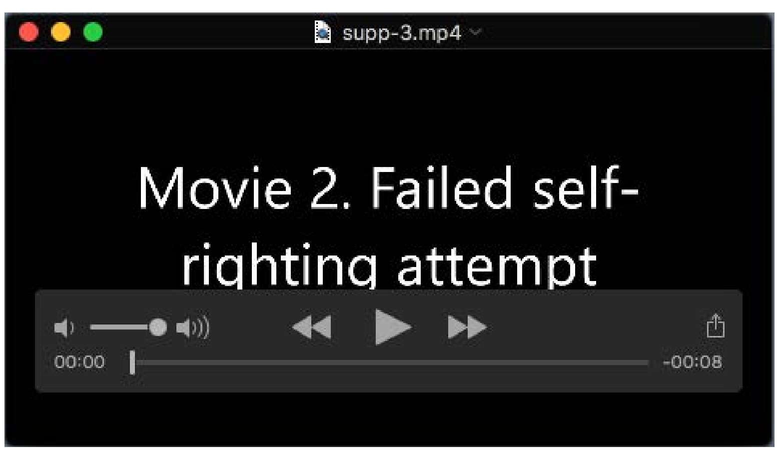
Supplementary Data for statistics

Click here to Download Data

Table S1. Mean ± SE values for failed (N = 32) and successful (N = 29) self-righting attempts.

	Failure	Success
Mean roll velocity (deg/sec)	26.13 ± 10.70	175.4 ± 22.81
Mean flipping moment (BWm)	0.07 ± 0.01	0.13 ± 0.03
Mean AP angle (deg)	41.23 ± 4.82	28.03 ± 3.79
Mean ML angle (deg)	15.55 ± 2.01	14.08 ± 1.32
Head angle (deg)	158.7 ± 6.82	177.4 ± 2.66
Total yaw (deg)	20.75 ± 4.03	10.11 ± 1.78

Movie 1. Successful self-righting attempt for *E. subglobosa* in frontal (left) and dorsal (right) views.



Movie 2. Failed self-righting attempt for *E. subglobosa* in frontal (left) and dorsal (right) views.