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Alligator ascension: climbing performance of *Alligator mississippiensis*

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Abstract. In tetrapedal locomotion, whether horizontal or during climbing, interactions between the foot and the contact surface or substrate influence the locomotor performance. Multiple previous studies of tetrapedal squamates (lizards) have reported that the animals used the same locomotor velocity, regardless of the angle of ascension. The present study was performed to determine if the American alligator (*Alligator mississippiensis*) would exhibit a stable climbing velocity and to determine to what degree, if any, this climbing velocity could be modified by substrate differences. Sub-adult *Alligator mississippiensis*, with body lengths around 170 cm, used the same stride velocity when moving at angles of 0°, 30°, and 55°. During these trials, both the sub-adult and juvenile alligators used a "low walk" gait, rather than a distinctive climbing gait. When the alligators traversed an open grate, their stride duration increased (and stride velocity decreased) presumably due to the insertion (and retraction) of their claws and digits into the grate. When climbing at 55° the juvenile and sub-adult alligators used the same stride duration; the sub-adults used a stride length that was significantly larger in absolute terms, but significantly shorter in relative terms. Despite their large size, and their more caudal center of mass, the climbing performance of *Alligator mississippiensis* is similar to what has been described in the previously-studied tetrapedal squamates.

Keywords: behaviour, Crocodylian, gait, locomotion, scaling, stride duration.

Introduction

In a now classic paper, Cartmill (1985) summarized the biomechanics of climbing in tetrapods. Though dry (Labonte and Federle, 2016.) and wet adhesive (Endlein et al., 2015) mechanisms have evolved, most terrestrial and arboreal vertebrates climb by clinging. Climbing performance for a clinging tetrapod depends, among other factors, on the location of the center of mass (Preuschoft, 2002), the interlocking or frictional interaction between the digits and the substrate (e.g., Zani, 2000), and the relative curvature/diameter of the substrate (Dunbar and Badam, 2000; Albanese et al., 2011). Viewed as a clinging climber, the American alligator (*Alligator mississippiensis*), has some significant challenges. The large tail of *Alligator* shifts the center of mass caudally (Willey et al., 2004), and the species mainly climbs on relatively flat (not rounded) substrate which hampers the alligator from using adductive or frictional force to increase the subtended angle (Cartmill, 1974; Kolbe, 2015). The feet of *Alligator* generate substantial forces during terrestrial locomotion (Willey et al., 2004), digging (Kley and Kearney, 2007), and anchoring (Walter et al., 2023), but lack the digital dexterity (e.g., D'Amore et al., 2018; Baeckens et al., 2020) and curved sharp claws (Birn-Jeffery et al., 2012) seen in arboreal reptiles.

The complex evolutionary history of crocodylians, including repeated transitions between terrestrial and marine habitats (Stubbs et al., 2021), are reflected in the evolution of the

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crocodylian manus and pes. In some marine forms, such as the Metriorhynchidae, the limbs terminated in paddle-like flippers (Young et al., 2010). In the terrestrial bipedal *Poposaurus*, the manus is significantly reduced and considered non-locomotor (Gauthier et al., 2011). Despite this morphological diversity, as Willey et al. (2004) noted, “no one has credibly suggested that arboreality plays a role in crocodilian evolution”.

Nevertheless, *Alligator mississippiensis*, and the more terrestrial of the extant crocodylians are known to climb. The older natural history literature has numerous accounts like that of Gadow (1901), who noted that of the *Crocodylus* he maintained, “The strongest specimen left the tank entirely, and took up its favorite place for basking on the stump of a tree, to reach which it had to climb up a rough wall of stone”. In the internet era, a simple image search will yield a multitude of images of crocodylians climbing chain link fences, trees, and screen doors. While the only published study on the subject (Dinets et al., 2014) confirmed that crocodylians can climb, it did not quantify any aspect of their climbing performance, and did not include coverage of *Alligator mississippiensis*. The present study was designed to quantify the climbing performance of different sized specimens of *Alligator mississippiensis* moving over differing substrates at different angles, and to assess whether the specializations of crocodylians (e.g., the caudal shift of the center of mass) influenced climbing ability.

Materials and methods

Animals

Three juvenile (51-53 cm total length) and seven sub-adult (167-188 cm total length) American alligators (*Alligator mississippiensis*) were used for this study. The juvenile alligators were obtained commercially, while the sub-adult animals were obtained through the courtesy of the Louisiana Department of Wildlife and Fisheries. The animals were housed communally in a 29 m^2 facility that featured three submerging ponds, natural light, and artificial lights on a 12:12 cycle. The facility was maintained at 30-33°C, warm water rain showers were provided every 20 minutes, which helped maintain the facility at >75% relative humidity. The alligators were maintained on a diet of previously frozen adult rats. The husbandry and use of the live alligators followed all applicable federal guidelines, and were approved by the IACUC of A.T. Still University (Protocol #228, approved 15 February 2023).

Climbing equipment

Three different climbing platforms were constructed. The small platform, used for the juvenile alligators, was 26 cm wide × 122 cm long and had a substrate of 0.6 cm metal mesh. The small platform was positioned at a 55° incline. The medium platform, used for the three smallest sub-adult alligators (167-174 cm total length; 11.8-17.2 kg), was 30.5 cm wide × 305 cm long × 41 cm tall; this platform had small LED lights on the inner surface and digital cameras (Action Camera 2K, YI Technology; recording at 1080p at 60fps) positioned at either end. The platform was built with a steel grate floor that was 2.5 cm thick and had 2.5 cm wide gaps between the bars of the grate. A second substrate, with 1 cm high wooden “rungs” positioned every 15 cm on an otherwise continuous smooth wooden surface, could be slid into the medium platform. An electric winch (DNYSYSJ) was used to position the medium platform in three different inclinations: 0°, 30°, and 55°. The large platform, used for the four largest of the sub-adult alligators (178-188 cm in length; 18.1-27.2 kg), was 122 cm wide × 729 cm long, it featured a 243 cm long central horizontal portion, between 243 cm long 35° inclination and 35° declination segments. The platform was constructed of wood and the substrate featured 1 cm high rungs positioned every 15 cm.

Climbing trials

Each juvenile alligator was placed at the base of the climbing platform and filmed while freely ascending, a total of six trials (2 from each animal) were made. For the sub-adult trials the animals were noosed and removed from their enclosure, their mouths taped closed with nylon tape, then they were released at the base of the climbing platform. Each of the three smaller sub-adult alligators was filmed moving over the medium climbing platform 12 times (two trials at each of three inclinations [0°, 30°, 55°] over both substrates). Multiple climbing trials were attempted using the four larger sub-adult alligators; because of the risk posed by the elevation of the large climbing platform (necessary given the size of the animals being studied) the animals could not be allowed to explore and voluntarily climb.

Quantification

Each of the trials was first evaluated simply as whether or not the alligator was capable of climbing (defined herein as moving the entire body mass up the incline for at least one step cycle). The video records of each trial were then examined using Kinovea (kinovea.org) and the stride velocity was calculated. Stride sequences were excluded from analysis if: any portion of the alligator (including the tail) remained on the floor; if the alligator paused during the stride cycle; if the

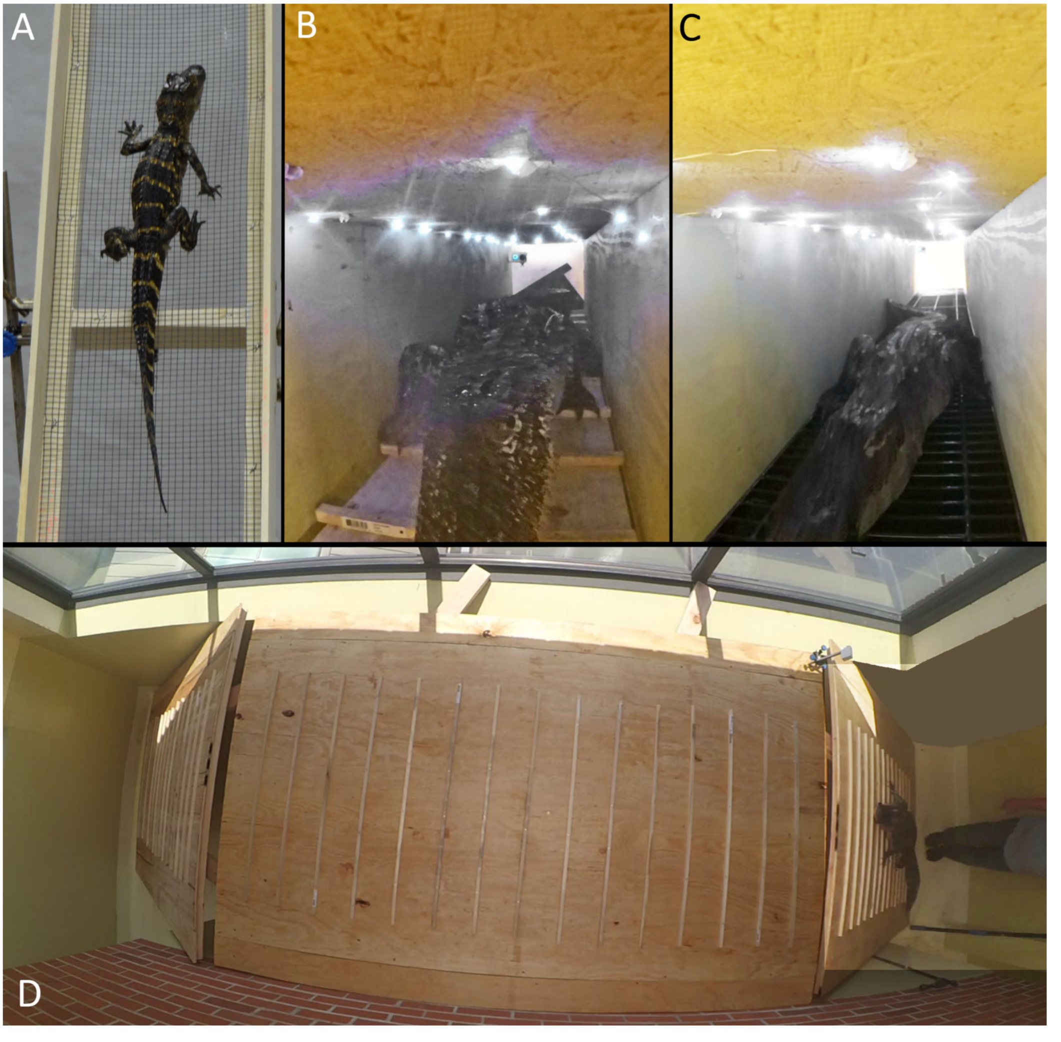

Figure 1. *Alligator mississippiensis* climbing trials. A) 52 cm total length juvenile climbing at a 55° incline; B) 171 cm total length sub-adult moving horizontally over the "runged" board substrate; C) the same alligator, climbing at a 55° incline over the steel grate; D) 188 cm total length sub-adult on the large climbing apparatus.

animal's paw came into contact with the side of the filming platform; or if anything about the step cycle appeared unusual (e.g., the alligator laterally flexed more than normal). Stride velocity was determined in cm/s and, since the animals had a three-fold range of body lengths, also in body length/s. Climbing performance of the smaller sub-adult alligators was compared using MANOVA. Both the smaller sub-adults and the juveniles climbed at a 55° incline over a grate (or mesh) substrate; their climbing performance was compared using two-tailed t-tests.

Results

Climbing ability

This study involved two general size classes of *Alligator mississippiensis*, three different inclinations, and two different substrates (fig. 1). In all of these trials, the alligators demonstrated their ability to move their body vertically or climb.

Table 1. Climbing performance of the juvenile and smaller sub-adult *Alligator mississippiensis*. Data are presented as mean ± s.d. Stride duration is in seconds, stride length is in cm, climbing velocity is in cm/s.

		Stride length	Stride duration	Velocity
		Smaller sub-adults		
Horizontal	board	53.3 ± 8.1	2.0 ± 0.3	27.4 ± 3.6
	grate	30.0 ± 7.3	2.1 ± 0.3	14.6 ± 4.5
35° incline	board	41.4 ± 7.4	2.0 ± 0.4	21.8 ± 6.8
	grate	37.8 ± 5.6	2.4 ± 0.5	16.6 ± 4.7
55° incline	board	28.3 ± 10.5	1.5 ± 0.5	19.0 ± 4.5
	grate	32.7 ± 2.7	1.9 ± 0.6	18.6 ± 6.1
		Juveniles		
55° incline	grate	14.9 ± 1.7	1.9 ± 0.4	8.3 ± 2.1

Climbing performance

The smaller sub-adult alligators were filmed moving over two substrates, each positioned at three different angles. The stride durations were significantly (F = 5.68, p = 0.022, df = 1) longer and the stride lengths significantly (F = 12.26, p = 0.0012, df = 1) shorter when these alligators climbed on a grate compared to a board (table 1). Regardless of the substrate, when they climbed at a 55° incline the smaller sub-adult alligators switched to significantly shorter (table 1) stride durations (F = 4.13, p = 0.024, df = 2) and stride lengths (F = 13.61, p = <0.0001, df = 2). These alligators were significantly (F = 14.9, p = 0.0004, df = 1) faster climbing over the board compared to the grate, but the angle of inclination (including horizontal) had no significant impact on velocity (table 1).

The juvenile *Alligator mississippiensis* were filmed moving over a grate which was positioned at a 55° incline, the same maximum slope climbed by the smaller sub-adult alligators. The juveniles climbed using a stride duration that was not significantly different (t = 0.244, p = 0.81, df = 1) from that of the smaller sub-adult specimens (table 1). The stride length of the juveniles was significantly (t = 13.34, p = 0.0001, df = 1) shorter than that of the smaller sub-adults (table 1), thus their climbing velocity was also significantly (t = 3.615, p = 0.0036, df = 1) lower.

Table 2. Performance of the juvenile and smaller sub-adult *Alligator mississippiensis* climbing at a 55° incline over a mesh (grate) substrate. Data are presented as mean ± s.d. Stride duration is in seconds, stride length is in body lengths, climbing velocity is in body lengths/s.

	Stride duration	Stride length	Velocity
Juveniles	1.9 ± 0.4	0.29 ± 0.03	0.16 ± 0.04
Sub-adults	1.9 ± 0.6	0.19 ± 0.02	0.11 ± 0.04

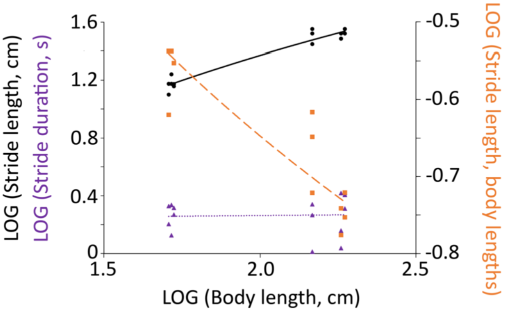

Figure 2. Changes in stride length during ontogeny. When climbing at a 55° incline, juvenile and sub-adult *Alligator mississippiensis* used the same stride duration (purple). The absolute stride length (black) increased with body size, while the relative stride length (orange) decreased. This meant that absolute climbing velocity was significantly greater in the sub-adults, while relative climbing velocity was significantly greater in the juveniles.

If the climbing performance up a 55° incline was evaluated in terms of body lengths (table 2), the pattern from the absolute data was reversed. The juvenile alligators used a significantly (t = 7.49, p = <0.0001, df = 1) longer relative stride distance, which resulted in a significantly (t = 2.471, p = 0.0294, df = 1) faster relative climbing velocity (table 2). This switch in velocities (the smaller sub-adults being significantly faster in terms of cm/s, but significantly slower in terms of body lengths/s) occurs, in part, because of the relative consistency of the stride duration (fig. 2).

Climbing tendency

The juvenile alligators showed no hesitation to climb. When placed at the base of the small climbing platform, they climbed to the top and "perched" every trial. The smaller sub-adult specimens were physically restrained and pointed at the medium climbing platform, which was lit and designed to resemble a secure hiding space. All of the smaller sub-adult specimens would enter the medium climbing platform, presumably as an escape behaviour, then traverse approximately 90% of the length of the climbing apparatus. They never voluntarily exited the far end.

The larger sub-adult alligators were physically placed on the inclined ramp of the large climbing platform. None of these alligators demonstrated any inclination to escape; they all moved up the ramp (demonstrating they were capable of climbing) but did so in a very inconsistent manner that prevented quantification of their performance. Primarily these alligators exhibited defensive, not locomotor, behaviours.

Discussion

A key finding of the present study is that when the alligators moved over the same substrate, but at inclinations of 0°, 30°, and 55°, there were no significant changes in velocity (table 1). This is the first study to quantify climbing performance of a crocodylian, but previous studies have looked at a variety of lizard taxa. Irschick and Jayne (1998) found no change in velocity between 0° and 30° in *Callisaurus*. Huey and Hertz (1982) noted that some small and medium sized lizards ran at the same velocity along inclines of 0° and 60°, but that large lizards ran "much slower" up the 60° incline. In this context, it is worth noting that the "large" lizards used by Huey and Hertz (1982) had roughly 0.5% the body mass of the sub-adult *Alligator mississippiensis* used in the present study. A study of climbing in chameleons (Krause and Fischer, 2013) also found no significant change in velocity among substrate orientations.

Simplistically, climbing velocity is determined by stride length and stride duration. In the present study, *Alligator* shortened both the stride length and stride duration with increasing inclination (table 1); shortening both is what kept the velocity similar. Jayne and Irschick (1999) found similar shifts when *Dipsosaurus* moved over inclines. Of the two lizards examined by Irschick and Jayne (1998), one reduced both stride duration and stride length with increasing inclination, while the other kept those features constant. (Krause and Fischer, 2013) found that the "reach" used by *Chameleo* was not influenced by inclination.

In this study the smaller sub-adult alligators climbed over two substrates; a smooth board with low "rungs" on it (designed to make the animal cling) and an open grate with enough space between successive bars that the alligator could insert not only the claws but even some of the terminal phalange. When moving over the grate the alligators used shorter stride lengths and longer stride durations than they used on the boards, this means they moved at a significantly lower velocity (table 1). The rungs on the board were spaced further apart (15 cm) than the openings in the grate (2.5 cm), which may have caused the alligator to stretch (extending stride length) to reach the next rung. The increased stride duration observed when the alligators moved over the grate may simply reflect time the animals spent inserting and retracting the digits from the grate. The performance difference over the two substrates may also reflect a difference in perspective; unlike the board, the grate was "see through" which may have made the alligator more hesitant resulting, in slower steps of shorter length.

Alligator mississippiensis has one of the largest ontogenetic size ranges among extant vertebrates (Platt et al., 2018). While the present study only sampled from a small portion of the size range of *Alligator*, the sub-adult alligators were roughly 3× larger than the juveniles. Despite the large difference in limb size, the juvenile and sub-adult alligators climbed using the same stride duration (table 1); the stride duration did shorten with inclination, and change with substrate, but was seemingly unaffected by body size. Other studies have found stride duration to scale with body size (Clemente et al., 2012), and larger bipedal birds have lower stride durations than smaller bipedal birds (Daley and Birn-Jeffery, 2018).

The present study found an ontogenetic decrease in relative stride length during climbing in *Alligator mississippiensis* (table 2, fig. 2). A similar decrease in relative stride length has been reported in this species during level locomotion (Iijima et al., 2023). This decrease in stride length is combined with the more caudal center of mass and the ontogenetic relative weakening of the crocodylian limb (Allen et al., 2010). This suite of scaling influences suggest that: 1) climbing mechanics are fundamentally different in hatchling/yearling alligators than they are in adult animals; 2) that climbing in even sub-adult alligator is likely mechanistically distinct from what has been described in lizards (most of which have a body size closer to that of the hatchling/yearling crocodylians); and 3) though not a formal part of this study, we found that the yearling alligators would readily climb the small apparatus even when it was positioned at a true vertical (90°). This behaviour may be impossible for larger adults.

The experimental design did not work well for the larger sub-adult alligators. These animals were large enough relative to the medium climbing cage that they made too much contact, either with their limbs or trunk, with the sides of the enclosure. This necessitated the construction of the larger climbing platform. The length of the larger sub-adult alligators, coupled with the requirement that the incline be long enough to accommodate two full step cycles after the entire length of the animal was off the horizontal, meant that the horizontal portion of the larger climbing platform was elevated nearly 2 meters off the ground. The risk of injury to an alligator falling off the platform meant that the animals could not be given a typical accommodation period to interact with the apparatus. The senior author has experience keeping *Alligator mississippiensis*, and has trained alligators of this size to do a variety of locomotor tasks, such as walking on a treadmill (Young and Cramberg, 2022). However, the size of the large climbing platform and the safety restrictions, precluded an iterative training approach. When placed on, or in front of the incline, these larger sub-adult alligators all took at least one step (demonstrating that they could climb), but invariably demonstrated defensive behaviours and moved down, rather than up, the climbing platform.

Another behavioural component to this study relates to gait selection. In all of the trials conducted, with different size alligators, different substrates, and different angles of inclination, the alligators always moved using what appeared to be the same "low walk" gait (e.g., Reilly and Elias, 1998). This present study did not include an analysis of limb kinematics [see Arias and Azizi (2023) for an analysis of limb kinematics in *Alligator* walking across 15° slopes]. Our observations and the analysis that was performed all suggest that the alligators simply walked up the inclines. Faced with steeper inclines, or different substrates, *Alligator mississippiensis* may utilize a distinctive climbing "gait", but no such gait was observed during the present study. A recent analysis of parrots (Young et al., 2023) provides a richer treatment of the distinction between inclined locomotion and climbing.

Though not the rationale for this study, our results do serve a cautionary role. There seems to be a popular misconception, judging by the abundance of photos online, that you are safe from alligator attack if you are on a bank over the water. The results of the present study suggest that an alligator can move up the bank nearly as quickly as it can over horizontal ground. The often repeated, and very valid, caution to stay away from the water's edge cannot be safely recalibrated because of a slight elevation difference.

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