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Getting Up to Speed: Acceleration Strategies in the Florida Scrub Lizard, *Sceloporus woodi*

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ABSTRACT

Small animals typically rely on quick bursts and intermittent pauses when moving in the wild. Hence, the study of acceleration capacity is important for understanding the ecology and evolution of locomotor performance. In this study, we investigate intraspecific variation in the acceleration capacity of a small lizard (*Sceloporus woodi*). To quantify animal acceleration performance, the momentum-impulse theorem is applied to data collected from high-speed video recordings of individuals accelerating from a standstill and over a subsequent distance of 0.4 m. Unlike earlier studies, the momentum-impulse approach allows one to directly and precisely quantify the per step contribution to acceleration capacity. Like other small vertebrates, we show that *S. woodi* is capable of accelerating to near maximum speeds ($\sim$2 m s^{-1}) within $\sim$0.4 m and needs only a few steps (at least five) to achieve maximum speed. However, considerable intraspecific variation in acceleration capacity exists; individuals take different numbers of steps (two to five steps) over the first 0.4 m, and only some individuals (10 of 19) reach their maximum speed over the first 0.4 m. Only acceleration performance in steps 1 and 2 is predictive of running speed at 0.4 m; accelerations in steps 3, 4, and 5 are not related to individual differences in speed. Individual variation in acceleration strategy is considerable, with individuals using one of three strategies to reach maximum speed. Muscle mass-specific power during acceleration approaches the maximum power output measured for lizard hindlimb musculature ($\sim$900 W kg^{-1}), suggesting that *S. woodi* accelerations approach the limit of their musculoskeletal system. This study highlights the utility of the momentum-impulse approach to study acceleration performance and the importance of elucidating the per step contribution to acceleration capacity.

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Introduction

Animals use locomotion in a variety of ecologically relevant contexts, such as predator evasion, prey pursuit, and territorial defense (Swingland and Greenwood 1983). As such, how well an individual can perform within these contexts is predicted to affect survival and reproduction (Garland and Losos 1994; Irschick and Garland 2001). Studies have shown that both natural and sexual selection can act on maximum locomotor performance (reviewed in Irschick et al. 2008) and that locomotor performance has undergone evolutionary adaptation to the structural environment (e.g., *Anolis*; Losos 1990) and has evolved with foraging behavior (Garland 1999; Miles et al. 2007). Clearly, the study of locomotor performance is important for broadening our understanding of organismal ecology and evolution.

Historically, studies of locomotor performance focused on steady-speed, maximal performance (i.e., sprint speed and endurance capacity). This large body of work greatly enhanced our understanding of how locomotion is related to organismal ecology and evolution. Unfortunately, few of these studies provide insight into how animals actually move in the wild or attain high speeds. Most small animals move intermittently using quick bursts and pauses (Irschick 2000; Mattingly and Jayne 2005; McElroy et al. 2007) such that the ability to escape a predator or defend a territory is more likely dependent on explosive acceleration to fast speeds than it is on absolute maximum sprint speed (Huey and Hertz 1984; Webb 1986; Miles 2004; Vanhooydonck et al. 2006*a*, 2006*b*). Thus, an understanding of acceleration capacity as animals move from a standstill to maximum speed is required if we are to more completely understand the relevance of locomotor performance to animals in nature.

The study of acceleration capacity is gaining momentum. Over the past several years, new studies have emerged showing accelerations' morphological correlates (Vanhooydonck et al. 2006*b*), biomechanical underpinnings (Biewener and Blickhan 1988; Irschick and Jayne 1998; Roberts and Scales 2002; Aerts et al. 2003; Roberts and Marsh 2003; McGowan et al. 2005; Scales and Butler 2007; Clemente et al. 2008; Williams et al. 2009), muscle physiological predictors (Wilson et al. 2000; Curtin et al. 2005), and ecological relevance (Vanhooydonck et al. 2006*a*, 2006*b*; Schuett et al. 2009). These studies have clearly demonstrated that acceleration capacity is an important facet of overall locomotor performance. One commonality of these investigations is that acceleration decays exponentially with step

number (Huey and Hertz 1984; Irschick and Jayne 1998), which suggests that acceleration in the first couple of steps is the most important for achieving large speeds. However, each of these earlier studies uses peak acceleration per step (defined as the maximum value of the acceleration-time curve for a whole animal bursting from a standstill) or "average" acceleration over short intervals (Huey and Hertz 1984; Irschick and Jayne 1998).

By studying only peak acceleration or average acceleration, previous studies have conveyed only a partial understanding of how acceleration affects running speed. Acceleration is defined as the increase in speed over time. When animals accelerate from a standstill, they use successive steps to generate the accelerative force necessary to increase the speed of the whole animal. We define acceleration performance as the total increase in speed over time (where time could be a step or stride); thus, maximum acceleration performance is the maximum increase in speed an animal can achieve over a given time. Defined this way, acceleration performance can be quantified using the momentum-impulse theorem such that the integral of the acceleration-time curve associated with each step is equivalent to the change in velocity of that step. The utility of using this approach is that one can account for the total effect that acceleration has on increasing speed; this cannot be achieved by quantifying only peak acceleration (a single value along this curve) or average accelerations (the mean value of this curve). Using this viewpoint, one can show that animals can achieve greater acceleration in two ways. First, an animal could lengthen the time component of the integral by increasing ground contact time (T_c) to increase impulse (Williams et al. 2009). Second, an animal could increase peak acceleration while keeping T_c very small (Vanhooydonck et al. 2006a; Williams et al. 2009). Each of these strategies appears to have a biological limit. Contact time cannot be too long because it will ultimately slow the entire burst locomotor event. While contact time cannot be too long, neither can peak acceleration be too large because it may exceed the ability of bone to withstand high peak stress (Biewener 2003) and/or the ability of muscle to generate short, high-power contractions (Swoap et al. 1993). Unfortunately, the relative contribution of these two strategies to burst locomotion remains relatively unexplored.

In this study, we demonstrate that by using the momentum-impulse approach one can quantify acceleration performance as the per step change in velocity associated with the integral of the acceleration-time curve (acceleration performance). Studying acceleration on a per step basis using the momentum-impulse approach is advantageous because it allows one to unequivocally identify which steps result in the greatest increase in speed. This is important because animals are hypothesized to reach maximum speed either by taking very few large accelerative steps or by taking many smaller accelerative steps (Hildebrand 1985; Irschick and Jayne 1998). By identifying which steps are crucial for increasing speed, one can then examine how T_c and peak acceleration contribute to acceleration performance and thus gain a better understanding of the biological limits of animal acceleration.

We first discuss the momentum-impulse approach and how it can be used to quantify per step acceleration performance capacity. Next, we provide data on intraspecific variation in acceleration performance in the lizard *Sceloporus woodi*. Animals used successive steps to accelerate from a standstill through 0.4 m; therefore, we were particularly interested in uncovering the relative contribution of successive accelerative steps to whole-animal speed at 0.4 m away from its starting position. We expected individuals with greater speeds to have greater per step acceleration performance and to take more steps over the first 0.4 m. In addition, we expected that high acceleration performance in the first few steps would be the most important for generating the highest speeds. Next, we explore the relative contribution of peak acceleration and contact time to altering per step acceleration performance for the first two steps of burst locomotion. Finally, we quantify whole-animal power over the 0.4-m locomotor burst and compare how individuals differ in power output. The examination of whole-animal mechanical power is highly relevant to studies of speed and acceleration since, by definition, power is the product of speed and acceleration and is well known to have biological limitations (Curtin et al. 2005; Scales and Butler 2007).

Methods

Biomechanical Analysis

The goal of our analysis was to estimate the contribution of successive accelerating steps to achieving maximum speed. To accomplish this goal, we employed a momentum-impulse approach to study acceleration capacity. This approach states that a change in a body's linear momentum must be achieved via the application of an impulsive force and is represented by the following equation:

$$\Delta \text{ momentum} = \int \text{force dt}. \tag{1}$$

Thus, the time integral of a ground reaction force must equal the change in momentum of the animal's center-of-mass. Expansion of the terms in equation (1) yields equation (2), which simplifies to equation (3) because whole-animal acceleration is being considered:

$$\Delta \text{ mass} \times \text{velocity} = \int \text{mass} \times \text{acceleration dt,} \tag{2}$$

$$\Delta \text{ velocity} = \int \text{acceleration dt.} \tag{3}$$

Equation (3) shows that any change in the center of mass velocity is equivalent to the time integral of the acceleration profile that caused that change in velocity. Studying an animal accelerating from a standstill (velocity = 0) to its maximum speed reduces the left side of equation (3) to maximum speed. The accelerations involved to achieve this maximum speed are

the integral of the acceleration-time curve, which results from craniocaudal ground reaction forces produced by successive steps. Thus for our study, the momentum-impulse principle can be written as follows:

$$\text{Maximum velocity} =$$
$$\int \text{acceleration 1 dt} + \int \text{acceleration 2 dt} \ldots \int \text{acceleration } k \text{ dt},$$

(4)

where k is the step in which maximum velocity is achieved. This simple mathematical approach allows one to determine the relative contribution of each step's acceleration performance to achieving maximum speed. In addition, this approach allows one to calculate the per step change in velocity via digitized high-speed video or normalized craniocaudal ground reaction forces.

A custom LABVIEW VI was written to graphically display the acceleration profile and automatically calculate the accelerative integral for each step. The position of touchdown for each step on the acceleration profile was manually selected using footfalls quantified from high-speed video. We chose to calculate the accelerative integral for each step from the time a hindfoot contacted the substrate until the next opposite-side hindfoot contacted the substrate. Thus, the total amount of acceleration was calculated for each full step (contact time and aerial phase). For simplicity, we refer to the per step accelerative integral as acceleration performance.

Animals

We captured 19 adult male *Sceloporus woodi* from the Ocala National Forest in central Florida during April and June 2009. Animals were housed individually in 10-gallon aquaria with a loose sandy substrate; they were fed vitamin-dusted crickets three times weekly and misted with water daily. We used only healthy individuals for experiments.

Before all experiments, nontoxic white correction fluid was used to paint a small dot at the base of the occiput on the dorsum of each lizard. This marker was then digitized, and its position, velocity, acceleration, and power were estimated for each video frame of each trial.

Animals were placed in an incubator set at 35°C for 1 h before each trial and in between trials on the same day.

At the end of the locomotor study, 13 individuals were released at their point of capture. The other six were killed. Captive care and euthanasia procedures followed approved Institutional Animal Care and Use Committee protocols (College of Charleston: 2009-009; Georgia Southern University: I08009).

Locomotion Trials

Lizards ran down a flat racetrack toward a dark hide box. The racetrack was 3 m long and 0.35 m wide with wooden sidewalls 0.4 m tall. The surface of the track was covered with cork bark,

which provided excellent traction with minimal slippage as observed during video review. A Casio EXILIM EX-F1 camera (resolution 512 × 384) was suspended and collected video of the lizard's dorsum over the first 0.4 m of the racetrack. This distance seemed appropriate for achieving near maximal sprinting speed on the basis of distances reported in previous studies (~30 cm; Huey and Hertz 1984; Curtin et al. 2005). Video was collected at 300 frames per second, as suggested by Walker (1998) and following previous studies (Bergman and Irschick 2006; Vanhooydonck et al. 2006a, 2006b).

Lizards were positioned in a resting, motionless posture at the beginning of the racetrack with the entire body in the camera's field of view. Hand clapping or a tail pinch induced a rapid locomotor burst from this resting posture. Lizards were encouraged to move down the length of the entire racetrack by continued clapping. We classified trials as good or bad. Good trials were those in which the lizard ran in a straight line down the entire length of the racetrack, with no or very few pauses. Bad trials were those in which the lizard turned, attempted to climb the sidewall, or refused to run the entire length of the track. Only good trials were used in subsequent analyses. Each individual was run four to 10 times down the raceway. For further analysis, we used only the best trial from each individual, which was defined as either (1) the only trial in which that individual met our criteria for good or (2) the trial with the highest instantaneous speed while under the camera (i.e., the first 0.4 m of the 3-m racetrack).

The racetrack was equipped with Keyence fiber-optic sensors (FS-V32) placed at 0.25-m intervals along its length. Analysis of the speed data obtained from photocells showed that lizards increased their speed by a maximum of 1.61 m s^{-1} (range = 1.46–1.73 m s^{-1}) over any pair of photocells (e.g., between 1 and 2; 0.25 m) and 1.85 m s^{-1} (1.65–2.14 m s^{-1}) over every other pair of photocells (e.g., between photocells 1 and 3; 0.5 m). In addition, for the trials included in our subsequent analyses, individuals obtained maximum running speed over the following pairs of photocells: pair 1, $n = 7$; pair 2, $n = 3$; pair 3, $n = 1$; pair 4, $n = 3$; pair 5, $n = 2$; pair 6, $n = 2$; pair 7, $n = 1$. These data show that *S. woodi* is capable of acceleration to near maximum sprinting speed over a distance of ~0.4 m, justifying our choice of this distance for studying acceleration performance.

Video Analysis

We imported video to a PC and manually trimmed the video files using Adobe Premiere Elements computer software. Individual trials were trimmed to 10 frames before the lizard began moving until the lizard had run completely out of camera view down the racetrack. This consisted of 0.4 m of burst locomotion.

Video from the dorsal view was used to estimate the animal's position for each frame. We used the program DIDGE (A. J. Cullum, 1999) to manually digitize a marker at the base of the occiput to obtain position. Next, we used the program GCVSPL (Woltring 1986) to fit a quintic spline to the position data and

to calculate the first (velocity) and second (acceleration) derivatives from the spline coefficients fitted to the position data. We manually chose the spline cutoff frequency (usually ∼25 hz) for each trial, such that it eliminated secondary oscillations in the acceleration data (Aerts 1998). The output from this procedure was the instantaneous velocity and acceleration for each frame of each video. We multiplied instantaneous velocity by instantaneous acceleration and individual body mass to estimate instantaneous whole-animal power. Position, velocity, acceleration, and power profiles were imported into a custom Labview VI for further analysis.

The customized Labview VI allowed us to manually position footfall data on the acceleration and power curves for the duration of each locomotor bout. Footfalls (touchdown and liftoff of each hindfoot) were recorded by reviewing the video. Contact time was then calculated by subtracting the time of touchdown from the time of liftoff. After positioning, the VI automatically calculated the peak acceleration and peak power associated with each step. As mentioned above, the VI also calculated the numerical integral of the acceleration-time curve per step to estimate acceleration performance. One issue with this approach is that we took the derivative of the velocity-time curve to calculate acceleration and then took the integral of the acceleration-time curve to calculate acceleration performance. This method was chosen because it allowed us to estimate the total amount of accelerative effort (acceleration performance) with each step. Finally, the VI automatically found the maximum instantaneous speed and its time for each trial.

We present whole-animal power calculations in three ways in order to compare our results with previous investigations: raw whole-animal power, mass-specific whole-animal power, and muscle mass–specific whole-animal power. Mass-specific animal power was calculated by dividing instantaneous power by individual body mass. Body mass was measured for each individual just before each day of experiments using an Ohaus Scout Pro balance accurate to 0.1 g. Body mass averaged 3.4 ± 0.1 g for the *S. woodi* in this study. Muscle mass–specific power was calculated by dividing raw power by the muscle mass of the hindlimb retractors and extensors (see Curtin et al. 2005). We quantified the mass of the main femoral retractor (mm. caudofemoralis) and knee and ankle extensors (mm. ambiens and mm. gastrocnemius) via dissection of three preserved *S. woodi* specimens. These dissections indicated that retractor and extensor muscle mass constitutes an average of 4% of body mass in *S. woodi*. To approximate individual muscle mass, we multiplied individual body mass by this average muscle mass. This method assumes that 4% is an accurate estimation of muscle mass across all individuals in this study; future studies should test the validity of this assumption.

Statistical Analysis

We used JMP7 (2007; SAS Institute, Cary, NC) for all statistical analyses. We ensured that all variables were normally distributed before analyses.

We used a single-factor ANOVA to test for differences in the

percentage of maximum racetrack speed achieved at 0.4 m (response) between individuals that used different numbers of steps (main effect) to accelerate over 0.4 m.

Separate multiple linear regressions were used to examine the relative contribution of acceleration performance and power in steps 1, 2, 3, 4, and 5. Acceleration performance on step numbers (i.e., 1–5) was entered as predictors, and final speed at 0.4 m was entered as the response.

The results of the above multiple regressions indicated that acceleration performance during steps 1 and 2 were the only
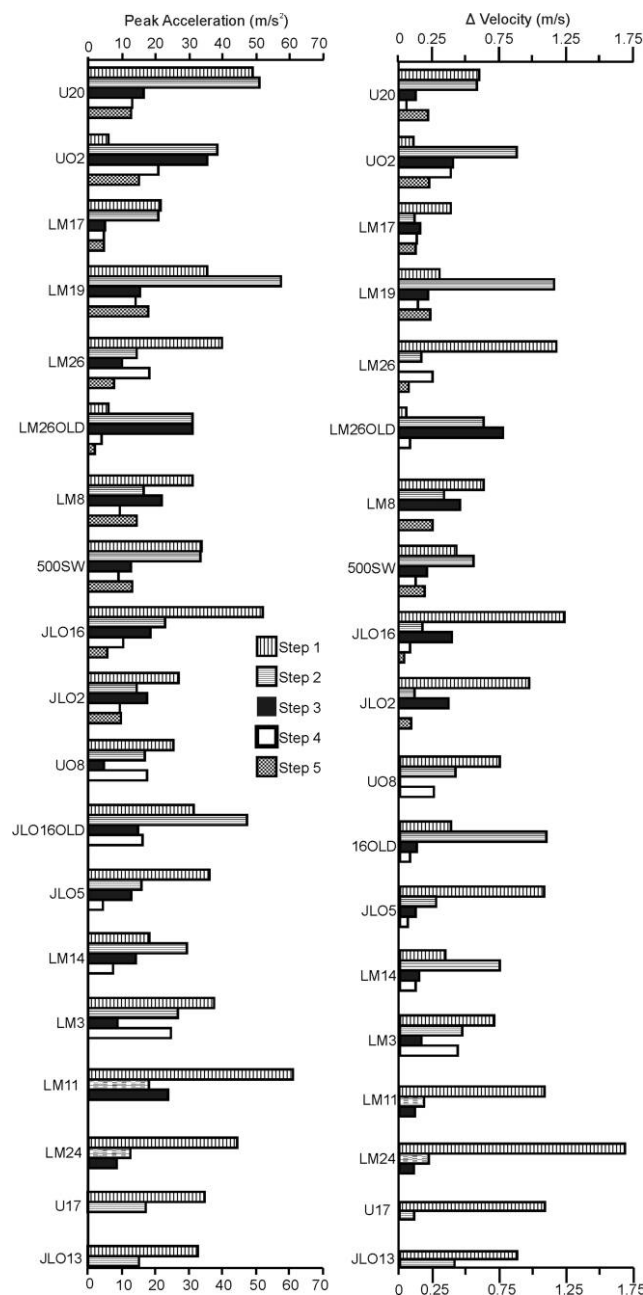

Figure 1. Bar diagrams for individual *Sceloporus woodi* (identifications along the vertical axis) showing per step peak acceleration and acceleration performance.

Table 1: Data for *Sceloporus woodi*

Steps to .4 m	n	Speed at .4 m (m s^{-1})	Maximum Racetrack Speed Reached (%)	Step 1 Acceleration Performance (m s^{-1})	CV	Step 2 Acceleration Performance (m s^{-1})	CV	Step 3 Acceleration Performance (m s^{-1})	CV	Step 4 Acceleration Performance (m s^{-1})	CV	Step 5 Acceleration Performance (m s^{-1})	CV
2	2	1.29 ± .07	54 ± 5	.98 ± .10	15	.25 ± .15	82						
3	2	1.74 ± .27	88 ± 8	1.38 ± .30	30	.20 ± .02	11	.11 ± .01	2				
4	5	1.69 ± .12	74 ± 5	.65 ± .14	47	.60 ± .15	54	.11 ± .03	56	.19 ± .07	84		
5	10	1.71 ± .14	96 ± 2	.59 ± .13	70	.47 ± .11	75	.31 ± .07	76	.12 ± .04	107	.14 ± .03	66

Note. Data include sample size (*n*), mean speed at 0.4 m, maximum speed reached at 0.4 m (%), per step acceleration performance ± SEM, and the coefficient of variation (CV) for acceleration performance. Data are split according to the number of steps required to reach maximum velocity.

significant predictors of speed. To further explore the inter-relationship between steps 1 and 2, linear regression (ordinary least squares) was used to test the relationship between step 1 versus step 2 acceleration performance. We also explored the relative contribution of ground contact time and peak acceleration (predictors) to per step acceleration performance (response) for steps 1 and 2. For all regression analyses, effect tests (*F*-tests) were used to test for significant predictors.

Analysis of steps 1 and 2 acceleration performance showed that *S. woodi* used three strategies to accelerate over the first two steps (see "Results"). To test the validity of this tripartite separation of the data, we used MANOVA with strategy as the main effect and acceleration performance in steps 1 and 2 as responses. Thus, we constructed planned linear contrasts (Quinn and Keough 2002) within two separate ANOVAs. One ANOVA compared the peak mechanical power on step 1 (response) between individuals with large accelerations on step 1 versus individuals using the two other strategies. The second ANOVA compared the peak mechanical power on step 2 (response) between individuals with large acceleration on step 2 versus individuals using the two other strategies. Finally, to explore the impact of mechanical power on speed and acceleration, we ran three separate multiple regressions. In all analyses, raw peak external mechanical power on steps 1 and 2 were entered as the predictor variables with the following as response variables (each a different analysis): (1) speed at 0.4 m, (2) step 1 acceleration performance, and (3) step 2 acceleration performance.

Finally, we calculated the coefficient of variation as a measurement of the variation in acceleration performance per step.

Results

Sceloporus woodi averaged 1.73 ± 0.09 (SEM) m s^{-1} (range = 1.11–2.57) at 0.4 m of the racetrack and 2.01 ± 0.09 m s^{-1} down the 3-m length of the racetrack. Over the first 0.4 m of the racetrack, individuals accelerated to an average of 86% of their overall maximum racetrack speed. However, individual variation in acceleration strategy was considerable. Individuals used from two to five steps to move across the first 0.4 m of the racetrack (Fig. 1; Table 1). The number of steps had a significant impact on the percent of maximum racetrack speed achieved over the first 0.4 m; individuals taking more steps

achieved a higher percent of their maximum racetrack speeds ($F_{3,15} = 19.15$, $P < 0.001$; mean percent maximum: two steps = 54%, three steps = 88%, four steps = 74%, five steps = 96%). Individuals using only two, three, or four steps never reached their overall maximum racetrack speed, whereas all of the individuals using five steps always achieved >84% of their maximum racetrack speed. Thus, *S. woodi* needs to take at least five steps over the first approximately half meter to achieve maximum running speed; fewer steps result in lower speeds over the first 0.4 m.

Acceleration performance during steps 1 and 2 was clearly the most important predictor of speed. For individuals using five steps, a multiple regression model with acceleration performance for steps 1, 2, 3, 4, and 5 as the predictor and speed at 0.4 m as the response found that acceleration performance in steps 1 and 2 was the only significant predictor of speed at 0.4 m (Table 2). To include all individuals, we also ran a multiple regression with acceleration performance in steps 1, 2, and 3 as the predictor and speed as the response. This model also

Table 2: Multiple regression models examining which steps' acceleration is the best predictor of speed at 0.4 m

Model and Predictor	Standard β	r²	F	df	P
Five steps		.94	12.12	5, 4	.016
Step 1*	.87				
Step 2*	1.22				
Step 3	.29				
Step 4	.11				
Step 5	.20				
All Individuals		.69	9.85	3, 15	.001
Step 1*	.82				
Step 2***	1.18				
Step 3	.32				

Note. Two separate analyses were run: (1) a model for individuals that used five steps to achieve maximum speed and included the acceleration performance from all five steps; and (2) a model with only steps 1, 2, and 3 as predictors but including all individuals, except those that took only two steps. Parameter estimates were standardized (standard β) by dividing the parameter by its standard error, which makes their values directly comparable. Statistically significant parameters determined via *F*-tests.
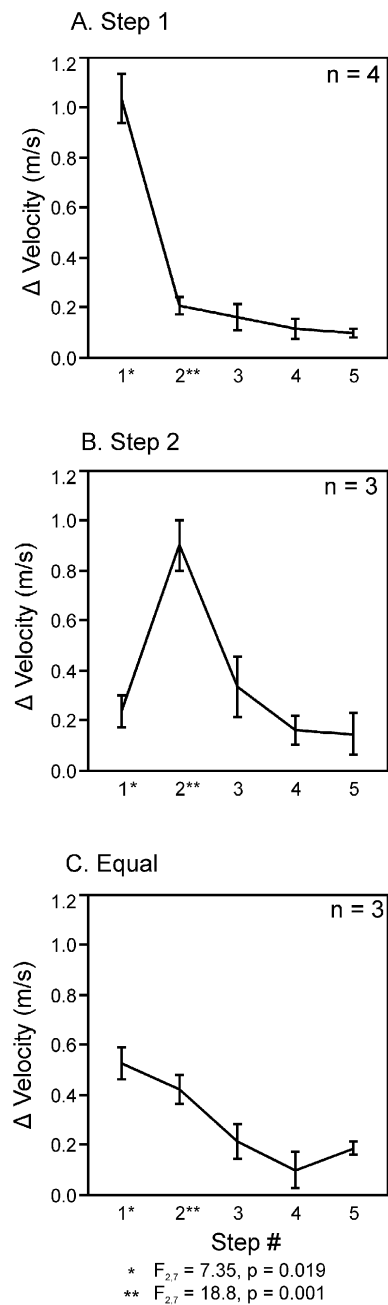
* $P < 0.05$.

*** $P < 0.0001$.

Figure 2. Mean values of per step acceleration performance for individuals reaching maximum acceleration performance on step 1 (A) and step 2 (B) and equal acceleration performance on steps 1 and 2 (C) in *Sceloporus woodi*. Only individuals that used five steps are shown; *n* indicates sample sizes. Error bars show ±1 SEM. Steps 1 and 2 are significantly different in acceleration performance between the three strategies. Steps 3, 4, and 5 do not differ (ANOVA, $P > 0.05$).

found that acceleration performance in steps 1 and 2 was the only significant predictor of speed (Table 2). Thus, larger accelerations in the first two steps are key to achieving faster speeds over the first 0.4 m of burst locomotion.

Although five steps were needed to achieve maximum speed within 0.4 m, the step in which an individual achieved peak

acceleration and the largest acceleration performance was variable (Fig. 1). Three acceleration strategies are apparent: (1) peak acceleration and acceleration performance on step 1, (2) peak acceleration and acceleration performance on step 2, and (3) equal peak acceleration and acceleration performance on steps 1 and 2 (Fig. 2). This tripartite grouping of the data is supported by the negative relationship between acceleration performance for step 1 and acceleration performance for step 2 ($\beta = -0.54$, $r^2 = 0.51$; $F_{1,17} = 17.76$, $P < .001$), such that individuals with a large acceleration performance in step 1 had a smaller acceleration performance in step 2 (Table 3; Fig. 3). In addition, a MANOVA with acceleration strategy as the main effect and steps 1 and 2 acceleration performance as the response variable shows that these groups are significantly different ($\lambda = 0.128$, $F_{4,30} = 13.48$, $P < .0001$). The top speed achieved by these strategies was statistically indistinguishable, although there was a tendency for individuals peaking on step 1 to be slower than those peaking on step 2 or with equal steps 1 and 2 (Table 3).

Separate multiple regression models for steps 1 and 2 with T_c and peak acceleration as predictors and acceleration performance as the response were generated to examine how *S. woodi* modulated these two variables to achieve maximum acceleration performance. These models found that peak acceleration and T_c have different impacts on step 1 versus step 2 acceleration performance. For step 1, *S. woodi* increases both T_c and peak acceleration in order to generate larger step 1 acceleration performance (overall model: $r^2 = 0.71$, $F_{3,15} = 12.11$, $P < 0.001$; effect tests: peak acceleration, $F_{1,15} = 10.28$, $P = 0.006$; T_c, $F_{1,15} = 25.57$, $P < 0.001$). For step 2, only increases in peak acceleration lead to an increase in step 2 acceleration performance (overall model: $r^2 = 0.75$, $F_{3,15} = 15.07$, $P < 0.001$; effect tests: peak acceleration, $F_{1,15} = 16.41$, $P = 0.001$; T_c, $F_{1,15} = 0.28$, $P = 0.60$). Thus, *S. woodi* modulates both ground contact time and peak acceleration to achieve larger acceleration performance and thus larger speeds.

The analysis of mechanical power indicated that individuals with large step 1 acceleration have higher peak power on step 1 when compared with the other strategies ($F_{1,18} = 4.62$, $P = 0.045$; Table 4; Fig. 4). Likewise, individuals with the largest step 2 acceleration had higher peak power on step 2 ($F_{1,18} = 5.31$, $P = 0.033$; Table 4; Fig. 4). Finally, individuals with the largest step 2 acceleration had higher peak power on step 2 than any other step by any other strategy ($F_{1,18} = 9.02$, $P = 0.005$; Table 4; Fig. 4). Mechanical power on steps 1 and 2 was predictive of both speed at 0.4 m and acceleration performance during steps 1 and 2 (Table 5). Results were similar for absolute, mass-specific, and muscle mass–specific mechanical power.

In general, variation in acceleration performance increased with step number (Table 1). Steps 1 and 2 had the lowest amount of variation, with increasing amounts of variation in steps 3, 4, and 5. The steps that had the lowest amount of variation (steps 1 and 2) were the best predictors of speed at 0.4 m, while those with the most variation (steps 3, 4, and 5) were the poorest predictors of speed (Tables 1, 2).

Table 3: Data for individuals that reached maximum acceleration performance on step 1 or step 2 or had equal acceleration performance on the first two steps

| Step of Maximum Acceleration | n | Speed at .4 m (m s^{-1}) | Step 1 | | Step 2 | |
			Acceleration Performance (m s^{-1})	Peak Acceleration (m s^{-2})	Acceleration Performance (m s^{-1})	Peak Acceleration (m s^{-2})
1	10	1.54 ± .10	1.03 ± .11[B]	37.5 ± 3.87	.22 ± .04[F]	16.9 ± .99[I]
2	5	1.99 ± .20	.24 ± .06[C]	19.5 ± 6.14	.90 ± .10[G]	40.8 ± 5.22[I]
1 and 2 equal	4	1.86 ± .10	.59 ± .06[C]	37.9 ± 3.94	.49 ± .06[H]	32.0 ± 7.29[J]
ANOVA:						
F		3.45	15.29	4.25	35.72	13.00
df		2, 16	2, 16	2, 16	2, 16	2, 16
P		.0568	.0002*	.0332	<.0001*	.0004*

Note. Data include speed at 0.4 m, acceleration performance, and peak acceleration ± SEM. The last three rows contain the results from ANOVAs with step of maximum acceleration as the main effect. Letters connect statistically similar values via a post hoc Tukey HSD.
* Denotes P values that remain significant after sequential Bonferroni correction (Quinn and Keough 2002).

Discussion

How Do Animals Accelerate Rapidly to Fast Speeds?

Two components are necessary to achieve the highest sprinting speeds within the first 0.4 m of locomotion: a high initial accelerative burst and at least five steps of acceleration. The initial burst from a standstill is critical; individuals with the greatest acceleration performance on step 1 and step 2 achieved the highest speeds by 0.4 m (Table 2). The acceleration performance achieved during steps 1 and 2 allowed *Sceloporus woodi* to reach ~70% of its maximum racetrack sprinting speed by the beginning of step 3 (Fig. 2; Table 1). Thus, as in previous studies (Huey and Hertz 1984; Irschick and Jayne 1998; Curtin et al. 2005; Vanhooydonck et al. 2006a, 2006b), we show that the superior acceleration performance in the initial steps of burst locomotion is key to obtaining high sprinting speeds that approach maximum speed over a very short distance (e.g., 0.4 m).

However, our analysis showed that more than just a good initial burst is required to reach a high speed. *Sceloporus woodi* must take at least five steps to reach near maximum sprinting speed (Table 1). Several lines of evidence support this finding. First, although steps 1 and 2 allow *S. woodi* to reach 70% of its maximum speed, it must continue with smaller acceleration on steps 3, 4, and 5 to reach maximum speed (Tables 1, 2; Fig. 2). Although maximum speed and acceleration performance have moderate to strong partial correlations across all steps, steps 3, 4, and 5 are not significant predictors of maximum
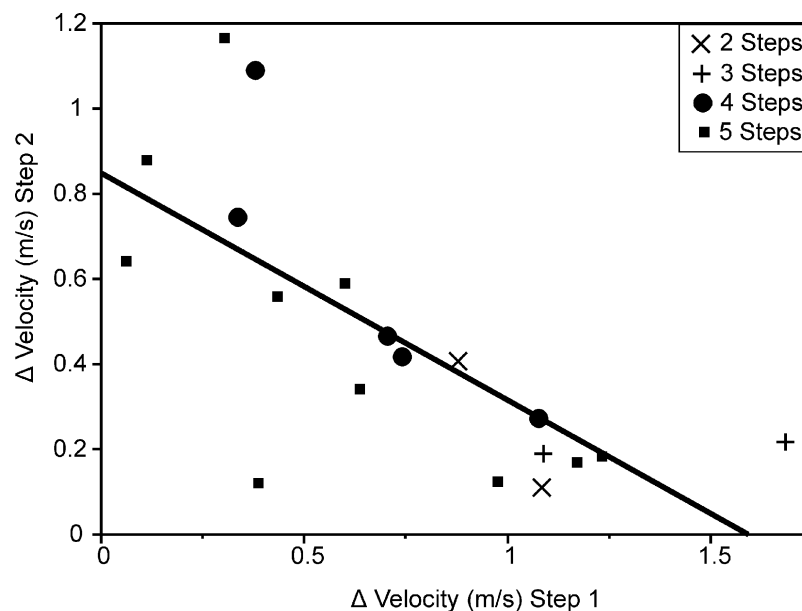

Figure 3. Linear regression showing inverse relationship between acceleration performance on step 1 versus acceleration performance on step 2 ($\beta = -0.54$, $r^2 = 0.51$; $F_{1,17} = 17.76$, $P < 0.001$).

Table 4: Data for burst locomotion in *Sceloporus woodi*

Acceleration Strategy	Peak Mechanical Power (W)		Body Mass–Specific Peak Power (W kg^{-1})		Muscle Mass–Specific Peak Power (W kg^{-1})	
	Step 1	Step 2	Step 1	Step 2	Step 1	Step 2
Step 1	.08 ± .02	.07 ± .01	23 ± 4	18 ± 2	576 ± 92	440 ± 43
Step 2	.02 ± .01	.13 ± .03	6 ± 3	39 ± 8	142 ± 73	983 ± 211
Equal	.06 ± .02	.07 ± .02	20 ± 7	27 ± 9	491 ± 179	676 ± 235

Note. Values are means ± SEM. Muscle mass–specific power was calculated assuming full activation of the hindlimb retractors and extensors, which constitute ∼4% of body mass in *S. woodi*. Data are divided into the three strategies used during the first two steps of burst locomotion (see "Results").

speed (Table 2), and this is likely due to the high variability of acceleration in those steps (Table 1). Thus, lizards must simply have some acceleration during steps 3, 4, and 5 to reach maximum locomotor speed over a distance of 0.4 m. This conclusion is supported by our finding that individuals that used five steps to reach maximum speed reached, on average, 96% of their maximum racetrack speed, while individuals taking fewer steps to reach maximum speed reached lower percentages (54%–88%) of their maximum (Table 1). We note that individuals taking fewer than five steps over the first 0.4 m likely need a greater distance than we filmed (>0.4 m) to take additional accelerative steps and achieve maximum running speed. An experimental setup with multiple cameras or sensors to measure instantaneous acceleration and speed over greater distances would be useful for addressing this issue. We urge future investigations of acceleration capacity to quantify acceleration performance for all steps to maximum speed in order to examine the generality of this finding.

In a running animal, acceleration performance (i.e., the acceleration integral) can be increased in two ways: (1) the time of ground contact (T_c) and/or (2) peak acceleration could be increased. However, which of these strategies results in the high-

est acceleration performance and the largest speed over a short distance? We show that both T_c and peak acceleration can be adjusted during the first two steps of burst locomotion. On step 1, increases in both T_c and peak acceleration result in greater acceleration performance, whereas on step 2, increases in only peak acceleration resulted in greater acceleration performance. Coupled with our finding that step 2 acceleration performance is the best predictor of maximum speed (Table 2), we conclude that increases in peak acceleration during step 2 will have the most profound impact on maximum running speed in *S. woodi*. We note that this finding is different from that of Irschick and Jayne (1998) and Vanhooydonck et al. (2006*a*), suggesting that lizard species are variable in how they accelerate and that different steps might be important in different species.

Interestingly, a trade-off exists between step 1 and step 2 in acceleration (Table 3; Fig. 2). Individuals with good accelerations on step 1 have poor acceleration on step 2 and vice versa. This result suggests that individuals that have a poor start on step 1 are able to quickly recover with a large acceleration during step 2 and achieve the same speed in the same number of steps. One explanation for this finding is that the initial limb
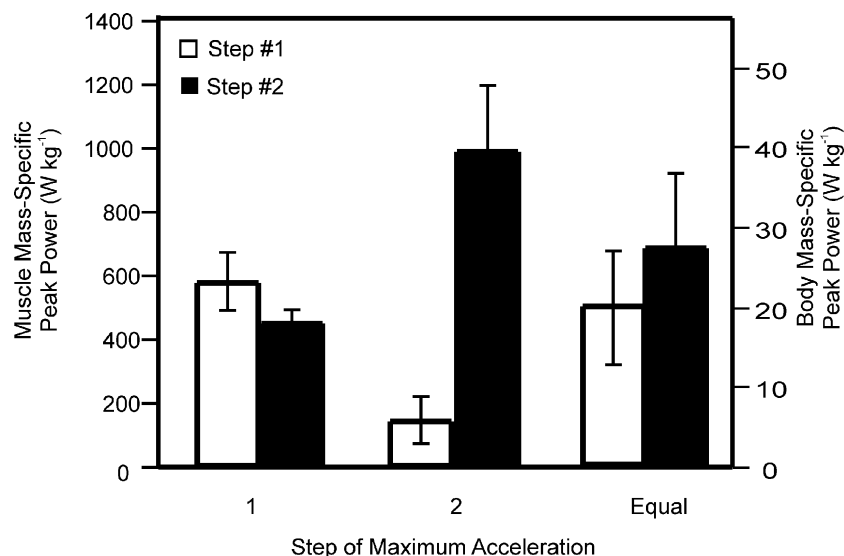

Figure 4. Muscle mass– and body mass–specific external mechanical power for steps 1 and 2. The data are split into the three ways that maximum acceleration was achieved (step 1, step 2, equal steps 1 and 2).

Table 5: Multiple regression models examining which steps' peak
external mechanical power output is the best predictor of speed at
0.4 m and acceleration performance

Model (Response) and Predictor	Standard β	r^2	F	df	P
Speed at .4 m		.71	19.37	2, 16	.001
Peak power 1	.005				
Peak power 2	.840***				
Acceleration performance:					
Step 1		.74	22.80	2, 16	.001
Peak power 1	.849***				
Peak power 2	−.390*				
Step 2		.86	48.11	2, 16	.001
Peak power 1	−.613***				
Peak power 2	.828***				

Note. Parameter estimates were standardized (standard β) by dividing the parameter
by its standard error. Statistically significant parameters were determined via F-tests.

  * $P < 0.05$.

  *** $P < 0.0001$.

configuration before step 1 may have been suboptimal for achieving maximum muscle activation and acceleration force in some individuals. Thus, these individuals may compensate for this initially poor configuration by maximally activating the musculature during step 2. Kinematic data are needed to test this hypothesis. This variability in per step acceleration performance must be accounted for in future efforts to understand the evolution and functional morphology of acceleration via adequate intraspecific sampling (Wainwright et al. 2008).

Does Mechanical Power Limit Accelerations and Running Speed?

Previous studies have suggested that mechanical power does not limit maximum locomotor speed during horizontal running in limbed animals (Farley 1997; Irschick et al. 2003). However, these studies also suggest that other aspects of performance, such as acceleration or maneuvering, may be limited by the mechanical power that the limb musculature can generate. One study supports this idea, showing that the first few steps of acceleration result in whole-animal mechanical power that approaches the limit of muscle power previously measured for lizards ($\sim$900 W kg^{-1} in *Acanthodactylus boskianus*; Curtin et al. 2005: Fig. 1, *right*). Our data reveal a similar amount of body mass–specific and muscle mass–specific mechanical power during step 2 in *S. woodi* (Table 4; Fig. 4), suggesting that available muscle power limits the mechanical power required to sustain large accelerations in *S. woodi*.

Could a power limitation on acceleration result in a power limitation on maximum speed? Imagine two animals that both accelerate from a standstill to the same maximum speed. Animal 1 initially uses high-power, large-acceleration steps and then shifts to low-power, low-acceleration steps as it approaches maximum speed. This situation is biologically realistic and has been observed in a number of small animals (Huey and Hertz

1984; Irschick and Jayne 1998; Curtin et al. 2005; Vanhooydonck et al. 2006*a*), including *S. woodi* (Tables 1, 4). Animal 2 produces very low acceleration initially but still reaches the same maximum speed. Animal 2 could reach the same maximum speed as animal 1 only by (1) taking more steps and adding up very small accelerations to achieve maximum speed or (2) using huge accelerations at higher speeds, because the animal has already taken two to three low-acceleration steps. Solution 1 is possible because muscles could continue to operate at submaximal power ($<\sim$1,000 W kg^{-1}) for many steps; however, it is unlikely in nature because most small animals achieve maximum speed with just a few steps (Huey and Hertz 1984; Irschick and Jayne 1998; Curtin et al. 2005; Vanhooydonck et al. 2006*a*; this study), and when moving in the wild, animals use an intermittent, burst locomotor strategy that precludes taking many low-power steps (Irschick 2000; McElroy et al. 2007). Solution 2 is probably impossible because the musculature cannot operate at the astronomically large power (e.g., 2,500–3,000 W kg^{-1}) needed to couple large peak accelerations (50–60 m s^{-2}) and very fast speeds (2 m s^{-1}). Thus, it seems likely that muscle power constrains small animals to using large accelerations within the first couple of steps of burst locomotion (when speeds are slow), as has been observed in many small animals (including in this study). Furthermore, if large accelerations are constrained to the first couple of steps (Table 1) because of a limit in muscle power (Table 4) and those steps are predictive of maximum speed (Tables 2, 5), then it is plausible that maximum speed could be limited by the available power during the first couple of steps during burst locomotion. This hypothesis could be tested via the use of loading experiments (Irschick et al. 2003), which examine power output, acceleration, and speed for each step involved in burst locomotion from a standstill to maximum running speed.

While the above argument applies to individuals reaching

maximum acceleration performance and power on step 2, what about individuals reaching maximum values on step 1 or having equal steps 1 and 2? In these strategies, power output is considerably less than the maximum power output the extensors and retractors are capable of producing (Fig. 4; Table 4). Thus, in individuals that reach maximum acceleration performance and power on step 1 or having equal steps 1 and 2, muscle power is operating at a suboptimal level. As mentioned above, suboptimal acceleration and power could result from disadvantageous initial limb configurations or kinematics. Another possibility as to why animals chose these strategies is that excessively large accelerations can cause the body to pitch upward and the lizard to topple backward (Aerts et al. 2003). We did not observe any subjects pitch upward at the start of a run, yet this hypothesis seems particularly relevant to taxa that use both quadrupedal and bipedal locomotion (see Aerts et al. 2003). Many lizard species (e.g., *Acanthodactylus*, *Aspidoscelis*: E. J. McElroy, personal observation) run bipedally within the first few steps and likely do so via large accelerations in steps 1 and 2. Other species run bipedally only after many steps or meters (e.g., *Callisaurus*: Irschick and Jayne 1999; *Crotaphytus*: E. J. McElroy, personal observation). These other species may apply solution 1 from above; they sum several steps each with smaller accelerations until they attain a high speed quadrupedally and then switch to bipedal locomotion (see also Clemente et al. 2008). Thus, per step acceleration performance, maximum acceleration, and power could be physiological factors that explain variation in gaits or locomotor modes that animals use in nature. Although we lack the data to test these hypotheses, the momentum-impulse approach could be applied to such problems, given the appropriate field data on gait transitions and bipedality.

Acceleration is clearly important for animal fitness (Miles 2004), is correlated with other ecomorphological variables (Vanhooydonck et al. 2006a, 2006b), and scales with body size (Huey and Hertz 1984; Vanhooydonck et al. 2006b); however, until now, a basic functional framework for studying acceleration performance was lacking. We demonstrate the utility of the momentum-impulse approach as a first step in identifying the strategies that small animals use to achieve high accelerations and maximal velocities in the first few steps of burst locomotion. We see this approach as an advance over previous studies because we show that T_c and peak acceleration account for only ~70%–75% of the variation in the change in speed over steps 1 and 2 (see "Results"), which is captured by using the momentum-impulse approach. Future studies could combine this method with measurements of limb kinematics, mechanics, anatomy, and gait transitions to develop an integrative functional framework for studying the biomechanics of acceleration capacity in terrestrial animals.

Acknowledgments

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