Are powerful females powerful enough? Acceleration in gravid green iguanas (*Iguana iguana*)

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Synopsis One demand placed exclusively on the musculoskeletal system of females is maintaining locomotor performance with an increasing load over the reproductive cycle. Here, we examine whether gravid (i.e., “pregnant”) iguanas can increase their force and power production to support, stabilize, and accelerate the additional mass of a clutch of eggs. At any acceleration, gravid iguanas produced very high mechanical power (average total power = 673 w/kg; total peak power = 1175 w/kg). While the increase in total power was partly a result of greater propulsive power (average propulsive power = 25% higher, peak propulsive power = 38% higher), increased vertical power (roughly 200% increase) was the main contributor. Gravid iguanas were also able to increase peak forces (propulsive = 23%, mediolateral = 44%, vertical = 42%), and step duration (44%) resulting in greater impulses (i.e., the sum of force produced during a step) to accelerate, balance, and support their increased mass. The increase in step duration and smaller increase in peak propulsive force suggests that gravid iguanas may be force-limited in the direction of motion. We discuss how biomechanical constraints due to females’ reproductive role may influence the evolution of the female musculoskeletal systems and contribute to the evolution and maintenance of ecological dimorphism in lizards.

Introduction During the lifetime of an animal, many different functional demands are placed on its locomotor system, including changes due to growth, reproduction, seasonal cycles in food supply, and predation intensity. These diverse life history and seasonal fluctuations may impose very different demands on the musculoskeletal system, brought about by changes in mass, overall size, nutritional status, or increased performance requirements. However, most locomotion studies consider only a single state at steady speed (the few studies exploring the range of functional capabilities are reviewed by Biewener and Gillis 1999). Understanding how organisms cope with the fluctuations experienced throughout the life cycle is critical to understanding the selective pressures and constraints responsible for the design of the musculoskeletal system.

One demand placed exclusively on females is maintaining locomotor performance during the large increase in mass as females produce offspring or eggs ( gravidity). Since the females of many taxa carry large reproductive loads, often repeatedly throughout life, this is a widespread and potentially important selective pressure that has received relatively little study. Are females designed for the gravid state, implying that their musculoskeletal systems are overengineered for the majority of the year? Or, alternatively, do they suffer a great performance decline when they are gravid?

Gravidity is known to reduce sprint speed or endurance in many taxa (birds: Lee et al. 1996; Veasey et al. 2001; Kullberg et al. 2002; fish: Ghalambor et al. 2004; salamanders: Finkler et al. 2003; snakes: Seigel et al. 1987), thereby increasing the vulnerability of females to predators. Lizards, which have often served as a model for locomotor adaptation (Irschick and Garland 2001), have commonly shown similar reductions in sprint speed with gravidity (Shine 1980; Bauwens and Theon 1981; Van Damme et al. 1989; Sinervo et al. 1991). In addition, female lizards with greater performance capacity may have a competitive advantage for the best home ranges or nesting sites. Therefore, females that can effectively undergo locomotion while carrying a reproductive load may enjoy a fitness benefit over those that cannot.

One ecologically important locomotor task is acceleration. Many animals use intermittent locomotion, which requires frequent accelerations.
Additionally, acceleration is important in determining the outcome of predator–prey interactions (Elliot et al. 1977; Huey and Hertz 1984). The increased mass of a clutch, however, will directly reduce acceleration unless greater force is applied in compensation (by Newton’s second law, we know that acceleration is force divided by mass). Therefore, a female carrying a reproductive load must increase her production of force proportionally to her increased mass to achieve the same acceleration.

In terrestrial animals, production of force can only occur while the foot is in contact with the ground. Therefore, animals carrying loads may compensate by either increasing the magnitude of force produced, or by producing the same magnitude of force but instead increasing the time over which it is applied. The first will result in increased power, as power is the product of force and velocity (all values are instantaneous), whereas the second will not.

Green iguanas and acceleration while gravid

Green iguanas (Iguana iguana) provide an exceptional opportunity to investigate whether females can accelerate when burdened with a clutch. Female iguanas are excellent runners and carry very large clutches (ranging from 31% to 63% of their nongravid body mass). Despite this large reproductive load, female iguanas travel long distances to reach their preferred nest sites, which presumably increases their exposure to predators (Rodda 1992). Upon arrival at the nest site, they excavate large nests in the sand, all the while fighting off competing females (Rand 1968). Thus, female iguanas are probably under strong selection for locomotor ability, precisely at the time when they perform their most demanding locomotor tasks.

Additionally, acceleration is especially relevant for escape of predators by iguanas. Iguanas commonly use short sprints to refugia (e.g., burrows, bodies of water) to avoid predators such as crocodiles, boa constrictors, large birds of prey, tayra, coatis, wild cats, and humans (Greene et al. 1978, personal observation).

While most lizards show a reduction in performance during gravidity (see references cited previously), we found in a previous study that iguanas exhibit impressive compensation (Butler, in review). Despite reproductive loads of 31–63% of maternal mass, gravid iguanas were able to match the acceleration of non-gravid iguanas in the initial burst from a standstill. This was a kinematic study only, where forces were not measured. In the present study, we used force plate analysis to test whether gravid iguanas can increase their force and power production during a step, in order to support, stabilize, and accelerate the increased mass of a clutch.

Materials and methods

Thirteen gravid iguanas were collected from Boca Raton, Florida (February, 2005) and transported to a laboratory at the University of Tennessee. The iguanas were group housed on a 12 h : 12 h D : L cycle with food and water available ad libitum. UV lights and ceramic heat lamps provided a temperature gradient suitable for basking, while room temperature was maintained at 29°C. Animal collection, care, and experimental protocols were approved by the UTK IACUC (protocol no. 1203).

Reproductive conditions

Presence of eggs was determined by ultrasound, and all iguanas were initially gravid. After 50 days recovery from oviposition, females were rerun as controls in running trials. Trials continued from 50 to 80 days postoviposition and no difference in performance was found over this time. At this time, iguanas had recovered a normal body tone, resumed normal eating behavior, and had put on significant weight. Furthermore, these animals returned to normal rates of activity and resistance to being handled by humans. We call this group “postgravid”.

Acceleration trials

Prior to all running trials, iguanas were brought to a standard body temperature of 35–37°C by placing them in a warm water bath. Body temperatures were verified immediately prior to all runs. Iguanas were placed immediately in front of a force-plate embedded in a 7 m trackway. A startle-response was elicited by rapid movements of a large cloth, lunging movements towards the animal, or clapping the tail of the iguana. Video and ground reaction forces were recorded as the iguanas accelerated across the force-plate. Gravid iguanas were run 1–2 times per day, while recovered iguanas were run 2–3 times per day. Iguanas were given a minimum of 15 min rest between runs, and 2 days rest between trial days. Only runs in which the iguana ran straight down the trackway and an isolated hind limb landed on the force-plate were considered for analysis (other limbs were in contact with the ground, but not on the force plate). Of these trials, the run with the highest acceleration was selected for each individual for each reproductive condition, gravid and recovered. Therefore, while over 300 runs were collected, only 19 trials were used in the analysis. The health of the iguanas was monitored continuously throughout the experiment. Animals were removed from the
experiment if they showed signs of fatigue, injury, or poor health.

**Video analysis**

In order to digitize video images, reflective markers made of retro-reflective tape (3M Scotchlite 8850 Silver Pressure Sensitive Adhesive Film, Motion Lab Systems, Inc.) covering 4 mm balsa wood spheres were attached above the middle of the iguana’s pelvis. The pelvis was chosen to represent the center of mass because it is an easily located landmark and is near the estimated center of mass of iguanas. Dorsal and lateral views of lizards running on the track were simultaneously recorded using two Photron™ Fast Cam high-speed video cameras operating at 125 Hz. Kwon CC was used to calibrate the two camera views and compute DLT parameters for reconstructing camera coordinates in three dimensions. Video recordings were digitized using Kwon 3D 3.0 and position data were smoothed using QuickSAND’s MSE quintic spline algorithm (Walker 1998). Velocities and accelerations of the center of mass were calculated by differentiating QuickSAND’s MSE quintic spline (Walker 1998).

**Work and power**

Ground reaction forces were measured using a Kistler 9286A force-plate with signals acquired using Bioware® software (Kistler). Force signals were initially acquired at 125 Hz for gravid iguanas, while force signals were collected at both 1000 Hz and 125 Hz for recovered iguanas. As we could not recollect data on gravid individuals, we tested for an effect of low collection rate. Having found no significant difference (see Results section), we report only data collected at 1000 Hz for recovered iguanas. Force signals collected at 1000 Hz were filtered in Bioware using a second-order low-pass Butterworth filter with a cutoff frequency of 50 Hz. Force signals acquired at 125 Hz were filtered in Bioware using a second-order low-pass Butterworth filter with a cut-off frequency of 30 Hz. Video recordings and force acquisition were synchronized using an external trigger.

Force, work, and power estimates are of isolated hind limbs, not taking the forelimbs into account. Therefore, the estimates are not of all force and work performed on the center of mass. However, the hind limbs provide the majority of propulsive force in running lizards (Aerts et al. 2003; Chen et al. 2006). Work can be measured as changes in kinetic energy (ΔKE) during hind limb footfalls. Thus, ΔKE was obtained by integrating the forces in each of three directions (fore-aft, mediolateral, and vertical) with initial velocities (v₁) of the center of mass obtained from the video analysis and final velocities (v₂) obtained from force data (work = ΔKE = 1/2 m[v₂² - v₁²], where m = mass). Fore-aft and mediolateral forces contribute to kinetic energy, while integration of vertical force contribute to both kinetic and potential energy. Net work was measured by summing work in all three directions. Power (P) was calculated by numerical differentiation of the change in kinetic energy with respect to time (P = ΔKE/Δt, where Δt = length of the time interval).

Hind limb extensor muscles constitute approximately 6% of body mass in the lizard species Acanthodactylus boskianus (Curtin et al. 2005). We measured total hind limb mass in three postgravid iguanas, and obtained a similar figure of 6.2%. We assumed that hind limb muscle-mass did not change with reproductive condition, so we estimated the hind limb mass for each individual based on this figure and their recovered body mass.

**Statistical analysis**

We tested whether gravid iguanas vary in measures of power, force, work, and step duration using general linear models. We included acceleration as an explanatory factor in these models because, although there was no significant difference between accelerations of gravid and postgravid iguanas, there was significant variation within groups. Also, the mean difference between groups (over 1 m/s²) may be biologically, if not statistically, significant (Table 1). Thus, for each of the above dependent variables, we tested models with the following independent variables: reproductive state (RS), acceleration (A), and their interaction (RS × A). We began with the full model, but dropped the interaction if it was not significant. The final models used in the analysis are reported in Table 1, where we report both the raw means and least-square means.

Gravid and postgravid iguanas did differ in step velocity (Table 1). However, velocity had no significant affect on work, power, or force differences between the reproductive classes. Thus, it was not included in the model for these variables. We also tested for effects of velocity on acceleration and step duration (Table 1). All statistical analyses were performed in the SAS statistical language (SAS 1994).

**Results**

**Differences in collection rate**

The difference in collection rate for gravid iguanas did not result in any significant error in force measurement. Specifically, it resulted in a 3.2% [±9.0% standard deviation (SD)] underestimation
in peak fore-aft force, an 11.3% (±14.6% SD) underestimation in peak mediolateral force, and a 1.3% (±15.3% SD) underestimation of peak vertical force. The difference in forces resulted in only 1.0% (±15.3% SD) underestimation in work, a 0.3% (±14.5% SD) overestimation of average powers, and a 3.5% (±8.7% SD) underestimation of peak instantaneous powers.

Change in mass and work during a step
Gravid iguanas weighed significantly more than did postgravid iguanas (Table 1). Individuals were, on average, 51% heavier during gravid trials than postgravid trials. Gravid iguanas produce 120% more net work with their hind limbs than did postgravid iguanas, respectively. Gravid iguanas produced 70% greater average (114% more if means are adjusted for acceleration) and 76% higher peak mass-specific total power (123% higher if means are adjusted for acceleration) in the hind limb than did postgravid iguanas (Table 1, Fig. 2).

Significant increases in the vertical direction are the main components of power increase for both average and total measures. Similar to net work, gravid iguanas increase power (average and total increased by about 200%, and over 230% if means are adjusted for acceleration) in the vertical direction, more so than in the propulsive, although both are significantly increased (Table 1, Fig. 2). Again, mediolateral power is very small in both groups (Table 1, Fig. 2).

Power production
Both gravid and postgravid iguanas produced extremely high hind limb power output, with the highest recorded average powers during a run at 1094 w/kg and 807 w/kg for gravid and postgravid iguanas, respectively (numbers given in Table 3 are averaged over individuals, whereas here we report maximal values). Maximal values for peak powers reached 1565 w/kg and 1344 w/kg for gravid and postgravid iguanas, respectively. Gravid iguanas produced 70% greater average (114% more if means are adjusted for acceleration) and 76% higher peak mass-specific total power (123% higher if means are adjusted for acceleration) in the hind limb than did postgravid iguanas (Table 1, Fig. 2).

Independent terms included in the general linear model (GLM) for each variable (9) are coded as: RS, reproductive state; A, acceleration; and V, velocity, and RS × A, interaction between reproductive state and acceleration. Dependent terms were those listed in row names. P-values (P) and F-statistics (F) given refer to differences between reproductive state, either before (5) or after adjusting for other terms in the model (10,11).

Change in mass and work during a step
Gravid iguanas weighed significantly more than did postgravid iguanas (Table 1). Individuals were, on average, 51% heavier during gravid trials than postgravid trials. Gravid iguanas produce 120% more net work with their hind limbs than did postgravid iguanas (209% greater if means are adjusted for acceleration; Table 1, Fig. 1A). Increases in propulsive and vertical work produce the increase in network, with vertical work contributing more (Table 1, Fig. 1). Neither group produces significant mediolateral work (Fig. 1D).

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directions of motion (Table 2, Fig. 3). Gravid iguanas, however, tended to increase mediolateral impulse with acceleration more than did postgravid iguanas (Table 2, Fig. 3).

The increased impulses in each direction can be partially attributed to gravid iguanas producing greater mass-specific peak forces in the hind limb than did post-gravid iguanas for a given acceleration, with a 23% increase in peak propulsive, 44% increase in mediolateral, and 42% increase in vertical forces. (Table 2, Figs. 3 and 4). The increase in impulses is also driven by a 44% increase in step duration (Table 2, Fig. 5).

**Discussion**

**Work, power, and acceleration**

The increase in mechanical power output by gravid iguanas is very impressive considering that when they are nongravid, females are already producing very high mechanical power (Table 1). Compared to the average and peak power outputs of other vertebrate locomotor systems, post-gravid female iguanas produce very high power, but it is even higher when gravid (Table 3). The increasing mass of females during gestation places a large demand on their musculoskeletal system during locomotion, and here we find that gravid iguanas are able to compensate for this increased load by greatly increasing vertical force and power.

Interestingly, the increases in vertical power approach, or exceed, 200%, which is much greater than their 51% increase in mass. A super-isometric increase is also observed in propulsive and vertical work, and impulses in all directions. Naively, to maintain the same sprint performance, one might expect that a fractional increase in mass would require the same fractional increase in force. The “extra” work, power, and force that we observed may result from lack of coordination, difficulties in maintaining stability, or other inefficiencies.

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**Fig. 1** Net work performed by the hind limbs (J/kg of hind limb mass) of gravid (black circles and dashed line) and postgravid (open squares and solid line) iguanas during accelerations. Trend lines shown are least-squares regression performed on each group independently. (A) Total, sum of all three directions of movement. (B) Propulsive, the direction of movement. (C) Mediolateral, side-to-side movements. (D) Vertical, movement normal to the ground.
Fig. 2 Hind limb power production (W/kg of hind limb mass) by gravid (filled circles, dashed lines) and postgravid (open squares, solid lines) iguanas during accelerations. Only peak powers are shown as both average and peak powers showed identical trends. See Fig. 1 legend for explanation of panels A–D.

Table 2 Force production and step durations of gravid and postgravid iguanas. See Table 1 for explanation of column/row names

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Peak forces (N/kg hindlimb)

| Propulsive | | | | | | | | | | | |
| Mediolateral | | | | | | | | | | | |
| Vertical | | | | | | | | | | | |

Step duration (s)

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P-values (P) and F-statistics (F) given refer to differences between reproductive state, either before (5) or after adjusting for other terms in the model (10,11).
Fig. 3 Hind limb force production (N x s/kg of hind limb mass) by gravid and postgravid iguanas during accelerations. Only impulses are shown as impulses and peak forces for total, propulsive, and mediolateral directions showed identical trends. See Fig. 1 legend for explanation of symbols and panels A, B, D. (C) Gravid iguanas tended to increase mediolateral impulse with acceleration while postgravid iguanas did not resulting in higher forces at higher accelerations. The trends in peak mediolateral forces appeared similar to those seen in impulse, but there was no significant difference in trends.

Fig. 4 Peak vertical force production (N/kg of hind limb mass) by gravid (filled circles, dashed line) and postgravid (open squares, solid line) iguanas during accelerations.

Fig. 5 Step durations of gravid (filled circles, dashed line) and postgravid (open squares, solid line) iguanas during accelerations.
Maintaining their acceleration while carrying a heavy load is a remarkable locomotor accomplishment performed by female iguanas. Two strategies could be employed by gravid iguanas, in order to produce the force necessary to maintain their acceleration: they could apply higher force over the same amount of time resulting in higher power output, or apply the same amount of force over a longer period of time resulting in a longer step duration. Gravid iguanas appear to use both strategies. While gravid iguanas do increase peak propulsive force (23% increase) and power (25% increase in average and 38% increase in peak), they do not fully compensate for their increased mass in this manner. Therefore, they also produce force for a longer period of time resulting in a 44% increase in step duration, suggesting that acceleration in gravid iguanas is force limited.

Also consistent with a force-limitation hypothesis are the changes in peak forces. While gravid iguanas increased peak vertical and mediolateral forces by 42% and 44%, respectively, peak propulsive force only increased by 23% suggesting that perhaps they could not increase peak propulsive forces further. Additionally, Butler (in review) found that gravid iguanas swing their legs faster than do recovered iguanas. In fact, even by the third stride during acceleration, gravid iguanas were swinging their hind limbs 21% faster than did recovered iguanas. The increase in swing speed would allow for longer force application per distance traveled, without increasing the duration of the step cycle. Therefore, for a given distance traveled, gravid iguanas would have more time for the force production required to accelerate their mass, but would not suffer a reduction in absolute performance. All these adjustments should significantly increase energetic cost. Thus, gravid iguanas are probably limited in the duration and number of sprinting bouts.

As a result of sprawling posture, lizards must exert more mediolateral force to maintain position of their center of mass than do animals with more upright postures. Here, we found that gravid iguanas increased mediolateral force production. Chen et al. (2006) found that ground reaction forces are likely important for providing dynamic stability in running lizards. Therefore, gravid iguanas may need to produce more mediolateral force in order to maintain the position and stability of their center of mass while carrying a clutch, but should not change mediolateral work or power (i.e., since they are running in a straight line, positive and negative work/power should sum to zero).

Given that recovered iguanas can produce such high power, which is what we observed, how do they increase power output when they are gravid? The ability for increased power output may come from the added mass of the clutch itself. In humans, external loading has been shown to increase short-term power output (Caiozzo and Kyle 1980; Kyle and Caiozzo 1985). While these authors concluded that optimal loading conditions must exist for maximizing power output, they do not apply this idea to sprinting. There is evidence, however, that this concept applies to sprinting animals. McGowan et al. (2006) found that guinea fowl were able to maintain locomotor performance while bearing an external load. This was partly achieved by increasing muscle activation. In addition, the loading increased the active stretching of the locomotor muscles. Active stretching of muscles enhances force production, which in turn, can enhance power output. Additionally, at high loads, stretch-induced power enhancement of muscle may last for an extended length of time (Cronin et al. 2001). Therefore, if nongravid iguanas are suboptimally loaded for maximum power output, the added mass of a clutch may load the locomotor muscles in a manner that prestretches them and enhances force and power output over the duration of a step.

**Locomotion, reproductive role, and ecological dimorphism**

Only females must contend with the problem of locomotion while carrying a clutch. If this is a
significant selective pressure, it may lead to sexual dimorphism in relative limb and body proportions. For example, accelerating with a reproductive load probably increases stress and strain on the musculoskeletal system of females. However, female lizards commonly have shorter limbs for a given body size than do males (Butler and Losos 2002; Irschick et al. 2005; Schwarzkopf 2005). This sexual dimorphism may be advantageous for accelerating with a load.

The relationship between limb length, posture, and joint mechanics in lizards is complex. The sprawling posture of lizards results in moment arms at joints, even when the animal is at rest. Shorter limbs would decrease moment arms, thereby reducing joint moments. Also, during acceleration, the shorter moment arm will result in greater force output. Additionally, one way to effectively support an increased mass effectively is to move the support limbs more directly under the mass. While lizards are capable of using a more upright posture, this increases stresses to their limb bones because of the details of their bone curvature (Blob and Biewener 2001). Therefore, shorter limbs in a sprawling animal will place the feet closer to the center of mass, without adopting a more upright posture. Smaller joint moments and lower bone stresses may be especially important for gravid animals, who need to increase propulsive force to counteract their increased load while remaining within safety factors for their bones and joints. Thus, the limb morphology of females may be constrained by reproductive role.

Relative limb length commonly reflects performance capabilities in lizards (Losos and Sinervo 1989; Losos 1990; Garland and Losos 1994; Bonine and Garland 1999 but see Vanhooydonck et al. 2006 for a study on limb muscles). Since the sexes differ in limb morphology and sometimes performance, biomechanical constraints may be responsible for this broad suite of sexual differences (Snell et al. 1988; Cullum 1998; Miles et al. 2001; Lailvaux et al. 2003; Irschick et al. 2005). Many studies have examined the influence of reproductive role on the evolution of performance and morphology, especially with regard to male behaviors (Garland et al. 1990; Perry et al. 2004; Husak et al. 2006). However, the mechanistic basis for these performance differences has been little studied. A research program integrating biomechanics, ecological pressures, and life-history changes is needed to understand the significance of sexual dimorphism in form and function.

Acknowledgments
The authors thank B. England, A. Fuller, K. Root, S. Tucker, M. Moses, C. Ross, T. Ives, S. Stanley, and J. Vandiver for assistance in care and running trials of iguanas. We thank D. Creer, K. Krysko, K. Enge, E. Lynk, J. Higa, R. Higa, and Crandon Park Zoo and Fairchild Tropical Gardens for help in animal collection. Helpful comments from Tom Roberts and Dave Carrier regarding data analysis and comments from two anonymous reviewers improved this manuscript.

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