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RESEARCH ARTICLE

Loading effects on jump performance in green anole lizards, *Anolis carolinensis*

Chi-Yun Kuo[1,*], Gary B. Gillis[1,2] and Duncan J. Irschick[1]

[1]Graduate Program in Organismic and Evolutionary Biology, University of Massachusetts Amherst, Amherst, MA 01003, USA and [2]Department of Biological Sciences, Mount Holyoke College, South Hadley, MA 01075, USA

*Author for correspondence (chiyun@bio.umass.edu)

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SUMMARY

Locomotor performance is a crucial determinant of organismal fitness but is often impaired in certain circumstances, such as increased mass (loading) resulting from feeding or gravidity. Although the effects of loading have been studied extensively for striding locomotion, its effects on jumping are poorly understood. Jumping is a mode of locomotion that is widely used across animal taxa. It demands large amounts of power over a short time interval and, consequently, may be affected by loading to a greater extent than other modes of locomotion. We placed artificial loads equal to 30% body mass on individuals of the species *Anolis carolinensis* to simulate the mass gain following the consumption of a large meal. We investigated the effects of loading on jump performance (maximum jump distance and accuracy), kinematics and power output. Loading caused a significant 18% decline in maximum jump distance and a significant 10% decline in takeoff speed. In other words, the presence of the load caused the lizards to take shorter and slower jumps, whereas takeoff angle and takeoff duration were not affected. By contrast, jump accuracy was unaffected by loading, although accuracy declined when lizards jumped to farther perches. Finally, mass-specific power output did not increase significantly when lizards jumped with loads, suggesting that the ability to produce mechanical power may be a key limiting factor for maximum jump performance. Our results suggest that mass gain after a large meal can pose a significant locomotor challenge and also imply a tradeoff between fulfilling energy requirement and moving efficiently in the environment.

Key words: loading, jumping, performance, kinematics, mass-specific power output, *Anolis carolinensis*.

INTRODUCTION

Locomotion is important for various tasks that are crucial to organismal fitness, such as foraging, finding mates and escaping from predators (Arnold, 1983; Wainwright, 1994; Biewener, 2000). In particular, maximum locomotor performance often directly impacts fitness in a variety of organisms in nature (reviewed in Irschick et al., 2008). Consequently, when extrinsic or intrinsic factors cause a decrement in locomotor performance, we might expect strong selective pressure to compensate for such a disadvantageous situation. One factor that is known to diminish locomotor performance is moving with loads, such as the consumption of a large meal (e.g. 100–150% of body mass in sea snakes) (Voris and Moffett, 1981) or the presence of voluminous offspring (e.g. litter masses of up to 25% of maternal body mass in bats) (Kurta and Kunz, 1987). As feeding and being gravid are by no means rare events in nature, moving effectively with added mass may represent a challenge that animals have to overcome or at least partially compensate for with kinematic, morphological and behavioral mechanisms.

Studying loading effects on locomotor performance can also advance our knowledge of the biomechanical basis of locomotion. Loading studies range from invertebrates (e.g. Kram, 1996), to lizards (e.g. Irschick et al., 2003), to mammals (e.g. Hoyt et al., 2000), and the general goal is not necessarily to mimic a natural condition (e.g. gravidity) *per se*, as such conditions impose their own physiological consequences, but rather to understand how animals respond to loads while keeping other such factors (e.g. hormonal mechanisms associated with gravidity) constant or nearly so. By investigating changes (or lack thereof) in kinematics of various body parts in response to additional loads, we can gain insights into how modulation of body movements translates into differences in locomotion in general (e.g. Lee et al., 2004; Seven et al., 2008). Additionally, as moving with loads requires increased mechanical power (assuming the animal moves at a similar speed), researchers have applied loading treatments as a means to testing whether the ability to produce mechanical power limits locomotor performance (Farley, 1997; Irschick et al., 2003). Maximum locomotor performance will decline when the amount of mechanical power produced per unit body mass (mass-specific power output) cannot increase to meet the demand for higher power when the animals have to move with loads (e.g. Irschick et al., 2003). Therefore, by applying loads as a means of imposing mechanical demands on the animal, we might be able to understand how the musculoskeletal system responds to physical perturbations through alterations in kinematics and power output.

Although many studies have examined loading effects on striding locomotion (walking or running), jumping has received considerably less attention, except for studies of humans in sport science (e.g. Moran and Wallace, 2007; Seven et al., 2008). However, jumping may be a better model for understanding the kinematic and functional impacts of loading for several reasons. Jumping is a mode of locomotion that demands considerable muscular work within a short amount of time (i.e. high levels of power) during takeoff (Alexander, 1985). Because of its greater power demands, load carrying is likely to impact jump performance and, potentially, kinematics to a greater extent than striding locomotion. If true, this could particularly

impact animals that use jumping as their primary means of locomotion or to elude predators. Indeed, jumping is widely employed among animals as a mode of locomotion, from fleas to humans, and this broad usage means that any effects of loading could have general applicability. For the above reasons, we sought to understand how loads affected maximum jump performance and kinematics by following the empirical framework established in previous studies (e.g. Carrier, 1994; Marsh, 1994; Krasnov et al., 2004; Toro et al., 2006).

Previous studies have typically defined whole-organism performance capacities as ecologically relevant traits that are likely to have an impact on fitness, and common examples inlcude maximum sprint speed, endurance and bite force (Arnold, 1983; Bennett and Huey, 1990; Garland and Losos, 1994; Aerts et al., 2000; Irschick and Garland, 2001). Most often, such traits are 'maximum' performance capacities (as opposed to average speed, or other such traits), but although such traits are often clearly important to animals in nature (Irschick et al., 2008), other aspects that are not typically defined as performance capacities, such as how accurately an animal performs a task, are less often considered. In this context, studying jumping provides a subtle advantage relative to striding locomotion, as far fewer studies have examined locomotor accuracy compared with maximum performance. However, for arboreal animals that regularly jump between branches (often when elevated quite high above the ground), jumping accurately (which we define as the ability to land close to the intended target) may also be important to fitness. Inaccurate jumps could have deleterious consequences, such as physical injury, increased vulnerability during the process of falling and extra time needed to return to territory. Thus, in this paper, we examine both typical performance traits (e.g. maximum jump distance) and other aspects, such as kinematics (e.g. take-off angle) and jump accuracy. We recognize that few studies have examined whether locomotor accuracy has influenced fitness, but we believe that it nonetheless merits study for the reasons cited above. As opposed to maximum performance, performing a task accurately may be energetically inexpensive but requires a high degree of coordination between the sensory and musculoskeletal systems (Bertram, 2004). No study to our knowledge has tested the effect of loading on jumping accuracy in arboreal animals. One possibility is that load carrying will disrupt the coordination between involved body parts and therefore result in a reduction of jump accuracy; alternatively, it is possible that load carrying will have no effect on accuracy.

We studied the effects of loading on maximum jump performance (distance), jump kinematics (takeoff speed and angle) and accuracy in the green anole lizard (*Anolis carolinensis* Voigt 1832), a common model for jumping studies. Green anoles are excellent subjects for studying loading effects on jump performance for several reasons. As a member of the trunk-crown ecomorph (Williams, 1983), they frequently use jumping to move around their habitat, escape from predators or capture prey (Losos and Irschick, 1996; Irschick and Losos, 1998). In addition, measurement of the mass of food items and that of lizards in the laboratory showed that green anoles are able to regularly consume prey that make up 20–30% of their body mass (C.-Y.K., unpublished results). Another advantage of using green anoles as study organisms is that their unloaded locomotor performance has been thoroughly studied in a series of laboratory and field experiments (Bels et al., 1992; Losos and Irschick, 1996; Toro et al., 2003), which serve as both a reference for experimental settings and a baseline for comparisons with the present study.

We addressed the following three questions in this study. First, will jumping with an additional 30% body mass (equivalent to the amount of a large meal) significantly reduce maximum jump distance or jump accuracy? As mechanical power expenditure is often proportional to the amount of mass gain (e.g. McGowan et al., 2006; Taylor et al., 1980) (but see Kram, 1996), we predict that a 30% load will cause a significant reduction in maximum jump distance (assuming a similar takeoff angle). Because of the lack of *a priori* data examining loading effects on jump accuracy, we tested each of two alterantives: no effect of loading on jump accuracy *versus* a significant decline in accuracy as a result of loading. If the latter were true, there is also reason to believe that this effect of loading on accuracy would become more apparent as lizards jump to farther perches. Second, how do jump kinematics change in response to increased loading? We predict that takeoff speed, an important determinant of jump distance, will decrease in the loaded condition. Finally, we will also address how mass-specific power output changes in response to loading. Answering this final question may provide some insight into whether power output limits maximum jump performance in green anoles.

MATERIALS AND METHODS

Performance trials

We used four female and 10 male adult lizards in the experiment (mean body mass=4.26 g). Lizards were housed separately in plastic terrariums (42.9×15.2×21.6 cm length×width×depth) with topsoil bedding. We placed a perch in each terrarium to provide lizards with a place to thermoregulate. Lizards were sprayed with water daily, and fed with calcium-enriched crickets twice a week (Flukers Farms, Port Allen, LA, USA). Feeding and performance trials (see below) were at least 1 day apart. We painted white dots (~0.3 cm in diameter) at the positions of the pectoral girdle, center of the trunk and pelvic girdle on both the dorsal and left lateral surfaces of the lizards. These marks were later used to measure performance and kinematic variables with computer software (see below). Before performance trials, lizards were heated to a preferred body temperature of 30°C for 45–60 min to induce maximum performance (Huey, 1983; Lailvaux and Irschick, 2007). Following Irschick et al. (Irschick et al., 2003), we used lead weights attached to a piece of cloth that wrapped around the center of the body to create a 30% weight gain condition. We measured the position of the center of mass (COM) in a male lizard (snout-to-vent length=6.2 cm) with and without the load. The COM was 3.22 and 3.21 cm posterior to the tip of snout in unloaded and loaded conditions, respectively. Therefore, the loading treatment did not substantially alter the position of COM in our lizards. For the unloaded treatment, we wrapped a piece of paper of a size similar to the cloth (representing 0% body mass) around the same position of the trunk as a sham control of the loading manipulation, as in Irschick et al. (Irschick et al., 2003). We chose this method, as opposed to alternative methods such as providing food items or injection of saline into the body cavity, because the former method would introduce extra variability in terms of subtle differences in the mass of food items, and the latter method has not (to our knowledge) been used with lizards, and could be harmful.

Prior to performance trials, lizards were randomly assigned to the loaded or unloaded condition and were tested in random order. At the beginning of each trial, we placed the lizard on a jump platform in a cardboard arena with raised edges. The platform was raised 11 cm high and covered with fine sandpaper for traction. We presented the lizards with a perch (diameter=1.24 cm) at the same height of the platform to provide an incentive for jumping. Although

we could not know definitively a lizard's intended target, the fact that lizards almost always jumped towards the presented perch suggested that they did aim at the perch we presented. In a performance test, the distance between the platform and the perch was 15, 25 or 40 cm. We randomized the sequence at which lizards were presented with the different distances. The perch distances of 15 and 25 cm were within the jumping distance of all lizards, so we used them as targets for the lizards to jump towards to test the effect of loading on jump accuracy. The 40 cm perch distance was beyond reach for all lizards, but the lizards still attempted to reach this distant perch, and were likely to achieve maximum jump distance. Immediately after placing the lizards on the platform, we induced them to jump by gently tapping the base of their tails. All trials were filmed at 500 frames s^{-1} with a Photron 1280 PCI high-speed video camera (Photron, San Diego, CA, USA) and saved into separate AVI files for further analyses.

For trials with 15 and 25 cm perch distances, we recorded the results of the jumps as either a success (if the lizard managed to stabilize itself with four feet on the perch surface) or failure (otherwise). We excluded trials where the lizards did not make contact with the perch because we were unable to discern whether the lizards failed in their attempt or simply did not aim at the perch. Including those trials would lead to an overestimation of failure rate. For trials with the 40 cm perch distance, we used ImageJ (Rasband, 1997-2009) to calculate takeoff duration and jump distance. We measured takeoff duration as the time elapsed from the end of the posturing phase to when the lizard completely left the platform (Bels et al., 1992). We also measured jump distance as the distance traveled by the front edge of the same body mark (whichever was the most clearly visible during the whole process) on a lizard between takeoff and landing. The longest jump distance obtained from at least five trials with the 40 cm perch distance was used to measure an animal's maximum jump distance. We calculated the instantaneous speed of the lizard as the distance traveled by the front edge of the same body mark (either on the pectoral or pelvic girdle, depending on which was more clearly visible) divided by the time between two consecutive frames. As digitizing the position of those marks inevitably involved measurement error, using only one instantaneous speed obtained from the last two frames prior to takeoff likely led to biased estimates. To reduce the influence of measurement error, we followed the approach of Gillis et al. (Gillis et al., 2009) by using the mean value of five instantaneous speeds immediately before takeoff. We were aware that this procedure might result in an underestimation of the real takeoff speed, but we considered reducing the influence of measurement error a more important issue. The takeoff angle was measured, using the same software, as the angle between a line connecting the marks on pectoral and pelvic girdles and the horizontal at the time of takeoff. At the moment of takeoff, the hindlimbs were fully stretched and the mark near pelvic girdle was therefore not blocked. Therefore, we could connect the two marks without difficulty. The external power generated during takeoff (P) was calculated using the following equation (modified from Marsh, 1994), which served as an approximation of external power when no direct force measurements were available:

$$P = (M_a V^2 / 2 + M_a \boldsymbol{g} h_c) / t_c , \quad (1)$$

where M_a is the total mass being accelerated, V is the takeoff speed, $\boldsymbol{g}$ is the gravitational constant, h_c is the height of the center of mass at the point of taking off and t_c is the takeoff duration. In anoles, h_c is approximately $1.46H\sin\theta$, where H is the hindlimb length and θ is the takeoff angle (Toro et al., 2004). Mass-specific power output was then calculated by dividing external power by animal body mass.

Statistical analyses

We compared the mean values of maximum jump distance, takeoff duration, takeoff speed and takeoff angle between the two loading treatments using paired t-tests. Because we had reason to believe that a load of 30% body mass would not increase maximum jump distance or takeoff speed, we used one-tailed tests when comparing mean values of those two variables between unloaded and loaded conditions. The tests for takeoff duration and takeoff angle were two-tailed. To test loading effects on jump accuracy, we arranged the numbers of successful and failed landings from all individuals into a contingency table (landing outcomes by loading conditions) for each perch distance (15 and 25 cm). We then applied one-tailed Chi-square tests with Yates correction for continuity to each table to test the difference in the distribution of successes and failures between the two loading treatments. To determine whether mass-specific power output limited locomotor performance, we compared mass-specific power output between the two loading treatments using paired t-test. The test was one-tailed because mass-specific power output is unlikely to decrease under the loaded condition. To maintain the overall Type I error rate of 0.05, we used Bonferroni corrections to adjust the significance level of all comparisons between loaded and unloaded conditions to 0.01.

RESULTS

The maximum jump distance decreased by approximately 18% when lizards were loaded, a difference that was statistically significant (t=5.77, d.f.=13, P<0.0001; Fig. 1A, Table 1). We also observed corresponding alterations in takeoff speed (~10% decrease; t=3.8, d.f.=13, P=0.001; Fig. 1B, Table 1) but not takeoff angle (Fig. 1C, Table 1), indicating that lizards took off at lower speeds under the loaded condition. We did not observe a significant difference in takeoff duration between loading treatments (t=1.21, d.f.=13, P=0.25; Fig. 1D, Table 1). The magnitudes of the takeoff speed and

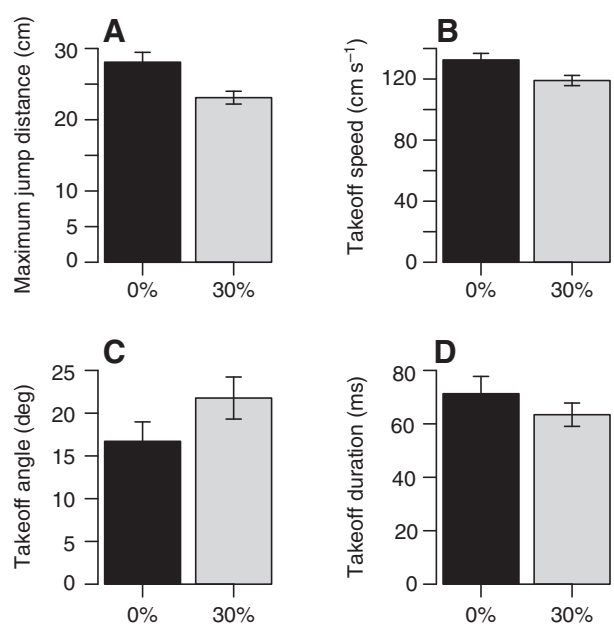

Fig. 1. Mean values of jump performance and kinematic variables of green anoles in unloaded (0%) and loaded (30%) conditions: (A) maximum jump distance, (B) takeoff speed, (C) takeoff angle and (D) takeoff duration. Error bars denote standard errors. Sample sizes for all variables were 14.

Table 1. Descriptive statistics (means ± s.e.m.) and results of paired *t*-test of maximum jump distance, takeoff speed, takeoff angle and mass-specific power output in unloaded (0%) and loaded (30%) conditions

Variable	0%	30%	t_{13}	*P*
Takeoff duration (ms)	71.29±6.47	63.43±4.37	1.21	0.25
Maximum jump distance (cm)	28.08±1.38	23.10±0.90	5.77	<0.0001
Takeoff speed (cm s^{-1})	132.51±4.29	119.02±3.34	3.80	0.001
Takeoff angle (deg)	16.71±2.27	21.77±2.46	2.39	0.03
Mass-specific power output (W kg^{-1})	17.63±2.17	17.93±2.13	0.13	0.45

Sample sizes for all variables were 14. *t*-tests for all variables except takeoff angle were one-tailed. The significance level for all comparisons was 0.01 after Bonferroni correction.

angle under the unloaded treatment were comparable to those reported in previous studies of this species (Toro et al., 2003; Gillis et al., 2009), indicating that the lizards exhibited normal jumping behavior in our study.

The probabilities of successful landings were 62.5 and 69.6% in unloaded and loaded conditions, respectively, when the perch was placed 15 cm away, a difference that was not statistically significant (χ^2=0.25, d.f.=1, *P*=0.69; Table 2, Fig. 2). The probability of successful landings declined sharply to 25.6 and 21.1% in unloaded and loaded conditions, respectively, when the perch distance increased to 25 cm, but there remained no significant difference between the two loading treatments (χ^2=0.04, d.f.=1, *P*=0.42; Table 2, Fig. 2). However, the probability of successful landings when the perch was 15 cm away was significantly higher regardless of loading condition (χ^2=9.40, d.f.=1, *P*=0.002; Table 2). Therefore, perch distance seemed to affect jump accuracy more profoundly than the presence of the load. External mass-specific power output did not differ between the unloaded and loaded treatments (*t*=0.13, d.f.=13, *P*=0.45; Table 1). Mechanical power generated to increase potential energy during takeoff contributed on average 12 and 18%, respectively, to external mechanical power in unloaded and loaded conditions. This finding was consistent with the hypothesis that mass-specific power output limits locomotor performance during jumping.

DISCUSSION

Our results confirmed our hypothesis that loading would negatively impact jump distance, which declined by approximately 18% with the addition of a 30% load, but jump accuracy was not significantly affected. Further, mass-specific power output did not increase significantly when the lizards were loaded, suggesting that lizards were unable to recruit additional power, which is consistent with the hypothesis that power is the limiting factor to maximum jump performance.

In both invertebrates and vertebrates, load carrying (mainly as a consequence of carrying offspring) often reduces locomotor performance (Table 3). The substantial decrease in maximum jump distance in our study suggests that mass gain after a normal feeding event, for example, might create a short-term performance decrement for green anoles in the field, although how long such a decrement might last remains an open question. We are aware that we only examined mass gain associated with loading *per se*, and not feeding, which could have other influences and could affect the position of the COM. Comparing locomotor performance before and after a real feeding event would be a fruitful next step. We did, however, detect significant alterations in jump kinematics as a consequence of loading; takeoff speeds declined by approximately 10% with increased loading. In other words, loading caused green anole lizards to jump shorter and slower. However, the magnitude of the reduction in locomotor performance in this study was not particularly high compared with previous studies, even after taking percent mass gain into account (Table 3). We were surprised that jumping was affected to a lesser degree than running, as jumping can be more power intensive. One implication of this result is that the musculoskeletal system of green anoles might be well suited to cope with such a regular increase in total mass. The property of the load itself might also be responsible for our observation, as extrinsic loads listed in Table 3 were mainly the result of gravidity. One major consequence of gravidity, as opposed to our loading treatment or feeding events, is that the former is often associated with significant changes in body shape, endocrinological state, muscle strength and even motivation (Bauwens and Thoen, 1981; Sinervo et al., 1991; Olsson et al., 2000; Shine, 2003a; Zani et al., 2008), whereas our treatment likely incurred no such effect. It is likely that the decline in locomotor performance observed in those studies was also due to other factors other than mass gain, whereas the decrease in locomotor performance in our study was attributed mainly to loading effect and was thus lower in magnitude.

Experimental manipulations such as loading have been demonstrated to result in alternations in locomotor kinematics. For example, loading studies with geckos running vertically (50–200% body mass) show that loading causes lizards to take smaller but

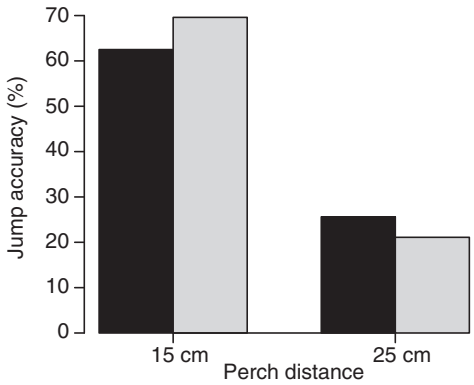

Fig. 2. Jump accuracy of green anoles at different perch distances (15 and 25 cm). Black bars, unloaded lizards; gray bars, loaded lizards.

Table 2. Number of successful jumps at two perch distances under unloaded and loaded treatments

15 cm		25 cm	
Unloaded	Loaded	Unloaded	Loaded
30 (48)	32 (46)	10 (35)	8 (27)

Numbers in parentheses are total number of trials.

Table 3. Summary of loading effect on locomotor performance from previous studies that provided quantitative data on the percentage of weight gain and decline in locomotor performance

Species	Source of load	Affected locomotor performance	Weight gain (%)	Decline in locomotor performance (%)	Reference
Invertebrates					
Centruroides vittatus	Offspring	Running speed	46.7	16	Shaffer and Formanowicz, 1996
Vertebrates					
Reptiles					
Lacerta vivipara	Offspring	Running speed	80	35	Bauwens and Thoen, 1981
Eumeces laticeps	Offspring	Running speed	54	27	Cooper et al., 1990
Anotis macoyi	Offspring	Running speed	33	20–30[a]	Shine, 1980
Lampropholis guichenoti	Offspring	Running speed	35	20–30[a]	Shine, 1980
L. guichenoti	Offspring	Running speed	21	18	Shine, 2003b
Leiolopisma coventryi	Offspring	Running speed	30; 46[b]	20–30[a]	Shine, 1980
L. entrecasteauxii	Offspring	Running speed	21; 42[b]	20–30[a]	Shine, 1980
Sceloporus occidentalis	Offspring	Running speed	27; 28; 32[b]	20; 30; 45[b]	Sinervo et al., 1991
Lacerta vivipara	Offspring	Running speed	63	38	Van Damme et al., 1989
Niveoscincus ocellatus	Offspring	Running speed	50	26; 37[b]	Wapstra and O'Reilly, 2001
Thamnophis elegans	Food	Endurance distance	22	36	Garland and Arnold, 1983
T. elegans	Food	Endurance time	22	31	Garland and Arnold, 1983
Lampropholis guichenoti	Food	Running speed	21	19; 36[c]	Shine, 2003b
Hemidactylus garnoti	Artificial load	Climbing speed	100; 150; 200[d]	25; 24; 37[d]	Irschick et al., 2003
Gekko gecko	Artificial load	Climbing speed	100	31	Irschick et al., 2003
Terrapene ornata	Artificial load	Walking speed	50; 75; 100; 150[d]	10; 20; 25; 40[d]	Wren et al., 1998
Birds					
Sturnus vulgaris	Offspring	Angle of ascent	7	29	Lee et al., 1996
Sylvia atricapilla	Migratory fuel	Velocity	60	17	Kullberg et al., 1996
S. atricapilla	Migratory fuel	Angle of ascent	60	32	Kullberg et al., 1996
Erithacus rubecula	Migratory fuel	Angle of ascent	27	17	Lind et al., 1999
Sturnus vulgaris	Artificial load	Angle of ascent	10	40–50[a]	Witter et al., 1994

[a]The author only provided the range in the paper.
[b]From different populations.
[c]From non-gravid (19%) and gravid (36%) females, respectively.
[d]From different loading treatments.

more strides (Irschick et al., 2003). Our study was no exception. There are three primary factors that directly impact jumping: takeoff angle, takeoff speed and hindlimb length (Marsh, 1994; Toro et al., 2004). Because loading cannot enhance maximum takeoff speed, the lizards could only adjust takeoff angle to enhance jump performance. The optimal takeoff angle (for maximizing jump distance) for any species varies according to both hindlimb length and takeoff velocity, but it is likely that lizards increase their takeoff angle to improve jump distance, although this method was only partly successful. As noted above, this use of compensatory kinematics is not unexpected, but it would be informative to examine how species of differing morphology and body mass adjust kinematically in response to loading.

Loading seemed to have a minimal effect on jump accuracy, suggesting that it may not disrupt the neuromuscular coordination among body parts involved in jumping. Distance, however, had a more significant effect in determining jump accuracy. A trade-off between the distance to a target and spatial accuracy has been widely studied for spatially constrained motor tasks in humans (Plamodon and Alimi, 1997). The trade-off is thought to stem from the limitations of the neuromuscular system during signal transmission between its constituent elements. Because jumping towards a certain target is clearly a spatially constrained locomotor task, it is reasonable to extrapolate the results from existing human models to explain our results. We also encourage more studies using other animals to test the generality of our findings.

Whether mass-specific power output limits maximum locomotor performance has received mixed support (Ellington, 1991; Farley, 1997). A general result emerging from prior studies is that animals often have far more power than they need for everyday purposes (Chai and Dudley, 1995; Askew and Marsh, 1997; Chai et al., 1997; Farley, 1997), yet power is potentially a limiting factor during events such as explosive jumps for long distances, particularly with large loads. Within lizards, results from the present study and a study by Irschick et al. (Irschick et al., 2003), both of which used the same mass-loading method, seem to support the idea that power limits maximum performance. In their study on two gecko species, Irschick et al. (Irschick et al., 2003) observed a leveling off of mass-specific power output in a gecko (*Hemidactylus garnoti*) as it climbed vertically with an increasingly heavier load. They concluded that mass-specific power output is likely the limiting factor for maximum climbing speed, at least in that species. In contrast, Farley (Farley, 1997) examined changes in the magnitude of mass-specific power in two lizard species as they ran up along a set of increasingly steeper slopes but did not observe a leveling off of mass-specific power output. Farley's result, therefore, was not consistent with the hypothesis that mass-specific power output limits factor on maximum locomotor performance, although one can argue that the lizards in her study may not have been as energetically challenged (moving unloaded along slopes *versus* climbing vertically with load). It is worth noting that factors other than mass-specific power output may play a role in limiting locomotor performance [e.g. bone and tendon strength (Christiansen, 2002; Bianco et al., 2003; Bianco and Gambini, 2007), and skeletal muscle mechanics (James et al., 2007)]. Although researchers have measured bone strength in green anoles (Bels et al., 1992), its importance in limiting jump performance is still unclear and merits further study.

Our study also raises some intriguing questions that deserve further research. The first question is whether green anoles have the ability to make kinematic adjustments to optimize certain aspects of performance (e.g. jump height) over others (e.g. jump duration) when faced with a certain challenge. In our study, green anoles took off at steeper angles when the takeoff speed was reduced by loading (Table 1). Toro et al. also noted that anoles often take off at lower than optimal angles (when unloaded), likely in exchange for significantly shorter flight time and lower maximum height (Toro et al., 2004). The observations in our and Toro et al.'s (Toro et al., 2004) studies suggested that green anoles might have the ability to adjust kinematically to optimize some aspects of jumping for certain situations, although this idea was not tested in detail. Few studies have demonstrated that animals make anticipatory biomechanical adjustment during locomotion (but see Gillis et al., 2010). It would be interesting to experimentally test the hypothesis that animals can make anticipatory, compensatory adjustments in takeoff angle when they are forced to jump at a lower speed. Another interesting issue is how the impairment in jump performance manifests itself in the field. Many lizard species tend to modify their behavior to increase crypsis when locomotor performance is compromised as a result of physical or anatomical perturbations (e.g. Cooper et al., 1990; Martin, 1996). Therefore, it has been widely suggested that behavioral modifications toward increased crypsis serve as a compensation mechanism for reduced locomotor performance, though the hypothesis has only been tested indirectly (Bauwens and Thoen, 1981). Testing whether lizards might adopt the same behavioral strategy to compensate for reduced jump distance after they consume a large meal in the field would require a comparison of movement patterns before and after feeding.

In summary, our study suggests that the level of mass gain after a regular meal can pose a locomotor challenge for green anoles as it impairs their jump performance and alters underlying jump kinematics. Furthermore, the results imply a tradeoff between two elements of organismal survival: fulfilling energetic requirements and maximizing locomotor performance. Further research on the generality of the abovementioned tradeoff and how the animals might resolve it will lead us one step closer to understanding how organisms cope with conflicting demands from multiple fitness-related tasks in nature.

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