Spring 2022

Stop, Then Go! Rapid Acceleration Offsets the Costs of Intermittent Locomotion When Turning in Florida Scrub Lizards

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STOP, THEN GO! RAPID ACCELERATION OFFSETS THE COSTS OF INTERMITTENT LOCOMOTION WHEN TURNING IN FLORIDA SCRUB LIZARDS

by

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(Under the Direction of Lance McBrayer)

ABSTRACT

Intermittent locomotion is a commonly used escape strategy with a wide array of potential benefits. Pausing may aid in locating a predator, crypsis, lowering energy costs, and maneuvering around obstacles. Navigating a turning may also benefit from intermittent locomotion by allowing an animal time to assess its surroundings; therefore, decreasing the chances of stumbling. Florida scrub lizards live in environments with a variety of obstacles and typically must turn around an obstacle when pursued. The goal of this study is to quantify the locomotor behavior and performance by lizards while navigating a 45° or 90° turn. Lizards were run along both a 45° and 90° racetrack. The number of trials with pauses and pause placement was collected as well as the mean speed before, in, and after a turn. I predicted that scrub lizards would utilize intermittent locomotion over continuous locomotion when turning. The results show that the linear speed entering the turn and exiting the turn are not significantly different. This finding indicates that acceleration, not speed is crucial in escaping when presented with a turn and therefore offsets the cost of intermittent locomotion on speed.

INDEX WORDS: Intermittent locomotion, Lizard, Turning, Speed, Acceleration, Escape strategies

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B.S., Austin Peay State University, 2018

A Thesis Submitted to the Graduate Faculty of Georgia Southern University in Partial Fulfillment of the Requirements of the Degree

MASTER OF SCIENCE

COLLEGE OF SCIENCE AND MATHEMATICS

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Electronic Version Approved:

May 2022

ACKNOWLEDGMENTS

This accomplishment could not have been possible without the help of Georgia Southern University Biology Department. I want to thank my advisor, Dr. Lance McBrayer for his help developing my project, his input on each step of my thesis, and his support through the ups and downs of graduate school; and my committee Dr. Ray Chandler and Dr. Michelle Cawthorn for their reviews and edits on both my proposal and my completed document; and the Squamate squad—Sidney, David, Katie, and Mike—for helping me collect lizards and making my time in the field memorable. I want to also thank my family, friends, and fellow graduate students, specifically Anthony Sample and Juan Jeronimo, who offered their support and comfort over the last several years.

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CHAPTER I

INTRODUCTION

Animals use a mixture of behavioral and morphological characteristics to either avoid an interaction with a predator, evade a predator, or escape a predator once captured (Walker et al. 2005; Schall and Pianka 1980). They must avoid predation in a variety of habitats ranging from flat terrain with little or no vegetation to complex multidimensional habitats filled with vegetation or other structures that animals must negotiate. In open habitats or habitats with large areas of bare ground, reaching the maximum sprint speed is an effective escape strategy since there are fewer obstacles to maneuver around (Wynn et al. 2015). However, in habitats that have higher numbers of obstacles, such as vegetation and uneven terrain, sprinting at maximum speed can lead to stumbling, and thus in natural situations, most animals rarely reach their maximum speeds (Wynn et al. 2015). Consequently, quantification of high speed sprinting alone as a measure of predator evasion may oversimplify the entire predator-prey dynamic (Clemente and Wilson 2016). While it is true that many studies have shown that faster running animals are more likely to escape predation, the probability of escaping is also dependent on an animal's ability to outmaneuver its predators (Clemente and Wilson 2016).

The presence of obstacles, such as vegetation, woody debris, or rocks, requires turning, enhanced maneuverability, or alternative locomotor behavior (Wynn et al. 2015; Brownsmith 1977). Animals may choose to alter their posture (bipedal running), make a series of turns, or use intermittent locomotion (McElroy and McBrayer 2021). Intermittent locomotion (also referred to as stop-go running, pause-travel locomotion, and saltatory search) is defined as stopping for extended periods of time (usually only a few seconds) during bouts of running (Kramer and McLaughlin 2001). This type of locomotion has been documented in many animals from various fishes and birds to terrestrial and arboreal mammals and reptiles. Several studies have quantified the benefits of intermittent locomotion. For example, Amo et al. (2005), McAdam and Kramer (1998), and Stojan-Dolar and Heymann (2010) each showed that intermittent locomotion was useful in enhancing vigilance.

Vigilance may contribute to the use of intermittent locomotion. Intermittent locomotion aids in locating predators by sight and/or sound, avoiding obstacles, identifying refuge, and planning escape routes (Kramer and McLaughlin 2001; Trouilloud et al. 2004). While being pursued by a predator, an animal may stop briefly to locate the predator's current location by looking and/or listening. By pausing, noise created by movement is reduced, allowing the animal to hear its pursuer (McAdam and Kramer 1998; Vasquez et al. 2002). Pausing also alleviates motion blur, or the obstruction of sight cause by rapid movement (Land 1999; Carpenter 1988; Desimone and Duncan 1995). Pausing allows the animal to momentarily stabilize their field of view (Avery 1993; Probst et al. 1986). Brief visual stabilization may aid in locating the predator and may also give the prey a moment to identify nearby refuges and/or to decide on alternate escape routes (Stojan-Dolar and Heymann 2010; McElroy and McBrayer 2021; Zamora-Camacho 2020). Intermittent locomotion may also aid in crypsis and cause the animal to "disappear" in plain sight (Martel and Dill 1995; Kramer and McLaughlin 2001). Deciding to become cryptic mid pursuit may confuse the predator and cause the predator to lose sight of the prey (Herzog and Burghardt 1974). Because many animals use movement to locate potential food items, intermittent locomotion may enhance crypsis and thereby increase the chances of a successful escape (Kramer and McLaughlin 2001).

Intermittent locomotion may also be beneficial by reducing energy costs (Weinstein and Full 1999; Weinstein and Full 1999). Pausing mid pursuit may allow the animal to improve endurance and allow the animal to run for longer periods of time (Baker Edwards and Gleeson 2001; Gleeson and Hancock 2001). Intermittent locomotion may also allow high-energy phosphates time to replace the fatigue-producing products in the body, such as lactic acid, thereby increasing the ability to continue running (Kramer and McLaughlin; Kemp et al. 2009; Weinstein and Full 1999). However, the fatigue-reducing benefits may be dependent on temperature, duration of activity, and pause duration (Weinstein and Full 2000).

Intermittent locomotion may reduce stumbling in animals that need to turn or maneuver (Wynn et al. 2015; Nasir et al. 2017). A mixture of speed and maneuverability may lead to more successful escapes, especially in environments with vegetation and/or uneven topography (Wheatley et al. 2015). Approaching a turn quickly increases the chances of making a mistake or crashing, so pausing before the turn may be beneficial (Wynn et al. 2015; Wheatly et al. 2015) and aid in orientation prior to turning (Higham et al. 2001). While there are numerous studies exploring speed and intermittent locomotion on straight paths (Vasquez et al. 2020; Weinstein and Full 1999; McAdam and Kramer 1998), the use of intermittent locomotion when negotiating a turn is not very well understood. Many studies have documented that animals such as lizards will run at near maximal speed straight to a known refuge (McElroy and McBrayer 2021; Kramer and Bonenfant 1997), yet very little is known about turning locomotion and behavioral tradeoffs when fleeing predators to an unknown, or unseen, refuge. Quantifying how turns affect intermittent locomotion could help broaden our understanding of predator escape behavior and performance tradeoffs in terrestrial vertebrates.

The goal of this study is to quantify the locomotor behavior and performance by lizards while navigating a 45° or 90° turn. Due to their inability to see around the 45° and 90° turns, I predict lizards will choose intermittent locomotion more frequently than continuous locomotion. Therefore, pauses before, in, and after the turn will have a higher number of lizards who paused on the 90° turns than on the 45° turns. I also predict that linear speed just before a turn will be faster than the linear speed just after a turn. That is navigating a turn will come at the cost of reduced speed. Intermittent locomotion at any point is expected to reduce linear speed on both 45° and 90° turns. Finally, linear speed after the turn is expected to decline as lizards begin to slow down or stop near the end of the track.

CHAPTER II

METHODS AND MATERIALS

Study Species and Field Site

Sceloporus woodi is a small, diurnal, short-lived lizard endemic to xeric habitats in Florida, USA (Tiebout and Anderson 2001). The species is rare outside of a few protected areas in Florida (Clark et al. 1999; McCoy et al. 2004). Ocala National Forest is a recreation and wildlife area located between the Ocklawaha and St. Johns Rivers in Marion County, Florida (Parker and McBrayer 2016). This 72,000 ha forest cite contains two habitats, longleaf pine sandhills (LLP) which consists of long leaf pines, turkey oaks, and wire grass, and Florida scrub pine (FSC), which consists of sand pines, and a mixed substrate of open sand, leaf litter and shrubby vegetation (Tiebout and Anderson 2001; Jackson 1972, 1973; Kaunert and McBrayer 2015).Within the Ocala National Forest, *S. woodi* is abundant in both LLP and FSC habitats (Parker and McBrayer 2016; Tiebout and Anderson 2001). These habitats have a mixture of vegetation that produces a variety of obstacles within each habitat that scrub lizards must negotiate if fleeing predators.

I captured adult lizards (minimum SVL = 40 mm) by hand or with a slipknot lasso. Once captured, each lizard was measured (snout-to-vent) and weighed using a ruler and scale. A global positioning system was used to document the capture coordinates to return the lizards to the place of capture following running trials (typically 5-8 days). They were kept cool and transported to Georgia Southern University animal facility. The lizards were housed in individual 38 liter tanks with one hide on top of sandy substrate. Lizards were kept on a twelve-hour light/dark cycle with daily misting and cricket feedings every 4 days following day two of captivity. Immediately prior to sprint trials, I marked each lizard with reflective stickers or non-toxic white paint on the dorsal side of the shoulders, the pelvis, and the base of the tail to aid visualization during digitization of the video recordings.

Sprint and intermittent locomotion data collection

Data were collected by encouraging each lizard to run down either a 45° or 90° angled, cork-bottomed racetrack, made from particle board inside a room kept at 25°C. Each angled racetrack was 1.9-meters long with 0.4-meter-high particle board walls. The track's width started at 0.35 m then tapered to 0.15 m at the turn (0.5 m) to force the lizards to turn. Each track had green foliage at the end of the track as a hide for the lizards to run towards (Figure 1A). Lizards were run once on one track type then returned to a holding bag (25°C) for 30 minutes then run again for a total of five trials with 30 minute rest periods per lizard. The lizards were then allowed to rest over night before being run on the opposite track type. I filmed each trial from above with two high-speed cameras (Megaspeed TM) at 300 frames per second (Figure 2). Video from each camera was spliced together using Video Editor then uploaded into MATLAB and digitized using DLTdv8.

To measure the change in speed due to the turn, the lizard's running speed was calculated before the turn (at 0.9m from the start) and after the turn (at 1.1 m). I measured the mean linear speed for all trials at 0.9 m, the mean linear speed for all trials at 1.1 m, and the mean speed from 0.9 m to 1.1 m to quantify changes in speed. I recorded the number of pauses that occurred in the following sections of the racetrack: 1) from the beginning of the track (0 m) to the beginning of the turn (i.e. 0 m – 0.9 m), 2) from the beginning of the turn (0.9 m) and the end of the turn (1.1 m), and 3) the end of the turn (1.1 m) to 1.4 m. The pauses were recorded up to 1.4 m because to most of the lizards began to substantially slow or stop between 1.4 m and 1.9 m at the end of the track. I used the fastest trials with the least number of pauses to analyze data related to intermittent locomotion. By doing this, I could measure the affect that intermittent locomotion has on speed in the most effective way since simply counting the number of pauses in total would not produce usable data on the lizard's overall speed but would still take into count the pause. Each variable is described in Figure 1B. The lizards were kept unfed in the animal facility to rest for 24 hours before sprint trials and fed following trials. All procedures followed the GA scientific collection permit number 1000545737 and IACUC permit numbers I18020 and I21010.

Statistical Analysis

Few lizards ran continuously during trials. Thus, the data was pared down to 42 trials, from 42 different lizards, in which the lizards paused a maximum of one time. Paired, or repeated measures analyses were not possible due to low sample sizes. Thus, no individual is represented twice in any statistical test, and sample sizes vary across tests. I used chi square analysis to compare the number of trials with no pauses and trials which did contain a pause before, in, and after the turn. The effect of pauses on linear speed and speed of the turn were compared using one-way ANOVAs and t-tests. A Tukey HSD was used to confirm the effect of pauses on the speed of the turn. All the data were tested for normality and distributions met either the Shapiro-Wilkes or Anderson-Darling criteria for normality.

CHAPTER III

RESULTS

Number of trials and placement of pauses

Out of these 628 trials, 602 trails, or 95.86%, contained pauses in at least one location throughout the track. Out of the 87 lizards run on the track, only 42 met the requirements for the analysis (trial contained one or fewer pauses). The presence and/or absence of pause per trial was examined (Figure 3). The angle of the turn, whether 45° or 90°, had no effect on whether the lizards paused before ($\chi^2 = 0.94$, $p = 0.33$, DF = 1), in ($\chi^2 = 2.83$, $p = 0.09$, DF = 1) or after the turn ($\chi^2 = 0.38$, $p = 0.54$, DF = 1). Sex had no effect on pauses on either the 45° ($\chi^2 = 0.85$, p = 0.36, DF = 1) or 90° ($\chi^2 = 0.05$, p = 0.83, DF = 1) turn.

The effect of pauses on linear speed at 0.9 m and 1.1 m

The average linear speed of the lizards entering the turn at 0.9 m (the start of the turn) and exiting the turn at 1.1 m (the end of the turn) did not differ between the 45° and 90° tracks at either location (0.9 m: $F_{(1,17)} = 0.002$, $p = 0.96$ and 1.1 m: $F_{(1,17)} = 0.002$, $p = 0.97$) (Figure 4). The number of pauses and their placement on the track also had no effect on the average linear speed of the lizards entering the turn (at 0.9 m) and exiting the turn (at 1.1 m) on the 45° track (0.9 m: $F_{(1,35)} = 0.85$, $p = 0.36$; 1.1 m: $F_{(2,36)} = 1.44$, $p = 0.25$) or the 90° track (0.9 m: $F_{(1,16)} = 0.32$, $p = 0.58$; 1.1 m: $F_{(2,24)} = 0.36$, $p = 0.70$).

The effect of pauses on the speed of the turn

Trials that contained a pause in the turn had the lowest speed through the turn (Table 2, Figure 5). Trails without a pause before the turn (and no pause in the turn) had a significantly faster speed of the turn than trials that contained a pause in the turn ($F_{(2,34)} = 5.40$, $p = 0.01$; $F_{(2,27)} = 17.76$, $p = 0.0001$). Likewise, trials which contained a pause before the turn also had a significantly higher speed of turn than trials with a pause only in the turn ($F_{(2,34)} = 5.40$, $p = 0.007$; $F_{(2,27)} = 17.76$, $p = 0.0001$). Interestingly, the speed of the turn did not significantly differ in trials with no pauses and trials with pauses before the turn ($F_{(2,24)}$ = 5.40, p = 0.98; $F_{(2,27)}$ = 17.76, p = 0.99).

The effect of a pause before the turn (0.9) and in the turn (0.9-1.1) on the speed after the turn (1.4)

The average linear speed at 1.4 m was significantly slower when there was a pause after the turn compared to trials with no pauses or pauses located elsewhere on the track (Figure 6). This was true for both the 45° ($F_{(3,25)}$= 4.81; p = 0.009) and 90° ($F_{(3,20)}$ = 4.41; p = 0.02) tracks. There was no difference in linear speed entering the turn (at 0.9 m); (45°: $F_{(1,17)}$ = 0.005, p = 0.94; 90°: $F_{(1,16)}$ = 0.32, p = 0.58) or exiting the turn on the 90° track (at 1.1 m); (90°: $F_{(2,18)}$ = 0.11, p = 0.90) regardless of pause placement. However, the linear speed at 1.1 m was affected when there was a pause in the turn. Intermittent locomotion does not appear to be costly (cause a significant loss in speed) on either the 45° or 90° track unless there is a pause in the turn.

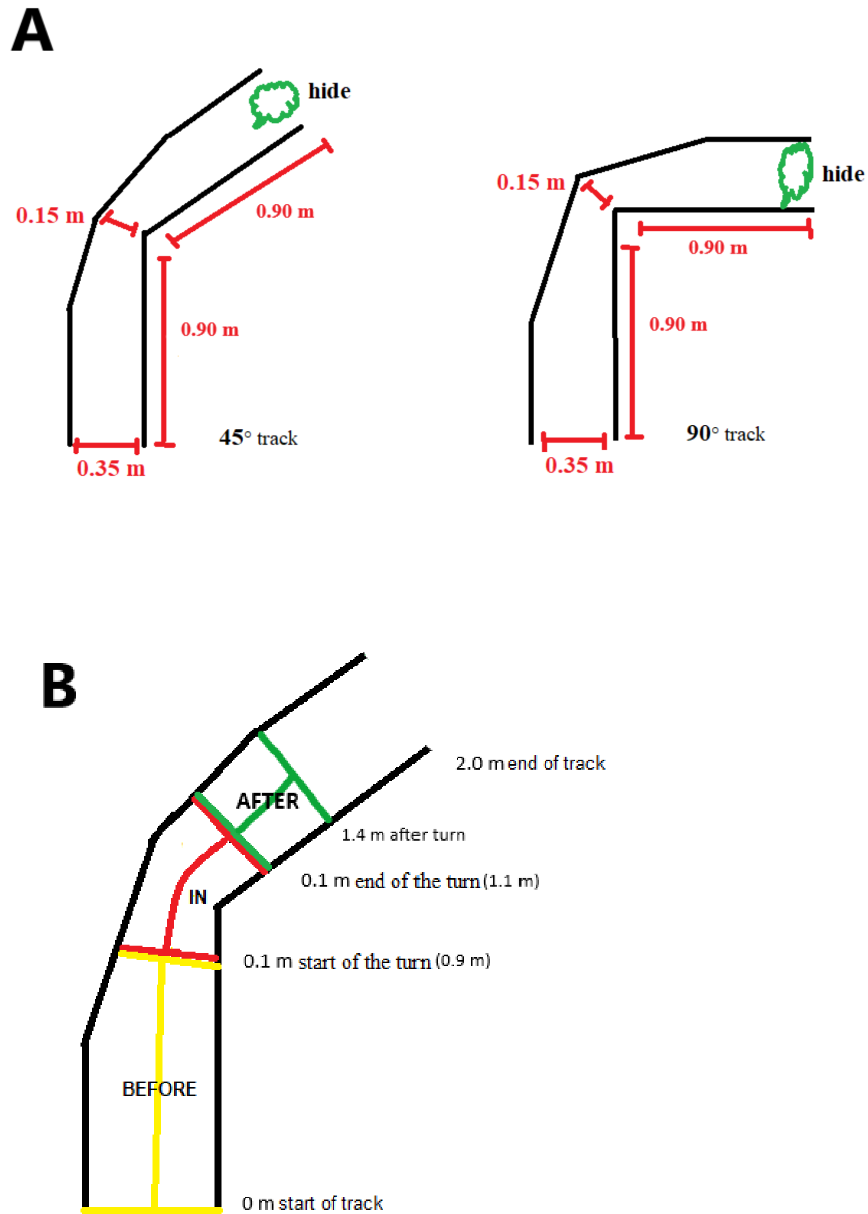

Figure 1: (A) The design of the 45° and 90° tracks. I defined the beginning of the turn as 0.1 m prior to its steepest angle (0.9m from the start). I defined the end of the turn as 0.1 m after its steepest angle (1.1m from the start). (B) The speed of the turn was measured between 0.1 m before the turn (0.9 m from the start) and 0.1 m after the turn (1.1 m from the start). The number of pauses was recorded and compared in each track segment (i.e., before = 0 - 0.9 m, in = 0.9 - 1.1 m, and after = 1.1 - 1.4 m).

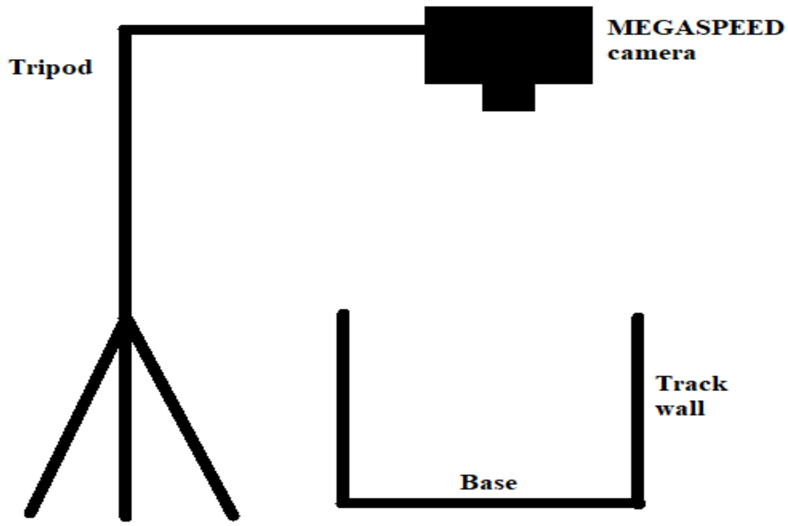

Figure 2**:** The track was constructed using particle board with a cork bottom to allow for better grip. In total, the track measures 2.0 in length with 0.4 m side walls and a width of 0.35 m which tapered to 0.15 m halfway down the track (0.5 m) to force the lizards to turn. The high speed cameras were positioned above the track to capture a dorsal view of the lizards during each trial.

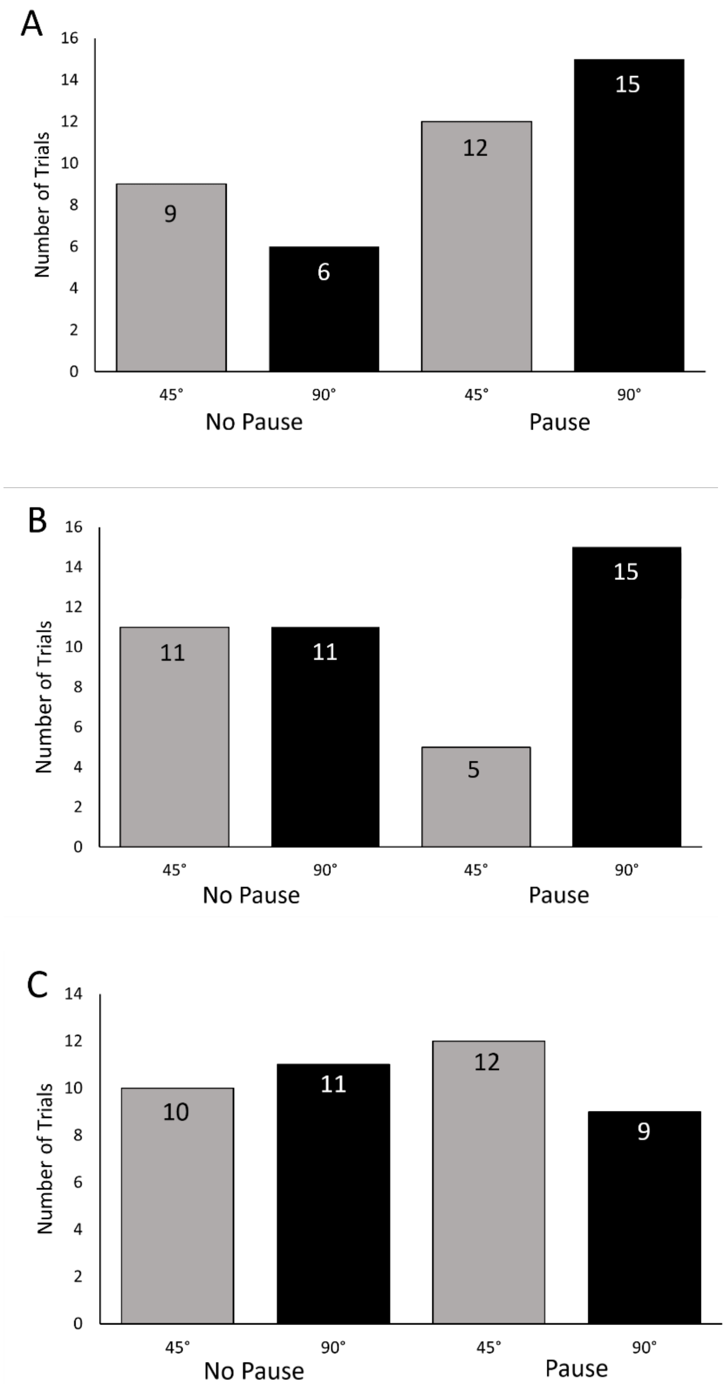

Figure 3: The presence or absence of a pause was not affected by whether the turn was 45° or 90°. (A) before the turn, (B) in the turn, and (C) after the turn. The number of lizards used in the analysis is shown in each bar.

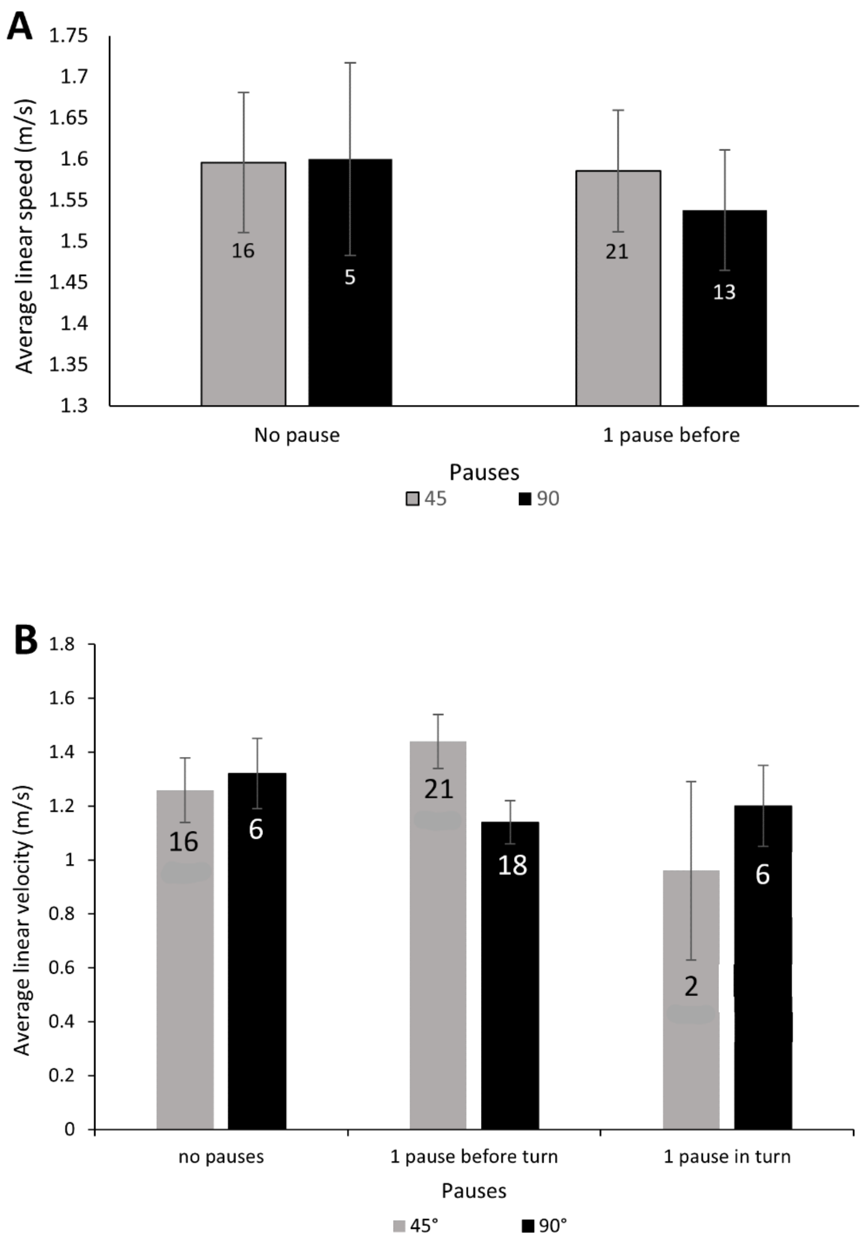

Figure 4: Mean linear velocities did not differ between the 45° and 90° tracks at 0.9 m and 1.1 m. The number trials and the placement of pauses on the track also had no effect on the mean linear speed of the lizards at (A) 0.9 m and (B) 1.1 m on the 45° turn or the 90° turn. The number of lizards used in the analysis is shown in each bar.

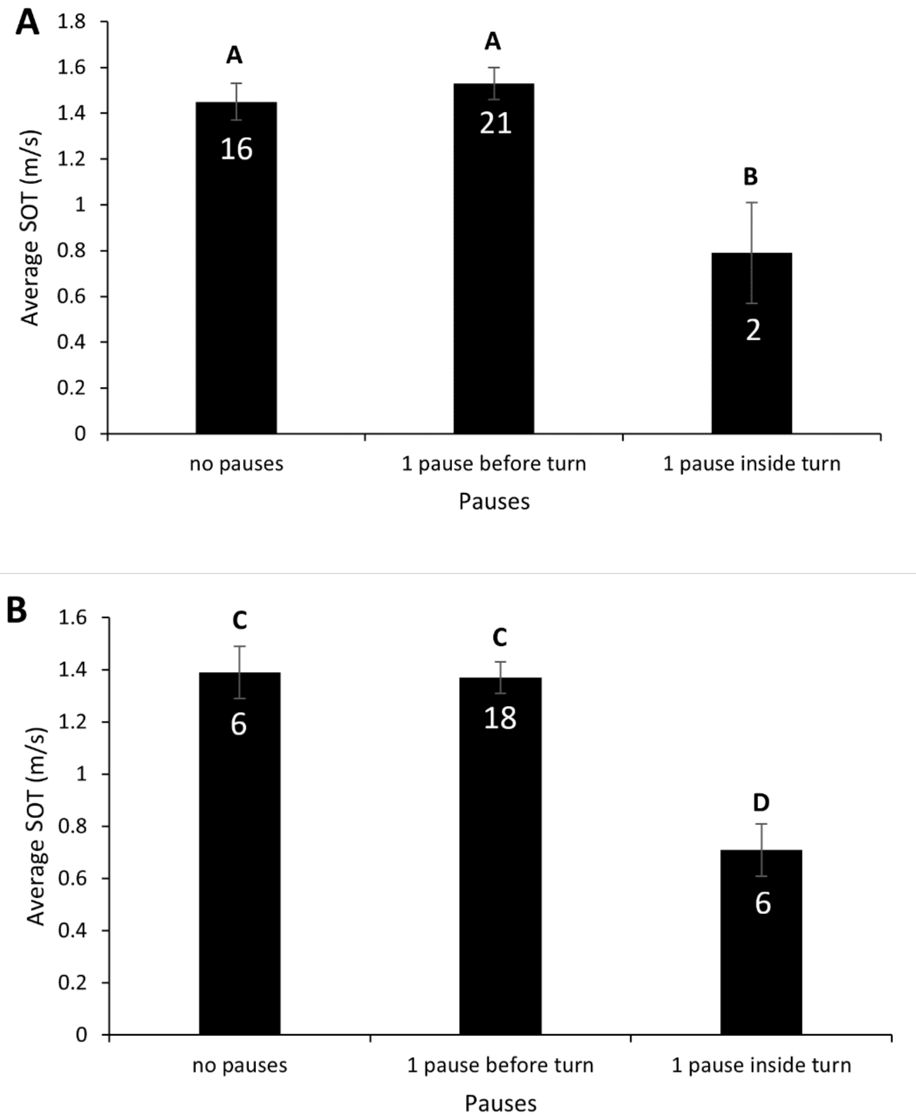

Figure 5: A) Mean speed of the turn in the 45° track ($F_{(2,34)}$ = 5.40, p = 0.01; $F_{(2,34)}$ = 5.40, p = 0.01). B) Mean speed of the turn on the 90° track ($F_{(2,27)}$ = 17.76, p = 0.0001; $F_{(2,27)}$ = 17.76, p = 0.0001. The speed of the turn of lizards with pauses in the turn also differed significantly from the speed of the turn of lizards with no pauses before the turn and of those with one pause before the turn. However, the speed of the turn did not significantly differ between lizards with no pauses before the turn and those with one pause before the turn (A: $F(_{2,34)}$ = 5.40, p = 0.01; B: $F_{(2,27)}$ = 17.76, p = <0.0001). The number of lizards used in the analysis is shown in each bar.

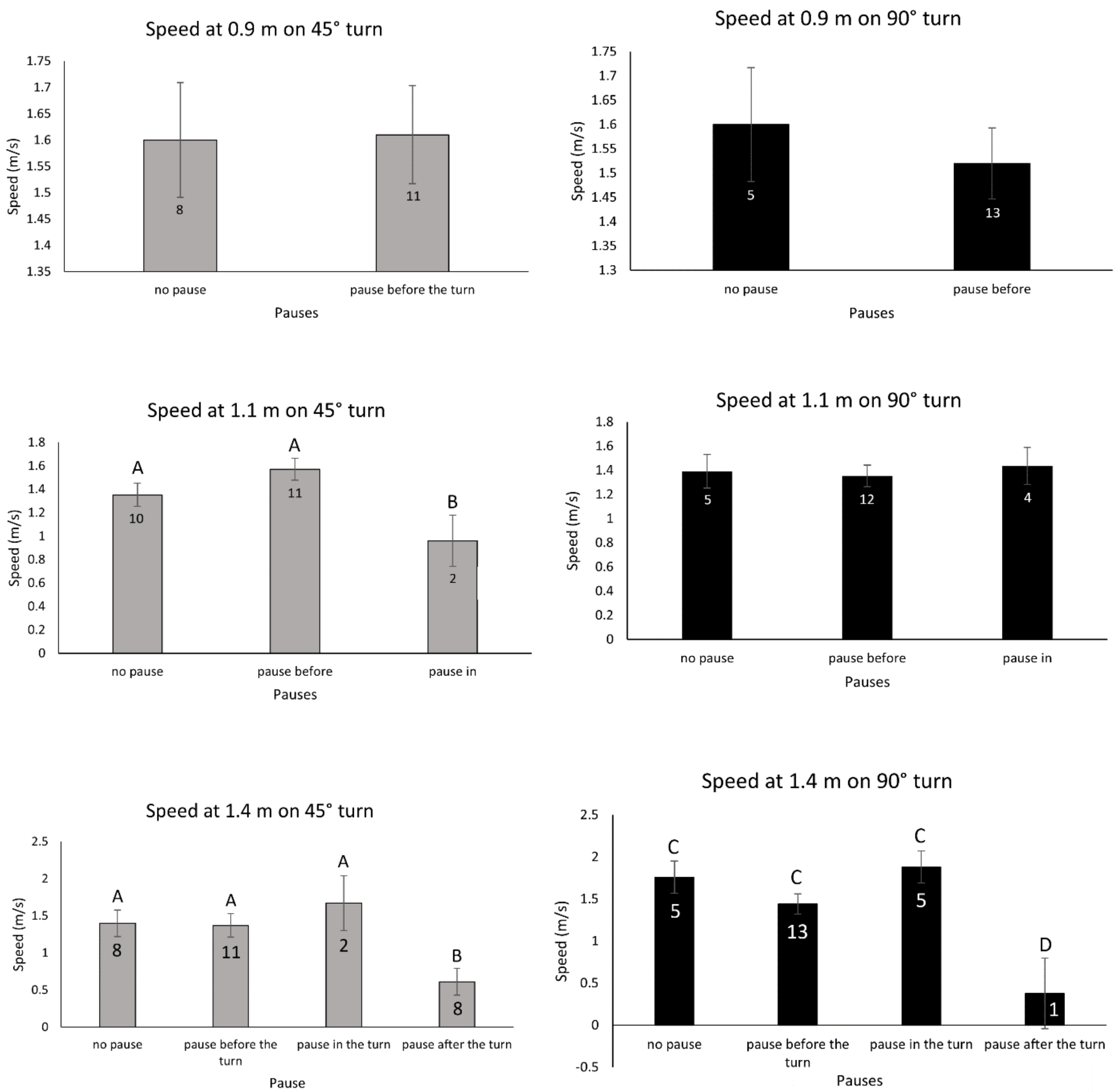

Figure 6: The mean linear speed at 0.9 m and 1.4 m (45°: $F_{(3,25)}$= 4.81; p = 0.01; 90°: $F_{(3,20)}$ = 4.41; p = 0.02) in trials with no pauses, trials with a pause before the turn, trials with a pause in the turn, and trials with a pause after the turn when pause after the turn data is included. There is no significant difference between the average linear velocities at 0.9 m on either the 45° or 90° track, however, the linear speed at 1.1 m on the 45° track was slower when there was a pause in the turn. There was also significant difference in the velocities at 1.4 m on both tracks

CHAPTER IV: DISCUSSION

The goal of this study is to quantify the use of intermittent locomotion when navigating a turn of either 45° or 90°. I predicted that a turn would influence the number of trials with pauses as well as the speed at which lizards negotiated the turn. In 95.86% of 687 trials, *S. woodi* used intermittent locomotion. The location on the track where the lizards paused was not influenced by the turn angle (45° or 90°; Figure 3). Pauses in the turn caused the speed to decrease significantly but pauses before the turn had no effect on the speed either entering the turn (0.9m) or exiting the turn (1.1m; Figure 5). These results demonstrate minimum cost to pausing and infer that intermittent locomotion may provide an advantage in predator avoidance when traversing a turn. This conclusion is supported by several previous studies of predator-related intermittent locomotion in various other types of animals. Amo et al. (2005) showed that intermittent locomotion was heavily utilized by lizards to avoid different types of predators, such as snakes and birds, and examine refuge. McAdam and Kramer (1998) demonstrated how chipmunks and squirrels use intermittent locomotion when moving towards food caches. The use of intermittent locomotion was also shown to enhance vigilance in mustached tamarins (Stojan-Dolar and Heymann 2010), chipmunks (Trouilloud et al. 2004), degus (Vasquez et al. 2002), and toads (Zamora-Camacho 2020).

Number of trials and Placement of Pauses

Of the total trials (95.86%), scrub lizards used intermittent locomotion in lieu of continuous locomotion. Several reasons may explain the frequent use of intermittent locomotion when encountering a turn. Pausing either before, in, or after the turn, may give the lizard time to locate the predator (in this case the human pursuer) while also stabilizing its field of view and alleviating motion blur (Trouillound et al. 2004; Kramer and McLaughlin 2001). In addition to offsetting the effects of “motion blur”, intermittent locomotion while evading a predator may also aid in finding alternate routes of escape (Stojan-Dolar and Heymann 2010; McElroy and McBrayer 2021). The placement of pauses was not affected by the turn angle (Figure 3). This finding suggests that lizards will use intermittent locomotion when presented with a turn regardless of the tightness (or angle) of the turn. These pauses may give scrub lizards time to evaluate their environment and determine the best way to avoid obstacles and locate refuge (McElroy and McBrayer 2021; Zamora-Camacho 2020). The use of intermittent locomotion may help scrub lizards identify nearby refuges or re-conceal themselves on the substrate or by the surrounding vegetation (Druell et al. 2019; Higham et al. 2010; Vasquez et al. 2002).

During flight from a predator, turns may generate confusion about where to go and how to get there due to the inability to see past it. Pausing is shown to increase in unfamiliar settings (Kramer and McLaughlin 2001; Zani et al. 2009), so it would be reasonable for lizards to use caution when maneuvering a blind turn. Pausing in this case would also allow the lizards to determine the most reliable route and create alternate routes and/or identify closer refuge once they have completed the turn (McElroy and McBrayer 2021).

Movement can increase the likelihood of being detected by a predator, so many animals use crypsis as a defense strategy (Kramer and McLaughlin 2001). Scrub lizards rely heavily on crypsis to avoid predators (Orton et al. 2018; Orton and McBrayer 2019), so increases in intermittent locomotion while running may give the advantage of blending into the surroundings and losing the threat before being detected (Martel and Dill 1995). The brief pause that enhances crypsis may allow lizards a brief period when the threat is distracted and thus avoid being detected again.

The effect of pauses on speed of the turn

Understandably, pausing should affect the average speed during sprint locomotion, especially during a more complicated maneuver such as a turn. My study supports the hypothesis that only trials with pauses in the turn would significantly decrease the speed of the turn, while pauses before and after would have no effect. This suggest that acceleration, not maximum speed, may be more important to escaping predators in scrub lizards. Scrub lizards reach maximum sprint speeds at 0.4 m from a standstill (McElroy and McBrayer 2010). Thus, they are able to rapidly accelerate following a pause making acceleration, not top speed, a critical performance variable for predator escape. Since the turn portion of the track is only 0.2 m in total, it would be impossible for the lizards to reach high velocities (Huey and Hertz 1984) in such a short distance. Combined with the deceleration caused by turning, and the lizard pausing, the distance required to speed up is even smaller. Therefore, high velocities are not reached within the turn. This was true for both the 90° and 45° turns. Interestingly, because there was no significant difference in the linear speed before (0.9 m) or after (1.1 m) the turn, this further suggests that acceleration is more critical in escape performance than turning (or agility) and linear speed in some situations.

Conclusion

Sceloporus woodi utilized intermittent locomotion over continuous locomotion when navigating a 45° or 90° turn. The presence of pauses on both tracks is consistent with previous findings. We showed that intermittent locomotion may be advantageous for lizards navigating turns. The linear speed did not differ between 0.9 m and 1.1 m on either track. Yet, the linear speed at 1.4 m was significantly slower than the linear speed at 0.9 m and 1.1 m on both the 45 and 90 track. Thus, there is a cost of the turn whereby linear speed declines. Because the speed between 0.9 m and 1.1 m were not different, this indicates that acceleration is a more critical variable to escape than speed when combined with intermittent locomotion. The speed of the turn was significantly slower when there was a pause in the turn for trials with no pauses and for pauses before the turn. This result strongly suggest that scrub lizards accelerate fast enough that using intermittent locomotion may enhance predator escape.

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