The Company of **Biologists**

SHORT COMMUNICATION

Robust jumping performance and elastic energy recovery from compliant perches in tree frogs

Henry C. Astley*, Alison Haruta and Thomas J. Roberts

ABSTRACT

Arboreal animals often move on compliant branches, which may deform substantially under loads, absorbing energy. Energy stored in a compliant substrate may be returned to the animal or it may be lost. In all cases studied so far, animals jumping from a static start lose all of the energy imparted to compliant substrates and performance is reduced. Cuban tree frogs (*Osteopilus septentrionalis*) are particularly capable arboreal jumpers, and we hypothesized that these animals would be able to recover energy from perches of varying compliance. In spite of large deflections of the perches and consequent substantial energy absorption, frogs were able to regain some of the energy lost to the perch during the recoil. Takeoff velocity was robust to changes in compliance, but was lower than when jumping from flat surfaces. This highlights the ability of animals to minimize energy loss and maintain dependable performance on challenging substrates via behavioral changes.

KEY WORDS: Spring, Arboreal, Jump, Compliance, Recoil, Recovery

INTRODUCTION

Animals moving through natural habitats commonly encounter compliant substrates (Demes et al., 1995; Gilman et al., 2012; Gilman and Irschick, 2013), which yield when subjected to force, resulting in the absorption of mechanical energy. While some substrates, such as mud, may only dissipate energy, others, such as small-diameter plant branches, are elastic and may return a significant portion of their energy upon recoil (Cannell and Morgan, 1987).

Jumping from compliant substrates is particularly challenging. During a jump, an animal may apply several times its body weight to the substrate, potentially producing much greater deformation of the substrate and therefore greater energy loss than during activities like walking. Once the animal loses contact with the substrate, elastic recoil can no longer return energy to the animal, and any energy remaining in the substrate is lost (Demes et al., 1995). Prior studies have shown adverse effects of jumping from compliant substrates, typically associated with energy loss to the substrate (Gilman et al., 2012; Ribak et al., 2012). In all species previously examined, animals jumping from a static start lost contact with the substrate prior to recoil, preventing any recovery of the energy imparted to the substrate (Demes et al., 1995; Gilman et al., 2012).

Cuban tree frogs are arboreal frogs with long hindlimbs and extremely powerful jumps, and presumably must perform these jumps from branches with a range of compliances. These high-force jumps could potentially produce substantial deflections and energy loss in compliant perches, severely compromising the frog's performance. However, it is also possible that these arboreal specialists are capable of recovering energy temporarily stored in springy substrates. We examined the kinematics and kinetics of Cuban tree frogs jumping from perches of varying compliance in order to determine the effect of compliance on jump performance and the energy transfer between the frog and the perch. Using high-speed three-dimensional kinematics and a calibrated spring force–length relationship, we measured displacement, velocity, force, energy and power of both the frog and perch throughout the jump, in order to allow detailed understanding of the interactions between the frog and the complaint perch, including potential performance losses and elastic recoil.

MATERIALS AND METHODS

Animals

Six adult, wild-caught Cuban tree frogs, *Osteopilus septentrionalis* (Duméril and Bibron 1841), were used for this study [body mass: 22.0 ± 8.0 g, snout–vent length (SVL): 7.0 ± 0.8 cm, leg length: 10.2 ± 0.9 cm]. All experimental procedures and animal husbandry were approved by the Brown University Institutional Animal Care and Use Committee.

Perches

Perches were constructed from hollow latex surgical tubing anchored between two rigid metal supports approximately 50 cm apart. A rigid Teflon rod, 9 cm long, was inserted within the tubing midway along the perch to provide a rigid area for frogs to jump from. The perch was stretched to 0, 2 and 4 cm beyond the slack length, creating three different compliance levels (2.3, 1.8 and 1.1 cm deformation under 1 N vertical load; unloaded resonant frequencies of 8.4, 9.5 and 12.1 Hz, respectively) within the range of arboreal substrate compliance observed in their introduced range (Gilman and Irschick, 2013). For rigid perches, frogs jumped from a wooden dowel of equal diameter. This perch configuration is similarly compliant in horizontal and vertical directions, while 'diving board' setups are compliant only perpendicular to the axis of the perch, causing effective compliance to vary based on jump angle.

The relationship between perch spring force and displacement and angle was determined by pulling slowly with a uniaxial force sensor (Kistler model 9207) while simultaneously recording displacement and angle using the same methods as in the jumping trials (see below). We generated a function to calculate spring force based on three-dimensional perch position using MATLAB (2010a, MathWorks, Natick, MA, USA), though the effect of angle was small. Subsequent calculations of force included the initial displacement due to the frog's weight at rest.

Jumping trials

Jumping trials were performed at 21–23°C. Jumps were recorded at 500 frames s^{-1} using two high-speed cameras (Photron 1280 PCI, Photron Inc., Tokyo, Japan) positioned posterior to the perch and at an angle of approximately 60 deg to each other, and calibrated using a cube of 64 points spaced at 35 mm and DLT calibration software (Hedrick, 2008). Each frog was stimulated to jump five times from each compliance level by gentle

Department of Ecology & Evolutionary Biology, Brown University, Providence, RI 02912, USA.

*Author for correspondence (henry.astley@physics.gatech.edu)

contact to the posterior body with a soft paintbrush, and the best three jumps were selected for analysis. Perches were used in order of decreasing compliance.

The cloaca of the frog was tracked throughout the jump and for at least three frames beyond toeoff, which was determined visually, using MATLAB digitizing scripts (Hedrick, 2008). The linear motion of the perch was tracked via points at the upper edges of the two circumferential rings at the ends of the rigid portion of the perch. Position data were smoothed using polynomial splines. Angles were determined with reference to a hanging mass.

Calculations

In order to understand the exchanges of energy between the frog and perch, we must quantify the three forms that together comprise the total system energy (E_{sys}):

$$E_{sys} = E_{frog} + E_{spring} + E_{perch\,motion}, \qquad (1)$$

where E_{frog} is the summed kinetic and gravitational potential energy of the frog's center of mass, E_{spring} is the elastic energy stored in the perch, and $E_{perch\,motion}$ is the summed kinetic and potential energy of the perch center of mass as it moves throughout the jump. Changes in mechanical energy of the frog can be calculated from:

$$E_{frog} = \frac{1}{2} m_{frog} v_{frog}^2 + m_{frog} \boldsymbol{g} h_{frog}, \qquad (2)$$

where m_{frog} is the mass of the frog, v_{frog} is the magnitude of the velocity vector of the frog, $\boldsymbol{g}$ is the gravitational acceleration, and h_{frog} is the vertical displacement of the frog center of mass relative to its starting point. Spring energy (E_{spring}) is calculated as the area under the spring force ($\mathbf{F}_{spring}$) versus perch displacement (d_{perch}) curve:

$$E_{spring} = \int_0^{d_{perch}} \mathbf{F}_{spring}(d_{perch}, \varnothing_{perch}) \mathrm{d}(d_{perch}), \qquad (3)$$

where $\varnothing_{perch}$ is the angle of the perch relative to the vertical, d_{perch} is the total displacement of the perch relative to the unloaded state, $\mathrm{d}(d_{perch})$ denotes the variable of integration, and $\mathbf{F}_{spring}$ is the spring force of the perch, which is a function of both d_{perch} and $\varnothing_{perch}$ empirically determined via the calibration method described above. The energy of perch motion ($E_{perch\,motion}$) is:

$$E_{perch\,motion} = \frac{1}{2} m_{perch} v_{perch}^2 + m_{perch} \boldsymbol{g} h_{perch}, \qquad (4)$$

where m_{perch} is the mass of the perch, v_{perch} is the velocity of the perch, and h_{perch} is the vertical displacement of the perch relative to its starting point. The total energy of the perch (E_{perch}) is:

$$E_{perch} = E_{perch\,motion} + E_{spring}. \qquad (5)$$

Power was calculated by differentiating energy with respect to time, with losses from the frog to the perch signed as negative and increasing frog energy signed as positive. Additionally, the reaction force exerted by the perch on the frog ($\mathbf{F}_{frog}$) was calculated as:

$$\mathbf{F}_{frog} = m_{frog} \mathbf{a}_{frog} + m_{frog} \boldsymbol{g}, \qquad (6)$$

where $\mathbf{a}_{frog}$ is the acceleration vector of the frog's body, calculated from displacements (see above). Note that this approach avoids the assumption that $\mathbf{F}_{frog}$ equals $\mathbf{F}_{spring}$. By treating the perch as an object with mass, inertia and energy, we not only correctly account for this otherwise neglected component of the system energy but also show that $\mathbf{F}_{frog}$ and $\mathbf{F}_{spring}$ are often unequal, with the vector sum of these forces producing the acceleration vector of the perch:

$$\mathbf{a}_{perch} = \frac{(\mathbf{F}_{frog} + \mathbf{F}_{spring})}{m_{perch}}. \qquad (7)$$

Early in the jump, $\mathbf{F}_{frog}$ exceeds $\mathbf{F}_{spring}$ and the perch accelerates away from the frog, while this is reversed later in the jump (Fig. S1), as the perch movement slows and eventually begins recoil.

Frog impulse was calculated as:

$$\mathbf{I}_{frog} = \int_0^{toeoff} \mathbf{F}_{frog} \mathrm{d}t, \qquad (8)$$

where $\mathrm{d}t$ denotes the variable of integration. The relative recoil of the perch, measuring the proportion of energy lost to the perch (both spring and motion energy) which is returned to the frog, was calculated as:

$$\text{Relative recoil} = \frac{E_{perch,max} - E_{perch,toeoff}}{E_{perch,max}}. \qquad (9)$$

All energies were set to zero at the start of the jump, but alternative calculations that allowed non-zero starting energy (e.g. energy stored in the spring by frog body weight, potential energy) did not change the fundamental results of this paper. All powers and energies were normalized by frog mass, while forces were normalized by frog weight. Peak perch displacement was normalized by frog leg length.

We performed mixed-model ANOVA using JMP 7.0 (SAS Institute, Cary, NC, USA) in which individual was a random crossed factor and compliance was a fixed crossed factor. Because of the number of tests, we performed a stepwise Bonferroni correction (Table S1).

RESULTS AND DISCUSSION

All three compliant perches showed substantial deflections during the jump (Movie 1). Perch deflection increased with increasing compliance (Table S1), reaching a total deflection of 34% of leg length for the most compliant perch (Fig. 1, Fig. 2A). Perch deflection was initially vertical due to body weight and became more horizontal throughout the jump, with the most compliant perch showing the most horizontal perch deflection angle at toeoff (98±37 deg relative to vertical) compared with the stiffer perches (combined: 44±16 deg) (Table S1). The maximum energy stored in the perch ($E_{perch,max}$) during the jump also increased with increasing perch compliance (Table S1). Peak spring force ($\mathbf{F}_{spring,max}$) was unaffected by compliance (Table S1).

Although the effects of perch compliance on limb displacement were apparent, there were only two statistically significant changes in the mechanics of the jump, with decreasing compliance resulting in an increase in jump impulse ($\mathbf{I}_{frog}$) and a decrease in total mechanical energy of the frog ($E_{frog,toeoff}$) at toeoff (Table S1; Fig. 2C). Peak frog force ($\mathbf{F}_{frog}$) and takeoff angle showed non-significant decreasing trends with increasing compliance, while jump duration showed no significant effect (Table S1). A trend towards a decline in frog takeoff velocity with increasing compliance was not statistically significant (Table S1; Fig. 2B). Neither total system energy ($E_{sys,toeoff}$) at toeoff nor peak frog power was significantly affected by compliance (Table S1).

Substantial energy was stored in the spring during the first part of the jump (Fig. 1). In the two stiffer perches, nearly half of this energy was effectively returned to the frog (relative recoil) (Table S1; Fig. 1D–F, Fig. 2D). Spring energy that was not returned to the frog was transferred to the kinetic and potential energy of the perch itself (Fig. 1).

The most unexpected result of this study was the return of a substantial portion of the energy absorbed by the perch to the frog during recoil of the stiffer perches (Fig. 1, Fig. 2D). Other organisms jumping from compliant perches lose contact with the perch prior to recoil (Demes et al., 1995; Gilman et al., 2012), preventing any recovery of energy from the perch. Thus, the present results represent the first evidence that organisms jumping from a static start (i.e. without counter-movements or repeated loading cycles) from compliant perches can recover energy stored in the perch. If the work produced by the animal's muscles determines jumping
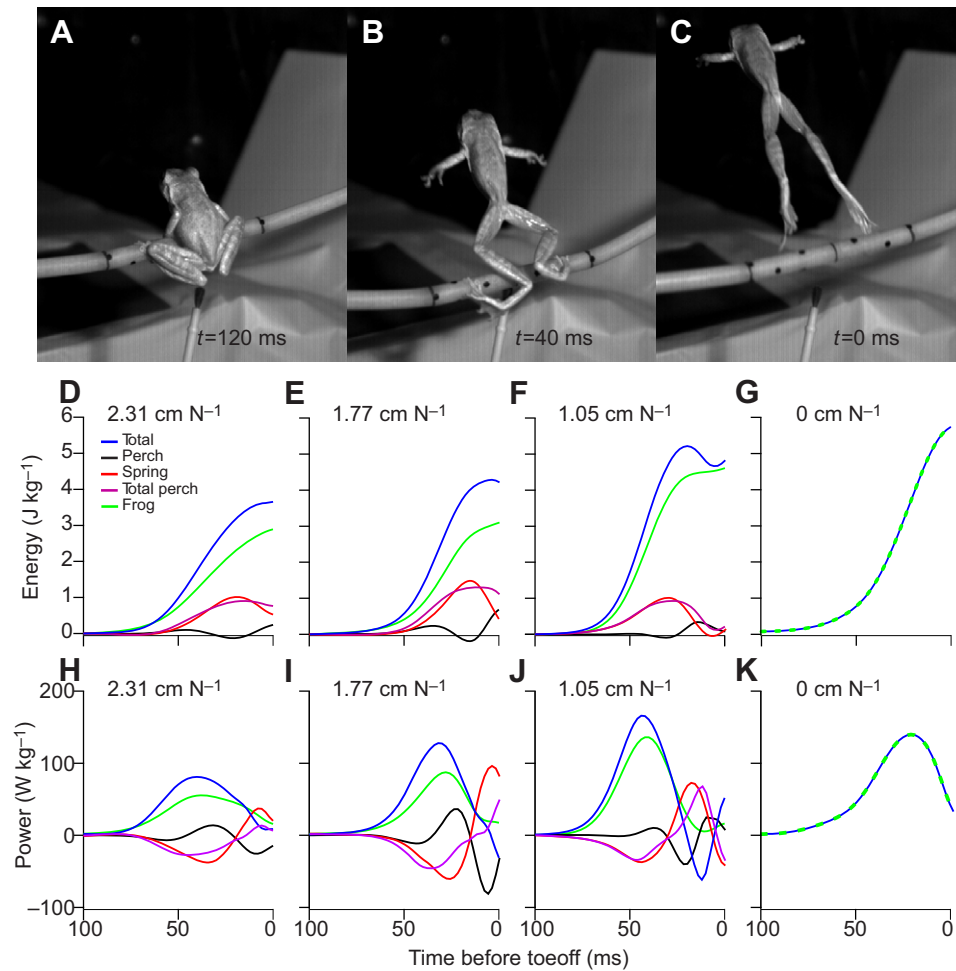
Fig. 1. Example jumps from compliant and rigid perches. (A–C) Sample high-speed video frames of a Cuban tree frog jumping from the most compliant perch prior to jump movement (120 ms before toeoff), at peak perch displacement (40 ms) and at toeoff (0 ms). (D–G) Total system mechanical energy (blue line), perch summed kinetic and potential energy (black line), spring energy (red line), total perch energy (purple line), and summed kinetic and potential energy of the frog (green line) are shown for example jumps ranging from the most compliant (D) to the least compliant (F) to a rigid (G) perch. (H–K) Power through time in four representative jumps, normalized by frog body mass. Compliance is given at the top of D–K.

performance, loss of energy to compliant perches will reduce jumping performance. The recoil of an elastic perch presents an opportunity to recover some of this energy to reduce the potential detriment to jump performance. The frogs in this study recovered some of the energy stored in compliant perches, allowing them to maintain performance on this challenging substrate.
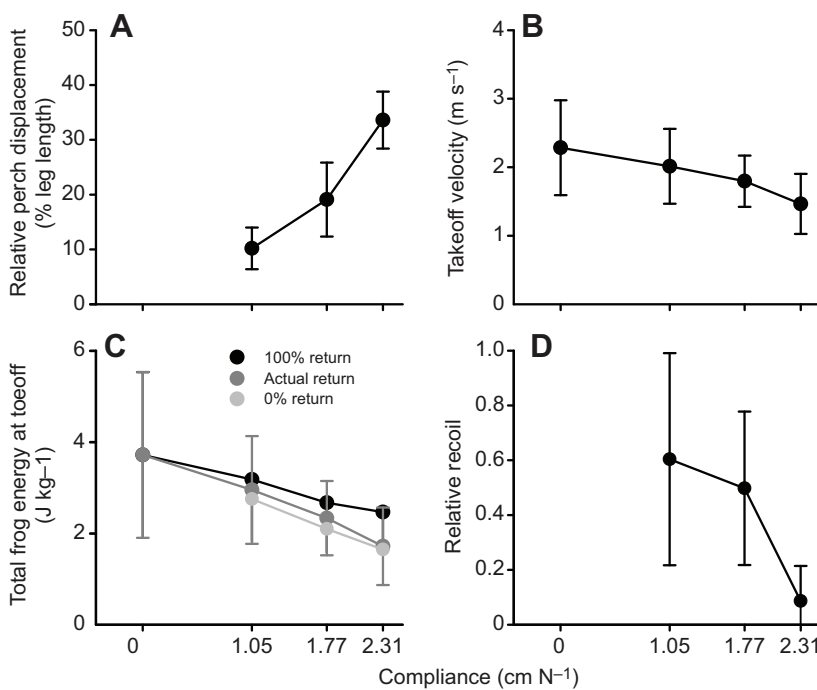

Fig. 2. Effects of compliance on jump variables.
(A) Maximal displacement of the perch, as a proportion of frog leg length. (B) Takeoff velocity. (C) Total mechanical energy of the frog at toeoff (actual return), as well as calculated frog energy in the hypothetical cases of 100% perch energy return and 0% perch energy return; 100% return was calculated by adding frog energy at toeoff to the remaining perch energy at toeoff, while 0% return was calculated by subtracting the relative recoil multiplied by the maximum perch energy, to simulate a state of zero energy recovery. (D) Relative recoil, the proportion of energy stored in the perch that is returned to the kinetic and potential energy of the frog at the time of toeoff. All energies are expressed per kg of frog body mass.

Jumping from a compliant perch presents several mechanical challenges. We focused on the loss of energy to the substrate, but perch displacement also influences the kinematics of limb extension, which may influence muscle velocity and power, as well as the kinetics of energy storage and release in elastic structures within the limb (Astley and Roberts, 2014). Furthermore, a substrate that moves with the application of force could present a challenge to balance, causing misalignment of the ground reaction force and the animal's center of mass, thereby inducing a rotational moment. Despite the motion of compliant perches, in no case did the frogs exhibit observable instability during the jump or following takeoff.

It is unclear whether tree frogs are unique in their ability to recapture significant portions of the energy stored in a compliant perch. The extremely long legs and adhesive toes of these frogs may allow them to remain in contact with the perch for longer than other jumpers. Neither jump force nor jump duration changed significantly across a range of compliances, suggesting that the frogs are not tuning their jumps to each perch. Because the relationship between perch spring force and displacement was non-linear, frogs could not infer the compliance of a perch at high force from its behavior under lower-magnitude arboreal walking forces, and thus tuning of the frog's jump to specific perch compliances may be less useful than simply adopting a robust strategy that preserves performance across a wide range of compliances.

Another feature of Cuban tree frog jumps is the 'catapult mechanism', in which the frogs store and release elastic energy in hindlimb tendons, which allows the frog to perform muscular work prior to body or joint movement (Astley and Roberts, 2012) without the deflection of the perch compromising muscle performance. For each compliance level, a minimum of 38% of jumps showed evidence of the catapult mechanism, with peak frog power normalized per unit muscle mass (14.7% of body mass) exceeding the isotonic muscle power of this species (322 W kg^{-1}; Roberts et al., 2011), and jumps below this threshold may still use the catapult mechanism (Astley and Roberts, 2012). It is unclear whether the catapult-like mechanism used in jumping holds any significance for the ability of frogs to recover energy from springy perches.

Although our results demonstrate that frogs reduce the effect of perch compliance by recovering energy, there is also a surprising reduction in performance for all perch-based jumps, regardless of compliance. Jumps from the rigid perches in our study had 57% of the takeoff velocity and 41% of the peak force seen in jumps from flat plates (Roberts et al., 2011). The cause of this performance loss remains unclear, though potential factors include the need to balance on a narrow perch and a behavioral strategy for maintaining jump performance on perches of uncertain compliance.

Author contributions
H.C.A. and T.J.R. designed the study, H.C.A. and A.H. performed the experiments, A.H. processed the data, and T.J.R. and H.CA. analyzed the data and wrote the paper.

References

Astley, H. C. and Roberts, T. J. (2012). Evidence for a vertebrate catapult: elastic energy storage in the plantaris tendon during frog jumping. *Biol. Lett.* **8**, 386-389.

Astley, H. C. and Roberts, T. J. (2014). The mechanics of elastic loading and recoil in anuran jumping. *J. Exp. Biol.* **217**, 4372-4378.

Cannell, M. G. R. and Morgan, J. (1987). Young's modulus of sections of living branches and tree trunks. *Tree Physiol.* **3**, 355-364.

Demes, B., Jungers, W. L., Gross, T. S. and Fleagle, J. G. (1995). Kinetics of leaping primates: influence of substrate orientation and compliance. *Am. J. Phys. Anthropol.* **96**, 419-429.

Gilman, C. A. and Irschick, D. J. (2013). Foils of flexion: the effects of perch compliance on lizard locomotion and perch choice in the wild. *Funct. Ecol.* **27**, 374-381.

Gilman, C. A., Bartlett, M. D., Gillis, G. B. and Irschick, D. J. (2012). Total recoil: perch compliance alters jumping performance and kinematics in green anole lizards (*Anolis carolinensis*). *J. Exp. Biol.* **215**, 220-226.

Hedrick, T. L. (2008). Software techniques for two- and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspir. Biomim.* **3**, 034001.

Ribak, G., Reingold, S. and Weihs, D. (2012). The effect of natural substrates on jump height in click-beetles. *Funct. Ecol.* **26**, 493-499.

Roberts, T. J., Abbott, E. M. and Azizi, E. (2011). The weak link: do muscle properties determine locomotor performance in frogs? *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **366**, 1488-1495.