Total recoil: perch compliance alters jumping performance and kinematics in green anole lizards (*Anolis carolinensis*)

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In Fig. 1B, the heading was given incorrectly as 'Lizards <3 g'. It should have read 'Lizards >3 g', as stated in the figure caption.

We apologise to the authors and readers for this error.

RESEARCH ARTICLE

Total recoil: perch compliance alters jumping performance and kinematics in green anole lizards (*Anolis carolinensis*)

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SUMMARY

Jumping is a common form of locomotion for many arboreal animals. Many species of the arboreal lizard genus *Anolis* occupy habitats in which they must jump to and from unsteady perches, e.g. narrow branches, vines, grass and leaves. Anoles therefore often use compliant perches that could alter jump performance. In this study we conducted a small survey of the compliance of perches used by the arboreal green anole *Anolis carolinensis* in the wild (*N*=54 perches) and then, using perches within the range of compliances used by this species, investigated how perch compliance (flexibility) affects the key jumping variables jump distance, takeoff duration, takeoff angle, takeoff speed and landing angle in *A. carolinensis* in the laboratory (*N*=11). We observed that lizards lost contact with compliant horizontal perches prior to perch recoil, and increased perch compliance resulted in decreased jump distance and takeoff speed, likely because of the loss of kinetic energy to the flexion of the perch. However, the most striking effect of perch compliance was an unexpected one; perch recoil following takeoff resulted in the lizards being struck on the tail by the perch, even on the narrowest perches. This interaction between the perch and the tail significantly altered body positioning during flight and landing. These results suggest that although the use of compliant perches in the wild is common for this species, jumping from these perches is potentially costly and may affect survival and behavior, particularly in the largest individuals.

INTRODUCTION

The ability of an animal to move effectively through its habitat is often essential for survival (Turchin, 1998), and adaptations of animals to locomotor challenges have provided insights into the evolution of many taxa (Biewener, 2003). Because of its general importance, many studies have examined locomotion from a variety of perspectives, including physiological (Ricciardella et al., 2010; Zhong et al., 2011), anatomical (Schoenfuss et al., 2010; van Casteren and Codd, 2010) and kinematic (Hugel et al., 2011; Larson and Demes, 2011), among others. Although these studies are representative of aspects of locomotion of many animals, few studies have directly addressed the locomotor challenges of animals that inhabit structurally complex arboreal habitats, with some exceptions (e.g. Bonser, 1999; Spezzano and Jayne, 2004; Vanhooydonck et al., 2006). For arboreal animals, the interaction between individuals and their habitat can be complex because of the variability in perch characteristics, such as diameter, length, angle and compliance (Irschick and Losos, 1999; Mattingly and Jayne, 2004). Perch compliance may be of particular concern for arboreal animals that use jumping as a means of moving through their habitat because of the high forces generated during takeoff (Crompton et al., 1993). The mass of the animal and the forces generated during takeoff cause compliant perches to bend, resulting in both potential and kinetic energy being lost to the perch (Alexander, 1991; Bonser, 1999;

Demes et al., 1995). If an animal is able to take advantage of the kinetic energy stored in the perch, the animal could use the perch as a springboard to propel itself, offsetting the initial energy loss. However, the use of perches as a springboard during jumping has thus far only been seen in humans (Channon et al., 2011). If a compliant perch is not used as a springboard, loss of energy to the perch could have marked effects on an animal's locomotion and behavior by decreasing the distance or speed at which the animal is able to jump. Therefore, perch compliance could ultimately affect an arboreal animal's ability to reach its intended target (the perch), which might have fitness consequences.

Thus far, research on the effects of perch compliance on jumping has been restricted to a few studies of primates and birds (Bonser et al., 1999; Channon et al., 2011; Crompton et al., 1993). These authors found that in laboratory jumping trials, common starlings (*Sturnus vulgaris*) do not compensate for the loss of energy due to a compliant perch, whereas in contrast, white-cheeked gibbons [*Hylobates* (*Nomascus*) *leucogenys*] minimize the effects of compliance by using low-power jumps to limit perch deflection. In the wild, bush babies (*Galago moholi*) chose larger-diameter (therefore less compliant and more energy efficient) perches for maximal jumps. Although these studies have been extremely valuable, the behavior and locomotor kinematics of birds and primates may inadequately represent the large number and wide

range of small animals that use compliant perches, such as frogs, lizards, small mammals and invertebrates. There may be other strategies that smaller animals employ, which would be useful to explore. Additionally, the effects of perch compliance on jumping across individuals of different size and age classes within a species have hardly been considered (but see Crompton et al., 2003). Finally, because of dramatic differences in morphology among taxonomic groups, it is possible that the effects of compliance could differ because of interactions of some body parts (e.g. the tail, such as in lizards) with the compliant perch.

One clear prediction and finding based on theory and empirical data is that if a small animal jumps from a compliant perch before the perch recoils, some kinetic energy of the jump will be lost to the bending of the perch, as seen with larger animals. Therefore, we predict that arboreal lizards will jump before the perch recoils, as observed in larger animals (Demes et al., 1995), and that increased perch compliance will negatively impact key aspects of jumping, particularly jump distance and takeoff speed, likely because of the loss of kinetic energy to the perch. We also predict that because jump distance in lizards is determined largely by takeoff speed and takeoff angle, lizards will increase takeoff angles from compliant perches to offset the negative effect on takeoff speed (Toro et al., 2004). Lastly, we anticipate that within a species, as mass increases, the negative effects of compliance on jump distance and takeoff speed for the same perch will increase. Larger animals cause greater displacement of compliant perches and generate greater absolute forces during takeoff than smaller animals, and therefore will lose more potential and kinetic energy of the jump (Alexander, 2003; Toro et al., 2003).

Arboreal lizards present an exceptional system in which to test the effects of perch compliance on behavior and jumping performance. For example, there are 400+ species of *Anolis* lizards, the majority of which use a variety of arboreal habitats and regularly use jumping to move around (Irschick and Losos, 1999). Anole ecology and locomotion has been widely studied (Calsbeek and Irschick, 2007; Irschick and Losos, 1999; Losos and Sinervo, 1989; Spezzano and Jayne, 2004; Vanhooydonck et al., 2006), although one anole species has been particularly well studied in terms of jumping, namely the green anole, *A. carolinensis* Voigt 1832 (Bels et al., 1992; Gillis et al., 2009; Kuo et al., 2011; Losos and Irschick, 1996; Toro et al., 2003; Vanhooydonck et al., 2005). However, the effect of perch compliance on this species, or any small (<65 g) species, is unknown. This species inhabits complex three-dimensional habitats, jumping between adjacent branches, from branches or tree trunks to the ground, and to branches, leaves and trunks above the original perch (Irschick and Losos, 1998) (D.J.I., unpublished). The green anole occupies a wide variety of perch types, from leaves and narrow branches to trunks, and therefore encounters a range of compliances that may affect performance (Irschick et al., 2005a; Irschick et al., 2005b) (C.A.G., unpublished). In this study we investigated how perch compliance affects several key jumping variables, including jump distance, takeoff duration, takeoff angle, landing angle and takeoff speed, across a range of body sizes in the arboreal green anole *A. carolinensis*.

MATERIALS AND METHODS
Perch characteristics in the wild
Studies of animal performance capacity are only valuable if they are performed in an ecologically relevant context (Irschick and Garland, 2001). To date, there are no published data on the compliance of the perches that anole lizards use in natural settings.

To determine whether the compliances of the flexible perches used in our study fall within the natural range found in the wild, we conducted a small survey of perch compliance in *A. carolinensis* at Riverbreeze County Park, Oak Hill, FL, USA. We walked through the park until we encountered an adult male or female *A. carolinensis*, and then noted the substrate type (leaf, vine, branch or trunk), and measured the perch diameter and compliance (*N*=54). To determine compliance, we measured the height of the perch, hung a fishing sinker of known mass from the perch at the exact spot where the individual was found, and measured the height of the perch again. We then calculated the compliance using the relationship between displacement and force:

$$C = \frac{d\delta}{dF} \, , \qquad (1)$$

where *C* is compliance, *F* is force [mass in kg $\times$ 9.81 m s^{-1} (gravitational acceleration)] and δ is the displacement of an object due to the force (Halliday et al., 2005).

Laboratory trials
We used five females (2.02±0.57 g, mean ± s.d.) and six males (4.30±1.79) of *A. carolinensis* for our jumping trials, which we acquired through the pet trade. All individuals were in good health with intact original tails. We marked each individual on its ventral surface with a permanent marker and housed them individually in plastic aquaria (42.9×15.2×21.6 cm) supplied with wood mulch and a wood basking perch. The cages were sprayed with water daily, and the lizards were fed calcium-dusted crickets twice a week and provided with a 12 h:12 h light:dark cycle using an aluminum clamp work light and a 65 W incandescent bulb.

We conducted jumping trials in a large glass aquarium (182×62×64 cm) that prevented lizards from escaping during the trials. Before trials commenced, we marked each lizard with Wite-Out® (BIC Corporation, Shelton, CT, USA) at six locations (three dorsal and three lateral: pelvis, mid-body and shoulder) to use as landmarks during analysis. To elicit maximal jump performance, we heated lizards to close to their preferred body temperature, 31°C (Lailvaux and Irschick, 2007), for approximately 1 h by placing them in individual cloth bags in a small Styrofoam cooler (30×30×30 cm) heated by an aluminum work lamp with a 65 W incandescent bulb. Each lizard was placed at the end of a horizontal balsa wood plank at one of three levels of compliance (rigid, flexible and most flexible) and was encouraged to jump by rapid hand gestures towards the lizard. Perch compliance was calculated by first measuring the flexural modulus of the balsa wood (*N*=5) in a three-point bend configuration (span length=75 mm) using an Instron 5500R (Instron, Norwood, MA, USA), and then using the formula:

$$C = \frac{4l^3}{Ewt^3} \, , \qquad (2)$$

where *E* is the measured flexural modulus of the wood, and *l*, *w* and *t* are the length, width and thickness of the wood, respectively. All planks measured 2 mm thick by 25 mm wide, with a 25×25 mm strip of fiberglass screen glued to one end for traction. Compliance was altered by changing the length of the wood. The rigid perch was fully supported by a steel file (3×16×150 mm) underneath the board that prevented flexion but did not interfere with the size characteristics of the board. The other two perches were 30 cm (flexible, *C*=0.27 m N^{-1}) and 40 cm (most flexible, *C*=0.64 m N^{-1}) long. All perches were placed 11 cm above the landing surface, which extended from below the perch to ~60 cm past the perch to allow lizards to jump at a natural range of distances. We presented

the lizards with a perch (wooden dowel, 1.24×10 cm diameter$\times$length) at approximately the same height as the jump perch, though slightly farther than their known maximal jump distance [~40–45 cm away (Bels et al., 1992)], to provide an incentive for jumping. This perch system, which was also used in Kuo et al. (Kuo et al., 2011), was designed to elicit maximal jumps, as it mimics the natural tendency of this species to jump from perch to perch in the wild. Lizards jumped from one perch type one to two times a week (one to two jumps per trial), and perch types were determined randomly before each set of trials. We filmed each jump at 500 frames s^{-1} with a Photron 1280 PCI high-speed video camera (Photron, San Diego, CA, USA). The glass aquarium contained a large mirror positioned on one side of the aquarium at a 45 deg angle to the perch and landing area, which allowed simultaneous recording of the lateral and ventral views of each jump.

We used the average of the two longest and straightest jumps per individual per perch type for kinematic analysis, and used ImageJ (Rasband, 1997–2009) to calculate the following variables: (1) jump distance, the distance traveled of a clearly visible mark on the lizard from rest to landing; (2) takeoff angle, the angle between a line from the pelvis to the shoulder girdle and the horizon just after the feet left the perch; (3) landing angle, the angle between the same line and the horizon when any of the lizard's feet first contacted the landing surface; and (4) takeoff duration, the time between the start of the jump to just after the lizard's feet left the perch. With these data, we also calculated takeoff speed as the average speed traveled during the last five frames of takeoff (Kuo et al., 2011).

All experimental procedures were conducted under the permission of University of Massachusetts Amherst Institutional Animal Care and Use Committee (protocol number 2011-0051).

Statistical analyses

We began our analyses by testing for the combined effects of compliance and mass on the dependent variables jump distance, takeoff duration, takeoff speed, takeoff angle and landing angle, using one-way repeated-measures analyses of covariance (ANCOVAs). Individual masses of some of the animals changed slightly over the course of the study (mean=–0.004 g), so we used mass at the time of the jump as a covariate, compliance level (rigid, flexible and most flexible) as a fixed factor and individual as a random factor. To better understand the effects of the interaction between compliance and mass on jump variables, we followed these analyses with one-way repeated-measures ANOVAs using either the full data set of the average of the best two jumps per individual per perch type ($N=33$), or with the data set separated by lizard mass (lizards <3 g, $N=21$; lizards >3 g, $N=12$). There were both males and females in the group of smaller individuals, so we tested for the effects of sex on the dependent variables using one-way repeated-measures ANOVAs. There were no differences between the sexes for any dependent variable in the small group, so the sexes were pooled (distance: $F_{1,18}=2.01$, $P=0.17$; takeoff duration: $F_{1,18}=0.90$, $P=0.36$; takeoff speed: $F_{1,18}=1.03$, $P=0.33$; takeoff angle $F_{1,18}=0.77$, $P=0.39$; landing angle: $F_{1,18}=0.75$, $P=0.40$). We separated the individuals into these two categories based on our observation that the size data naturally fell into these two distinct groupings (small lizards: mean=2.05 g, range=1.43–2.92 g, $N=7$; large lizards: mean=5.43 g, range=3.81–6.05 g, $N=4$). To account for multiple ANOVAs, a sequential Bonferroni test was used for each set of tests (Rice, 1989). To test for differences in jump distance and takeoff speed between the size groups we used Mann–Whitney–Wilcoxon tests for the rigid and most compliant perches.

RESULTS
Perch characteristics in the wild

Perch diameter and compliance of the perches measured at Riverbreeze County Park ranged from 0.2 to 1.0 cm and 0.01 to 1.67 m N^{-1} for branches, 0.3 to 1.0 cm and 0.01 to 0.53 m N^{-1} for vines, 1.4 to 13.0 cm and 0.01 to 0.17 m N^{-1} for palm fronds, 0.4 to 5.1 cm and 0.03 to 1.43 m N^{-1} for leaves, and 3.5 to 5 cm and 0.12 to 0.83 m N^{-1} for terminal branch leaf clumps, respectively.

Laboratory trials

Lizards jumped from the rigid perch with the same general kinematics as seen in other studies (Bels et al., 1992; Gillis et al., 2009): the jump started with placement of the hind feet towards the front of the body; lizards then used their hind limbs to propel themselves forward with a mean positive body angle of 12.1±1.7 deg and a mean speed and duration of 130.4±2.6 cm s^{-1} and 0.1±0 s. After the takeoff phase, the aerial phase followed with the forelimbs limbs tucked close to the body, and lizards landed with the body angled so that the hind feet contacted the landing substrate first (26.7±4.2 deg), at a mean distance of 34.4±0.9 cm.

When jumping from compliant perches, lizards began their jumps by placing their hind feet forward in a manner similar to that from the rigid perch. However, during the takeoff phase, extension of the hind limbs resulted in a downward deflection of the perch (supplementary material Movie 1). The lizards continued to push against the perch through takeoff, and the perch began to recoil after the lizards lost contact with it. No lizards remained on the perch during recoil.

From the rigid perches, large lizards had significantly greater jump distances than small lizards, and takeoff speeds similar to those of small lizards (Mann–Whitney test, distance: $W=120.5$, $P=0.006$; speed: $W=132.0$, $P=0.05$; Fig. 1). However, with increased compliance, large lizards jumped significantly shorter distances and had lower takeoff speeds than smaller lizards (distance: $W=193.0$, $P=0.03$; speed: $W=193.0$, $P=0.03$; Fig. 1). The ANCOVAs revealed significant interaction effects between animal mass and perch compliance for two of the jump variables, jump distance and takeoff speed (Table 1). Increased compliance resulted in significantly shorter jump distance in large lizards (23% decrease from rigid to most flexible perch types), but did not result in significant changes in jump distance in small lizards (large: $F_{2,8}=10.22$, $P=0.01$; small: $F_{2,17}=0.37$, $P=0.70$; Fig. 1A,B). Similarly, increased compliance had a negative effect on takeoff speed, but only for the large lizards (large: $F_{2,8}=9.71$, $P=0.01$; small: $F_{2,17}=2.69$, $P=0.10$; Fig. 1C,D). There was no significant interaction effect between animal mass and perch compliance for takeoff angle or duration (takeoff angle: $F_{2,26}=0.82$, $P=0.45$; duration: $F_{2,26}=1.27$, $P=0.30$; Table 1), and increased compliance did not significantly affect either variable (takeoff angle: $F_{2,29}=2.07$, $P=0.14$; duration: $F_{2,29}=0.20$, $P=0.82$; Fig. 2A,B).

Increased compliance resulted in significantly decreased landing angles for both small and large lizards ($F_{2,29}=6.55$, $P=0.004$; Fig. 2C). The negative landing angles appeared to be caused by the perch striking the lizard tail upon recoil (supplementary material Movie 1). We observed that when lizards jumped from rigid perches, they often dragged their tail along the perch during takeoff, as also noted in a previous study (Gillis et al., 2009). When jumping from compliant perches, the part of the tail that was still in contact with (or sometimes above) the perch was struck when the perch recoiled, thus lifting the tail and ultimately changing the body position of the lizard during flight and landing (Fig. 3A). This interaction resulted in the lizards, particularly the large ones, landing horizontally or
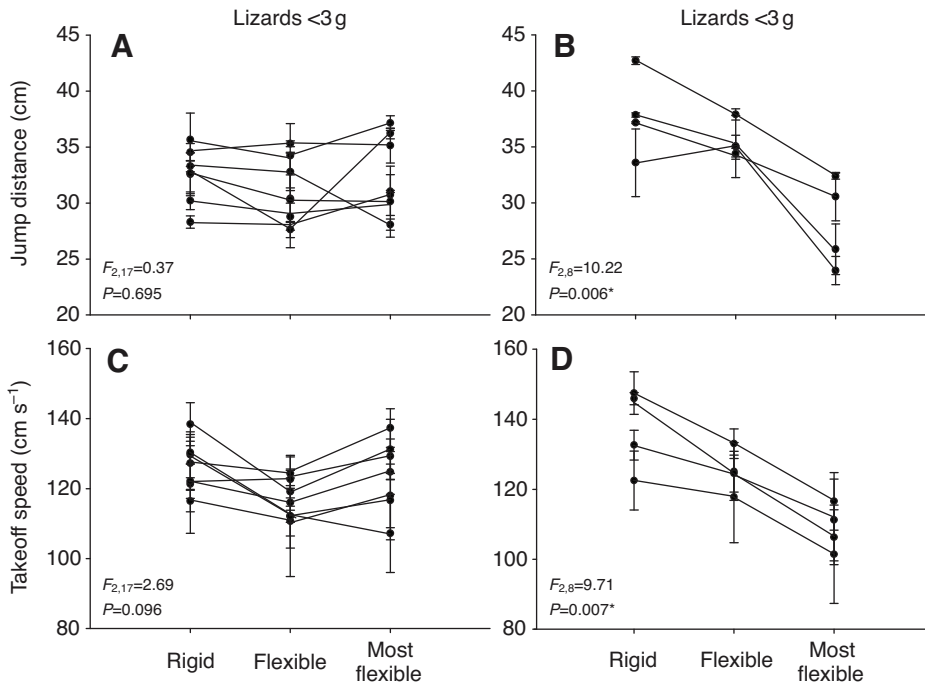
Fig. 1. The effects of three levels of perch compliance on the jump variables jump distance (A,B) and takeoff speed (C,D). Increased compliance significantly affected both variables in larger lizards (>3 g; B,D) but not smaller lizards (<3 g; A,C). Data are means ± s.e.m. of two jumps for an individual *Anolis carolinensis* from one perch type (<3 g, *N*=7; >3 g, *N*=4). Lines connect each individual's value across the three perch types. *F*- and *P*-values shown are from one-way repeated-measures ANOVA for each group. *Table-wide significance with the sequential Bonferroni test using α=0.05.

with a negative angle to the horizon (Fig. 3B). We also observed an effect of mass in general on landing angle, with larger lizards having lower landing angles from every perch type (mass: $F_{2,26}$=43.79, *P*<0.001; Table 1, Fig. 3B).

Because we observed an interaction between the recoiling perch and the lizard tail, we also analyzed the perch speed just before the perch contacted the tail to determine whether perch speed contributed to the negative landing angles of the larger lizards. The perch speed from the rigid perch was $0\,cm\,s^{-1}$, so we removed it from the analysis. Perch speed was not significantly different between compliant perch types for either group of lizards (paired *t*-test; small lizards: *t*=1.18, *P*=0.26; large lizards: *t*=0.93, *P*=0.39), but the tails of larger lizards were hit with significantly greater perch speeds than the small lizards for both perch types (flexible: *W*=122, *P*=0.009; most flexible: *W*=116.0, *P*=0.002; Fig. 3C).

We considered the possibility that the width of the perch we chose for our study may have contributed to the extreme perch–tail interactions, i.e. a compliant perch wider than the perch the lizards choose to jump from in the wild may result in abnormal interactions between the lizard and the perch. Although we did not formally test this possibility, we performed some preliminary trials to determine whether perch width was a confounding factor. We repeated jumping trials with three males (1.50, 4.75 and 5.90 g) using a compliant perch half the width of our original perch (13×3 mm,

C=0.30 m N^{-1}), using a similar setup as our other trials. We oriented the perch parallel to the landing pad, as before, and also angled the perch 45 deg to the landing pad. We were unable to set the perch perpendicular to the landing pad, but wanted to account for lizard orientation as another factor leading to non-typical jumps in our lizards. Regardless of perch orientation, perch–tail interactions resulted in forward pitching of all lizards from this narrow perch. The smallest lizard, however, was able to right itself mid-flight and land horizontally from both perch orientations. This mid-flight readjustment was typical of smaller lizards in our original set of trials.

DISCUSSION

Despite the frequent use of compliant perches by *A. carolinensis* in the wild, perch compliance negatively affected several aspects of jumping performance in this species during our laboratory trials. Because lizards lost contact with the compliant perches before the perches recoiled (i.e. they did not use the recoil like a springboard to propel themselves), they lost energy to the perch, resulting in decreased jump distances and takeoff speeds in large lizards. In addition, perch recoil following takeoff resulted in the perches striking the lizards on the tail, which pitched the lizards forward and resulted in significantly altered landing angles for all lizards. The perches used in the wild by *A. carolinensis* at this site span a

Table 1. *F*-values and associated significance levels for one-way repeated-measures ANCOVA for jump variables across three treatments: rigid perch, flexible perch and most flexible perch, with mass as a covariate

	Compliance level		Mass		Compliance level × Mass	
Variable	$F_{2,26}$	*P*	$F_{2,26}$	*P*	$F_{2,26}$	*P*
Jump distance	3.35	0.051	2.59	0.120	8.08	0.002*
Takeoff duration	0.26	0.770	9.86	0.004*	1.27	0.297
Takeoff speed	7.95	0.002*	0.14	0.708	9.76	<0.001*
Takeoff angle	2.14	0.138	2.34	0.138	0.82	0.450
Landing angle	16.79	<0.001*	43.79	<0.001*	2.25	0.126

N=11 for each treatment. *Table-wide significance with the sequential Bonferroni test using α=0.05.
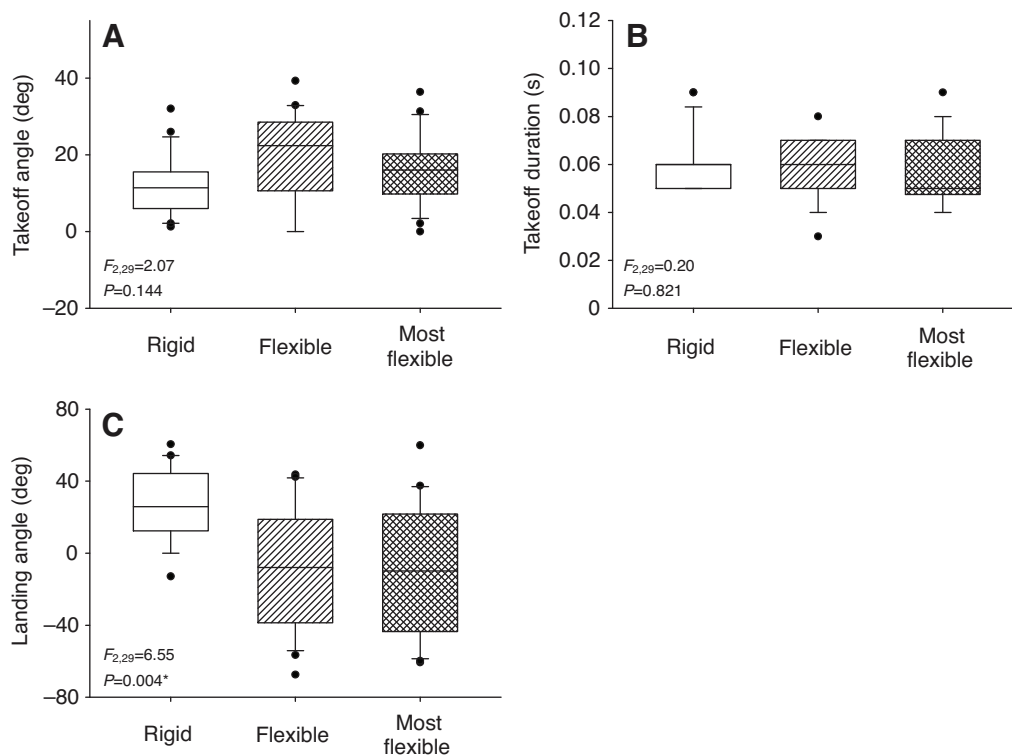
Fig. 2. The effects of three levels of perch compliance on (A) takeoff angle, (B) takeoff duration and (C) landing angle in *A. carolinensis*. Of the three jump variables, only landing angle was significantly affected by increased perch compliance. *F*- and *P*-values shown are from one-way repeated-measures ANOVA (*N*=11). *Table-wide significance with the sequential Bonferroni test using α=0.05.

large range of diameters and compliances. However, the perches we used in our study were similar in compliance (0.27 and 0.64 m N⁻¹) to those of many of the branches, vines and leaves. Therefore, although it is necessary to use caution when attempting to extrapolate laboratory-based performance results to performance in the wild, our results show that perch compliance could affect both performance and behavior in *A. carolinensis* in the wild, particularly in larger individuals.

Environmental perturbations, such as changes in substrate compliance or terrain height, and air or water flow speed and direction, are well known to influence locomotion in various animal taxa (Alexander, 2003; Biewener, 2003; Hildebrand et al., 1985; Hill et al., 2008). Because these perturbations can be energetically challenging and cause locomotor instability, their effects have been studied across a range of taxa, including cockroaches (Sponberg and Full, 2008), lizards (Korff and McHenry, 2011), turkeys (Gabaldón et al., 2004), fish (Webb and Cotel, 2010), gibbons (Channon et al., 2011) and humans (Moritz and Farley, 2003). In environments where these perturbations are common, animals often evolve behavioral means of compensating for the impacts on locomotion. For example, cockroaches run more quickly to offset the effects of rough terrain (Sponberg and Full, 2008) and, as mentioned above, gibbons use low-power jumps to compensate for the effects of perch compliance (Channon et al., 2011). Indeed, one of the themes from this body of work is the remarkable ability of animals to overcome quite formidable natural obstacles through morphological and behavioral specializations.

In this regard, it is notable that *A. carolinensis* did not compensate for changes in perch compliance by altering their kinematics or behavior, and individuals were affected quite dramatically. The largest lizards suffered a substantial loss of speed, distance and potentially accuracy (which was not measured but implied from the unstable jumps) when induced to jump from compliant perches. This lack of compensation has also been observed in common starlings,

which Bonser et al. posited might lead to decreased initial leap distance and an inability to escape from predators (Bonser et al., 1999). This suggests that these two animals do not necessarily strive for locomotor efficiency when choosing perches. Given these results, the use of compliant perches by green anoles in the wild, with its resultant diminished locomotor performance, might ultimately impact fitness in the wild by decreasing an animal's ability to catch prey or avoid predators, although this needs to be tested empirically. A recent review (Irschick et al., 2008) showed that poor locomotor performance can negatively impact fitness in a variety of lizard and snake species. Our results clearly show costs associated with compliant perch use in green anoles; however, it remains to be seen whether these costs do indeed affect fitness, and how this species is impacted by perch compliance in the wild.

The independent radiation of the genus *Anolis* into distinct ecomorphs has led to extensive study of the relationship between the morphology, ecology and behavior of these species (Losos, 1990; Losos, 2009; Williams, 1972; Williams, 1983). Although the preferred perch diameter, height and even length of the perches used by these species are well documented, the compliance of the perches used in the wild is unknown. The compliance of a structure depends on the material's modulus and the structure's geometry, and, as a general rule, as branches get thinner they become more compliant (Bonser et al., 1999). Although the degree of compliance will vary by substrate type (e.g. wood *versus* leaf), many of the small-diameter branches *Anolis* lizards jump from are somewhat compliant. The use of narrow, and likely compliant, perches is common in several of the *Anolis* ecomorphs. In particular, the truck-crown, twig and grass-bush ecomorphs, including *A. carolinensis*, often use perches that are 0.5 cm or less in diameter (Irschick et al., 2005a; Losos, 1990; Losos, 2009). Given the negative effects of perch compliance seen in the present study, it is likely that this habitat variable could be an important and underappreciated aspect of anole ecology and behavior, and potentially help explain some of the less well-
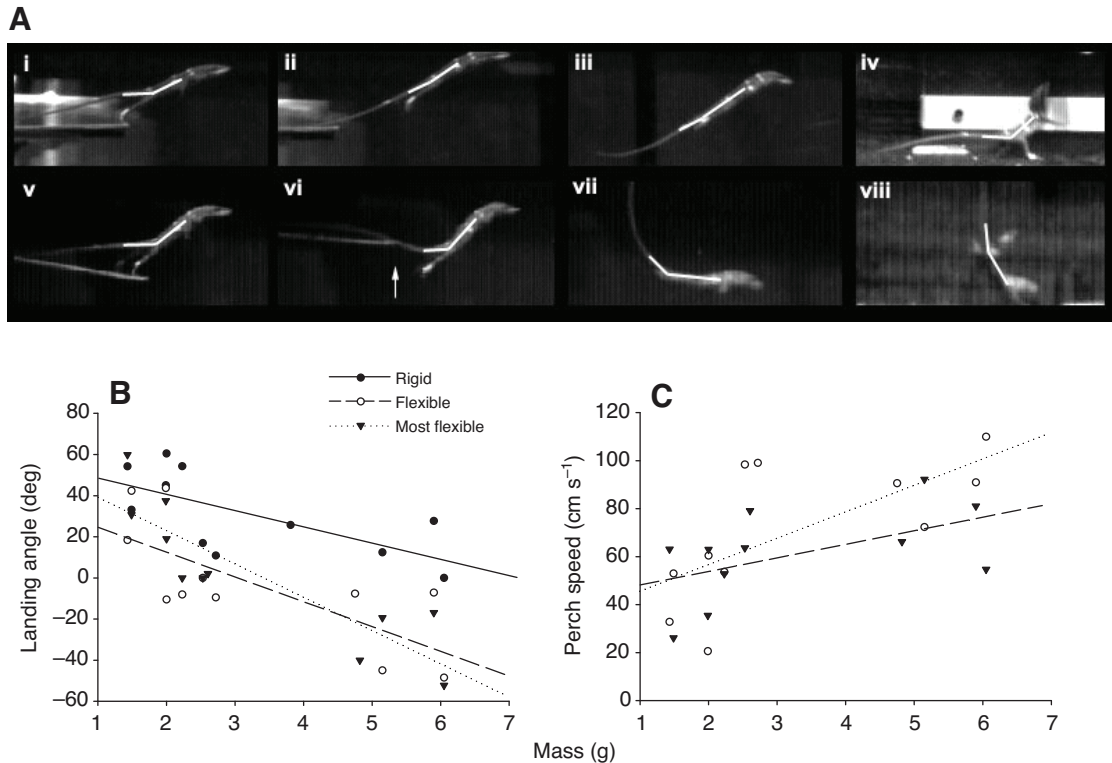
Fig. 3. Perch interference effects on takeoff, flight and landing angle in *A. carolinensis*. (A) Movie stills of the same lizard (6 g) jumping from rigid (i–iv) and most flexible (v–viii) perch types. White lines show body and tail base angles throughout the jump. This lizard had positive takeoff and landing angles from the rigid and compliant perch types (i, v), but the rebound of the most compliant perch hit the middle of the tail and caused the body to pitch forward (vi, vii), resulting in a negative landing angle (viii). (B) Relationship between mass, compliance and landing angle. Note that landing angles decrease as compliance increases, largely due to the pitching caused by perch–tail interactions (rigid perch: solid line; flexible perch: dashed line; most flexible perch: dotted line; longest jumps of *N*=11 lizards per perch type). (C) Relationship between mass, compliance and perch speed as the perch contacts the tail. Note the greater speeds for the larger lizards.

understood morphological and habitat-use correlations. As an example, *Anolis* ecomorphs that use broader perches tend to have longer legs and jump more frequently than ecomorphs that use smaller-diameter perches (Losos, 2009). However, some anoles use extremely narrow perches, but have long limbs and jump regularly. This latter group is often composed of small lizards, suggesting that size is a factor in determining compliant perch use.

The results from our preliminary tests of the effects of compliance using narrow perches suggest that perch–tail interactions may occur regardless of perch width or orientation. However, the structures of perches in nature are complex, and how they recoil depends on several factors, such as material properties and to what extent recoil is damped, for example by air drag if leaves are present on the branch. Additionally, green anoles jump at a variety of angles to and from a range of perch types in their three-dimensional habitat and perch–tail interactions may only occur under specific circumstances (Irschick and Losos, 1998) (D.J.I., unpublished). Therefore, more data are needed to test the importance of perch–tail interactions in the wild. In addition, more research is necessary to determine whether these lizards are able to sense the compliance of perches used in the wild, and, if so, whether their locomotor strategy changes to potentially compensate for this compliance. In our study we found that large lizards were generally more reluctant to jump from the most compliant perch, indicating that although they were forced to jump from these perches, they did have some sense of the compliance of the perch before jumping and perhaps

were aware of potential costs of jumping from compliant perches. They often hopped down to the substrate below them as opposed to jumping forward with a positive takeoff angle. After sufficient coercion, however, large animals jumped from compliant perches using the same takeoff angle and duration as they did from more rigid perch types, and as small lizards did from all perch types. Because all individuals we used for the trials were obtained through the pet trade, it is unclear whether this reluctance is due to an innate or learned response to this particular perch characteristic. Additionally, although our results support the prediction that large lizards would be affected to a greater degree than small lizards, more data are needed to understand whether this effect is stepwise or gradual.

Recent work has shown the value of examining locomotion in nature, and how animals interact with habitat structure (Fulton et al., 2001; Irschick and Losos, 1999; Johansen et al., 2007; Mattingly and Jayne, 2004; Youlatos and Samaras, 2011). Green anoles in the wild segregate perches across age or sex classes based on perch diameter: smaller animals use narrow perches, and larger animals use larger perches (Irschick et al., 2005a). Although laboratory trials have shown that perch diameter influences maximum running speed (Irschick and Losos, 1999) but not jump distance from non-compliant perches (Losos and Irschick, 1996), both jump distance and jump speed are reduced by compliant perches for larger animals. Therefore, perch segregation may reflect the constraints imposed by small-diameter compliant perches, alone or in

conjunction with other factors such as intraspecific competition. However, it is possible that larger individuals of *A. carolinensis* in the wild may occasionally choose compliant perches when the costs of jumping from these perches do not outweigh the gains, e.g. from better resources or for territorial defense. Understanding how this particular habitat characteristic affects the way animals move, and their ability to navigate their habitat, would provide greater insight into an important yet understudied aspect of locomotion.

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