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Jumping performance in tree squirrels: Insights into primate evolution

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ABSTRACT

Morphological traits suggesting powerful jumping abilities are characteristic of early crown primate fossils. Because tree squirrels lack certain 'primatelike' grasping features but frequently travel on the narrow terminal branches of trees, they make a viable extant model for an early stage of primate evolution. Here, we explore biomechanical determinants of jumping performance in the arboreal Eastern gray squirrel (*Sciurus carolinensis*, $n = 3$) as a greater understanding of the biomechanical strategies that squirrels use to modulate jumping performance could inform theories of selection for increased jumping ability during early primate evolution. We assessed vertical jumping performance by using instrumented force platforms upon which were mounted launching supports of various sizes, allowing us to test the influence of substrate diameter on jumping kinetics and performance. We used standard ergometric methods to quantify jumping parameters (e.g., takeoff velocity, total displacement, peak mechanical power) from force platform data during push-off. We found that tree squirrels display divergent mechanical strategies according to the type of substrate, prioritizing force production on flat ground versus center of mass displacement on narrower poles. As jumping represents a significant part of the locomotor behavior of most primates, we suggest that jumping from small arboreal substrates may have acted as a potential driver of the selection for elongated hindlimb segments in primates, allowing the center of mass to be accelerated over a longer distance—and thereby reducing the need for high substrate reaction forces.

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1. Introduction

Investigating the performance of possible fitness-critical behaviors is a key component of evaluating the functional consequences of variation in specific morphological traits. Measuring performance allows researchers to assess how well an individual can accomplish a given task along some ecologically relevant dimension, thus providing more direct correlates with phenotypic variation (Bock and von Wahlert, 1965; Bock, 1980; Arnold, 1983). Investigating the functional consequences of phenotypic variation is essential for improving the understanding of the selective pressures leading to speciation and for testing adaptive hypotheses that have been proposed to explain morphological changes in a lineage.

The hindlimb skeletons of many early crown primates (i.e., adapids and omomyids) are characterized by several features that have been argued to be mechanically linked to rapid and forceful hindlimb extension, including low intermembral indices, tall femoral condyles and talar bodies, and elongated hind- and midfoot regions (Gregory, 1920; Napier and Walker, 1967; Szalay and Dagosto, 1980; Dagosto, 2007; Boyer et al., 2013; Ni et al., 2013; Boyer et al., 2017). Such 'leaping' traits in early fossils have often been interpreted as synapomorphies reflecting the adaptative importance of powerful jumping abilities in the lineage leading to the ancestral crown primates. This fossil-based interpretation of early true primates in the Eocene (as opposed to primate ancestors in the Paleocene) has been supported by the study of Boyer et al.

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(2013) which showed that size-adjusted calcaneal elongation is associated with leaping proclivity in extant strepsirrhines. The authors therefore argued that patterns of increasing size-adjusted calcaneal elongation during early primate evolution suggest increasing jumping specialization across the phylogeny.

Compared to analogies based on correlations between morphology and behavior, performance data have a great potential to inform the likelihood of adaptive scenarios for primate origins by directly demonstrating the ecological utility of hypothesized structure-function complexes (Bock, 1980; Arnold, 1983). Several studies have used performance testing in an arboreal context (Herrel et al., 2013; Thomas et al., 2016; Boulinguez-Ambroise et al., 2019; Young and Chadwell, 2020). For instance, primate grasping performance has been investigated using a pull strength task, highlighting the functional importance of specific limb segment dimensions in determining grasping strength (Thomas et al., 2016; Boulinguez-Ambroise et al., 2019, 2021). Similarly, a recent comparative biomechanical study of Eastern gray squirrels (*Sciurus carolinensis*), common marmosets (*Callithrix jacchus*), and squirrel monkeys (*Saimiri boliviensis*) moving on variously sized laboratory supports showed that when transitioning to a narrower support (i.e., experiencing perturbation to stability), squirrels most often displayed the greatest magnitude of kinematic adjustment to remain stable (Young and Chadwell, 2020). The authors concluded that primatelike grasping ability may be an adaptation that specifically improves locomotor performance in a fine-branch niche, rather than merely permitting access to the environment (Young and Chadwell, 2020).

Despite arguments that powerful jumping was a key behavior in early primate evolution, jumping performance has rarely been evaluated in arboreal mammals, compared to the large volume of research on other locomotor modes, such as quadrupedalism (but see Aerts, 1998; Bobbert and Casius, 2005; Scholz et al., 2006; Bobbert et al., 2008; Channon et al., 2010; Channon et al., 2012; Legreneur et al., 2010; Bobbert, 2013; Bobbert et al., 2014). In this paper, we use the term jumping according to the definition of Emerson (1985: p. 58), restricted to the "locomotion mode in which both hindlimbs extend simultaneously to provide the total propulsive thrust". Emerson's definition of jumping therefore includes upward vertical leaping or vertical clinging and leaping, a common positional behavior in several platyrrhine, tarsier, and strepsirrhine species (Garber et al., 2009; Crompton et al., 2010; Gebo, 2011). Ballistic equations establish that jumping performance (i.e., height attained or distance traveled) is primarily dependent on the animal's center of mass (CoM) velocity at takeoff (TO). Therefore, to increase jumping performance—to jump high or far—the animal must maximally accelerate to increase the kinetic energy (KE) of the CoM, typically by extending the hindlimb joints and pushing their hind feet against the substrate. Because the change in KE is equal to the total mechanical work performed on the CoM (following the work-energy theorem), the animal has two fundamental strategies: (1) increase the mean substrate reaction force (SRF) magnitude or (2) increase the distance over which the SRF is applied (Bennet-Clark, 1977; Demes and Günther, 1989; Marsh, 1994; Alexander, 1995). Jumping animals should therefore be characterized by specific morphological traits that serve to either increase limb force production (e.g., relatively more hindlimb muscle mass) or increase CoM displacement during push-off (e.g., relatively longer hindlimbs). Comparative studies on *Anolis* lizards (Losos, 1990) and frogs (Gomes et al., 2009) provided experimental support that increased hindlimb length corresponds to increased jumping capability (i.e., jump distance). Hindlimb musculotendinous anatomy facilitating mechanical power amplification has also been highlighted in a particularly extreme example: the Senegal bushbaby (*Galago senegalensis*; Aerts, 1998). With a weight of 0.250 kg, these small strepsirrhines can achieve an upward vertical jump of 2.25 m (i.e., six body lengths, tail not included; Hall-Craggs, 1965).

In this study, we measured upward vertical jumping performance and investigated its biomechanical determinants in a nonprimate arboreal mammal, the Eastern gray squirrel (*S. carolinensis*). We focused on vertical jumping because jumping performance (i.e., height attained) in this context is solely dependent on how well the animal can use the musculoskeletal system to accelerate against gravity. Upward vertical jumping is thus a direct measure of jumping power, irrespective of other behavioral factors (Aerts, 1998; Scholz et al., 2006; Bobbert et al., 2008; Bobbert et al., 2014; see Marden, 1987 for an equivalent argument for studying lift production in flying animals). Though most specialized primate jumpers, including both strepsirrhine and platyrrhine species, mainly perform trunk-to-trunk leaping, often in the context of a vertical clinging and leaping locomotor mode (Kinzey et al., 1975; Garber et al., 2005, 2009; Garber and Porter, 2009; Gebo, 2011; Granatosky et al., 2016), this is primarily a horizontal jump—with a more or less important loss in height—from a vertical substrate to another substrate (either vertical or nonvertical). As such, horizontal jumping performance varies with parameters that are independent of power production per se, i.e., the trajectory of the velocity vector at TO and the relative vertical position of the launching and landing supports (Crompton and Sellers, 2007).

We focused on tree squirrels because, as generalist arboreal mammals, equally adept at terrestrial travel when required, they are a viable extant model for an early stage of primate locomotor evolution (Sargis et al., 2007), although—like all such analogies—the functional comparison between extant squirrels and primate ancestors is necessarily imprecise (Nyakatura, 2019). Nevertheless, understanding the biomechanical strategies that squirrels use to modulate jumping performance can therefore inform theories of selection for increased jumping ability during primate locomotor evolution (e.g., Boyer et al., 2013). *Sciurus carolinensis* live in hardwood or mixed forests and habitually forage in the small-branch niche (Thorington et al., 2012). Orkin and Pontzer (2011) reported that 54% of feeding and 48% of foraging events were on terminal branches (the remaining observations were either terrestrial or on four other branch sizes from small to very large). Jumps are frequently displayed as the habitat is discontinuous with gaps of varying magnitude between substrates (Youlatos, 1999; Thorington et al., 2012). In addition, free-ranging gray squirrels display various gaits when moving on arboreal substrates—including symmetrical walking and running gaits, gallops, half-bounds, and bounds—and adjust gait selection according to both the diameter and the orientation of the substrate (Dunham et al., 2019a), whereas some primate species instead adjust their grip postures according to substrate characteristics but maintain locomotor mechanics (in *Microcebus murinus*: Reghem et al., 2012; Boulinguez-Ambroise et al., 2020; in platyrrhine species: Dunham et al., 2019b). As with quadrupedal locomotion, substrate diameter has the potential to compromise jumping performance by challenging the overall stability or limiting the force production capacity (Fig. 1). Research on how substrate size affects jumping performance is limited. Previous studies found a minimal influence on jumping ability, but they focused on very small arboreal vertebrates (i.e., body masses <25 g; *Anolis* lizards: Losos and Irschick, 1996; Gilman et al., 2012; Gilman and Irschick, 2013; gecko species: Grabar et al., 2016).

Here, we used instrumented force platforms and poles to assess vertical jumping performance in Eastern gray squirrels and used launching supports of various sizes to test the influence of substrate diameter on the jumping kinetics. We used standard ergometric methods to quantify jumping from force platform data (Manter,

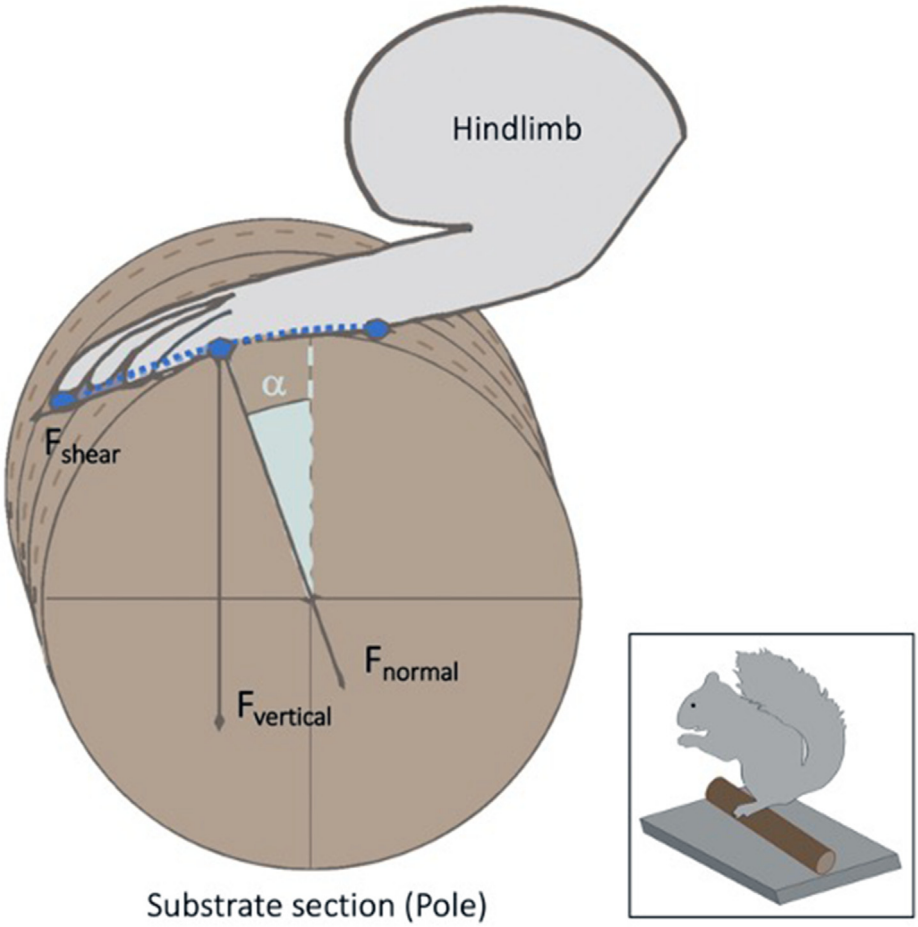

Figure 1. Force components related to foot position on branchlike substrates during vertical leaping in gray tree squirrels (*Sciurus carolinensis*). The blue dotted line represents the foot surface in contact with the substrate. As an indicator of the foot position, we measured the angle (a) between the center of this contact surface and the vertical axis of the substrate. For the animal standing on the pole, vertical forces can be resolved into a component normal to the support (F_{normal}) and a second component (F_{shear}) tangential to the pole surface. A decrease in substrate diameter may require the animal to adjust foot position to reduce an overdependence on F_{shear} (which is limited by frictional interactions between the foot and support and may generate slipping from the support if traction is insufficient). Squirrel silhouette modified from phylopic.org. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

1938; Cavagna, 1975; Bobbert et al., 2014). Specific biomechanical parameters included TO velocity—our primary measure of jumping performance—as well as total CoM displacement, peak vertical mechanical power, and net vertical mechanical work of the CoM during the push-off phase of upward vertical jumping. In order to compare the jumping performance of squirrels with the performance of primate species documented in the literature, we collected data on morphological traits to scale the available biomechanical output data. We collected hindlimb length measurements and leg muscle masses in *S. carolinensis*. We additionally collected hindlimb length measurements from μCT scans and data from the existing literature on jumping performance in small-bodied primates (i.e., *G. senegalensis*: Aerts, 1998; *M. murinus*: Legreneur et al., 2010; *C. jacchus*: Bobbert et al., 2014). However, we do not explicitly investigate morphofunctional correlates of jumping performance in this study. We test the following predictions.

P1) TO velocity (i.e., jumping performance) in squirrels will be jointly determined by maximal vertical force production and CoM displacement during TO.

P2) Given the unpredictable nature of the arboreal habitat, and the resulting need to reduce the magnitude of forces imparted to the substrate (Schmitt, 1999; Young, 2009), squirrels should modulate jumping height via increases in CoM displacement, rather than increases in force per se. The dependence on CoM displacement for mechanical work production during TO should be even greater when jumping from simulated arboreal supports.

P3) TO velocity should decline with decreasing support diameter, given that small diameter supports potentially compromise force production by requiring increasingly precise foot placement if the animal is to avoid an overdependence on shear/tangential forces to power the jump (Cartmill, 1985; Lammers, 2009).

P4) Given that Eastern gray squirrels frequently travel in terminal branch environments similar to those used by small-bodied primates (Orkin and Pontzer, 2011), we tested the null prediction that biomechanically relevant measures of squirrel jumping performance (i.e., size-adjusted vertical mechanical work, vertical power production, and maximal jumping height) would be similar to those of small-bodied primates (i.e., *G. senegalensis*: Aerts, 1998; *M. murinus*: Legreneur et al., 2010; *C. jacchus*: Bobbert et al., 2014). Finding similarity of jumping performance would indicate that the arboreal environment imposes similar constraints on small-bodied

mammals. In contrast, variation in performance—despite similarity in body size—would imply that phylogenetic history, clade-specific morphological adaptations, variation in locomotor ecology, or other factors result in variable selection pressures on jumping performance per se.

2. Materials and methods

2.1. Animal subjects and care

We studied three adult female gray squirrels (*S. carolinensis*), born and raised in captivity and obtained via the pet trade from a United States Department of Agriculture–accredited breeding facility (Hill View Exotic, Sunbury, USA). Animals were housed together in a large enclosure (122 cm wide × 183 cm deep × 244 cm tall) kept in indoor controlled conditions. The room in which the enclosure was kept was maintained under artificial light conditions (12 h light/12 h dark). Room temperature and humidity were maintained around 22 °C and at 25–35%, respectively. Animal keepers enriched the cage with dried branches, PVC pipes, wooden sticks for gnawing, and plastic nest boxes lined with straw to create sleeping holes. The three animals (individual mean body masses across the duration of study: 505 g, 516 g, and 600 g) were fed 5008 Rodent block *ad libitum* and produce once a day; a variety of fruits and vegetables were used according to the diet of the species. Before each session, an animal was transported individually from its home enclosure to the experimental room using an opaque metal transport box (44 × 18 × 22 cm) with the wire on the front. A sliding door on the side of the box allowed the animal to enter it, attracted by a food reward placed inside. After each session, the same procedure was followed in reverse to return the animal back to its home enclosure. Each session was carried out by two experimenters only. Animals were identified individually based on gross differences in fur distribution and markings, as well as differences in overall body size. Following the AVMA Guidelines for the Euthanasia of Animals for rodents, squirrels were euthanized at the end of the study via pentobarbital overdose (Fatal-Plus, Vortech Pharmaceuticals, Dearborn MI; dosage: 1 ml kg^{-1} of body mass). Prior to beginning the research, all procedures and housing conditions were approved by the Northeast Ohio Medical University Institutional Animal Care and Use Committee (i.e., IACUC; Protocols 17-04-069 and 17-04-069) and the Ohio Department of Natural Resources (ODNR Permit 16-63).

2.2. Performance measurements

We investigated jumping performance in gray squirrels by measuring mass-specific vertical mechanical work and vertical power outputs during vertical jumping. We performed the measurements using two HE6 × 6–16 small animal force plates (AMTI, Watertown, USA; 15 × 15 cm) measuring the ground reaction force during jumping. The force plates were mounted next to each other (with a 1-cm gap between them) and independently bolted to a laboratory benchtop (mass ≅ 50 kg), thus mechanically isolating them from each other and avoiding cross talk. We embedded the two force plates in a single custom-designed rectangular acrylic enclosure (122 × 34 × 34 cm), facilitating controlled vertical jumping to two 'stations' (i.e., target holes in the plexiglass enclosure; diameter = 4 cm) of different heights: 86 cm and 56 cm (Fig. 2). The height difference between the two stations was equivalent to approximately one squirrel body length. Individuals were trained to vertically jump to the targets using positive reinforcement (i.e., with a training clicker as a bridge and a mix of peanuts, blueberries, and grapes as a reward). During the test sessions, after releasing an individual into the enclosure at the ground level, experimenters used nuts, grapes, and other food rewards passed through the holes to motivate animals to jump to the two stations. To facilitate safe landing at the feeding stations, a wire mesh (40 × 27 cm) was attached to the plexiglass at targets' heights.

Animals were tested in four conditions, corresponding to different terrestrial and arboreal substrate types from which free-ranging animals might jump (Orkin and Pontzer, 2011; Dunham et al., 2019a): ground (i.e., flat force plates); wide pole (diameter = 9.1 cm); intermediate pole (diameter = 4.9 cm); narrow pole (diameter = 3.5 cm). The squirrels' foot length (measured from the proximal calcaneus to the top of the third toe) averaged 4.7 cm (SD ± 0.24), corresponding to 16.5%, 30.6% and 42.8% of the wide, intermediate, and narrow pole circumferences, respectively. Wide, intermediate, and narrow poles were constructed from stiff PVC pipe and mounted directly to the force plates. We collected between 22 and 57 trials per individual per experimental condition. Whereas animals jumped to both target heights in the ground condition, they jumped only to the highest target (i.e., 86 cm) in the three pole conditions.

We sampled forces at 1000 Hz and recorded synchronized video of each trial at 50 frames per second using three digital cameras (Xcitex XC-2; Xcitex Inc., Woburn). Video and force data were synchronously recorded using ProCapture v. 1.0.3.6 (Xcitex Inc., Woburn; Chadwell and Young, 2015; Young and Chadwell, 2020). All mechanical variables were calculated from the vertical force output alone, measured by the force plates. We recorded videos for three purposes: 1) to qualitatively score the quality of the trial, making sure that the animal's body weight was fully supported by the force plates (i.e., the animal was not holding onto the jump tower), 2) to record the actual height gained during the jump, independently of the projected height gain from SRF analysis (using the dimensions of the jump tower as a calibration object), and 3) to record details of foot placement on the launching pole immediately prior to TO (see below). The three cameras thus focused on three different fields of view: one frontal view camera focused on the animal on the force pole (purpose 1), a second frontal view camera filmed the entire jump box (purpose 2), and a final side (sagittal) view camera (purpose 3). Qualitative review of jumping videos showed that when jumping to the high target, squirrels fully extended their forelimbs in order to reach the landing point and occasionally pushed off the plexiglass case of the jumping enclosure in mid-flight, perhaps in an effort to gain or redirect momentum (Hunt et al., 2021). We interpret these behaviors as an indication that the squirrels reached their maximal performance when jumping to the high target.

2.3. Behavioral measurements: Average foot position on substrates

To assess how variation in support diameter could influence the squirrels' reliance on shear/tangential forces—rather than normal forces—to power the upward vertical jump, we quantified foot position on the branchlike substrates (i.e., wide, intermediate, and narrow poles). We measured the angle (α) between the vertical axis of the substrates and the central point of the part of the foot in contact with the substrate (Fig. 1), digitizing videos using the freely available DLTdv8a MATLAB v. R2018a application (Hedrick, 2008). Shear forces (F_{shear}) are equal to the product of total vertical force ($F_{vertical}$) and the sine of the foot contact angle (α; Cartmill, 1979):

$$F_{shear} = F_{vertical} \sin \alpha$$

Therefore, the ratio of shear force to total vertical force is itself equal to the sine of the foot contact angle (i.e., dividing both sides of the equation by $F_{vertical}$):

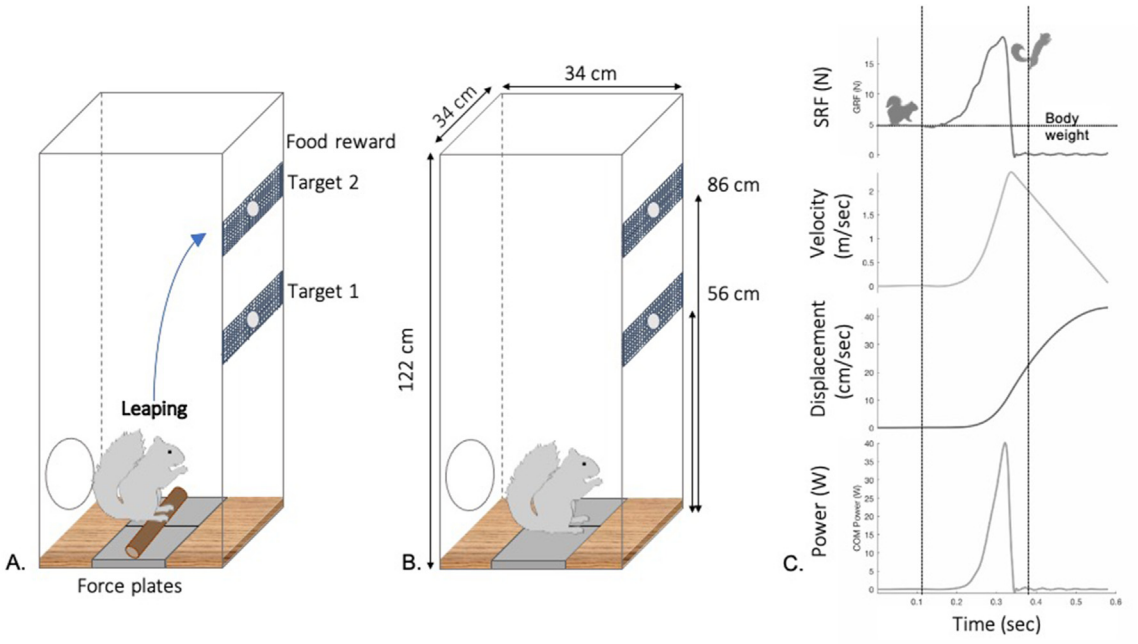

Figure 2. Experimental apparatus to assess vertical leaping performance in gray tree squirrels (*Sciurus carolinensis*). Food rewards were used to motivate animals to leap to two targets of different heights, eliciting a range of leap heights. Two small animal force plates (in gray) were used to record ground reaction forces during the push-off phase of the leap from: A) a branchlike substrate fixed on the force plates (i.e., poles of different diameters: 9.1 cm/large), 4.9 cm/intermediate, 3.5 cm/narrow); B) from the ground (i.e., the flat force plates); (squirrel's silhouette modified from phylopic.org); C) exemplar velocity, power and displacement curves of the center of mass obtained from substrate reaction force (SRF) data (using standard ergometric methods; Bobbert et al., 2014). Dashed vertical lines indicate the boundaries of integration, allowing us to calculate the CoM vertical velocity, displacement, and mechanical power from the vertical component of the substrate reaction force.

$$\frac{F_{shear}}{F_{vertical}} = \sin \alpha$$

Because the sine of α increases monotonically as α increases, variation in foot contact angle directly correlates with reliance on tangential forces to power jumping.

2.4. Determination of muscle mass

We estimated leg muscle masses for use in equations in this study from a carcass (*S. carolinensis,* 641 g) available in existing laboratory collections (Department of Anatomy and Neurobiology, NEOMED, USA). The whole body (frozen after death and kept at −20 °C) was thawed prior to the dissection. We used a digital balance (MRB-10000 compact scale, LW Measurements LLC, Rohnert Park, USA) to weigh the following functional muscle groups of both legs (Scholz et al., 2006; Bobbert et al., 2014): hip extensors (gluteus superficialis, gluteus medius, gluteus minimus/profundus, semitendinosus, semimembranosus, biceps femoris), hip adductors (adductor magnus, brevis, longus), knee extensors (vastus lateralis, medialis, intermedius, rectus femoris), and ankle plantarflexors (gastrocnemius, soleus, plantaris, tibialis posterior, flexor digitorum longus tibialis, flexor digitorum longus fibularis).

2.5. Hindlimb length measurements

We measured total hindlimb lengths in *S. carolinensis* and several primate species (*M. murinus, G. senegalensis, C. jacchus, Pan troglodytes,* and *Homo sapiens*) to compare squirrel jumping performance with existing data on primate jumping performance taken from the literature. For *S. carolinensis,* we measured hindlimb length directly from the animals used in this study. The euthanized specimens were scanned using μCT at the Duke University Shared Materials Instrumentation Facility. Scans were uploaded to Morphosource.org and are available for public download. Lengths of five hindlimb elements (femur, tibia, distal calcaneus, cuboid, and fourth metatarsal) were digitally measured on μCT scans in Avizo 3D v. 2021.1 (Thermo Fisher Scientific, Waltham). Measurements were chosen to represent 'functional' hindlimb length (hip joint to point of contact with substrate) and did not include projections of bone that function as muscle or ligament attachment sites (e.g., greater trochanter, medial malleolus, and calcaneal tuber).

For other primate species with available data on jumping performance (*M. murinus, G. senegalensis, C. jacchus, P. troglodytes, H. sapiens*), hindlimb measurements were taken from μCT scans of specimens downloaded from MorphoSource.org; original published data sources (Zihlman et al., 2008; Ward et al., 2011; Boyer et al., 2013; Prang, 2019; Aitken, 2021).

2.6. Data processing

Vertical velocity, displacement, instantaneous mechanical power, and net mechanical work of the center of mass For our calculations, we only considered the vertical component of the SRF. We summed the vertical force outputs of the two force plates, treating them as a single integrated transducer. We calculated vertical velocity, vertical CoM displacement, instantaneous vertical mechanical power, and the net vertical mechanical work of the CoM from vertical SRFs, collected by the force platforms, using standard ergometric methods (Manter, 1938; Cavagna, 1975; Bobbert et al., 2014). First, we calculated instantaneous CoM acceleration by dividing vertical SRF by body mass and then subtracting local gravitational acceleration (i.e., g: 9.81 m s^{-2}).

$$\overrightarrow{a_{CoM}} = \frac{\overrightarrow{SRF_v}}{m} - \vec{g}$$

Body mass (m) was measured for each squirrel immediately prior to data collection each day. To calculate the CoM velocity, we used the definition of the acceleration as the derivative of velocity:

$$\overrightarrow{a_{CoM}} = \frac{d\overrightarrow{v_{CoM}}}{dt} \text{ so that, } d\overrightarrow{v_{CoM}} = \overrightarrow{a_{CoM}}\, dt \quad (1)$$

and integrated the equation (Eq. (1)), with an initial velocity assumed to equal zero (i.e., jumping from a static start). We manually chose to start the integration as the final instant (t_0) before the animal crouched down to begin the jump (using the MATLAB function 'ginput' to register this point on a graph of the vertical SRF vs. time) and defined the end of the integration as the instant the SRF dropped to zero (t_f):

$$\overrightarrow{v_{CoM}} = \int_{t_0}^{t_f} \overrightarrow{a_{CoM}}\, dt, \text{ so that}$$

$$\overrightarrow{v_{CoM}} = \int_{t_0}^{t_f} \left(\frac{SRF}{m} - g\right) dt$$

To calculate the CoM displacement, we used the definition of velocity as the derivative of position(s)

$$\overrightarrow{v_{CoM}} = \frac{d\overrightarrow{s_{CoM}}}{dt} \text{ so that, } d\overrightarrow{s_{CoM}} = \overrightarrow{v_{CoM}}\, dt \quad (2)$$

and integrated the equation (Eq. (2)), assuming the initial position is zero, so that

$$\overrightarrow{s_{CoM}} = \int_{t_0}^{t_f} \overrightarrow{v_{CoM}} dt$$

The mechanical work (W, in J) occurs when the SRF is applied to the CoM during its displacement (in the same direction as that of force). As a transfer of energy related to the displacement, the mechanical work formula is the scalar product of the force (in N) and the displacement (Dy, vertical displacement in meters). Mechanical power (P, in W) is work per unit of time (i.e., the greater the amount of work transferred per second, the greater the mechanical power). We calculated the mechanical power as the scalar product of the net vertical force (F_{net})—i.e., the difference of vertical SRF and body weight—and CoM velocity (Bennet-Clark, 1977):

$$\text{As } W(t) = \overrightarrow{F_{net}}(t) \cdot d\overrightarrow{s_{CoM}}(t) \text{ and } P(t) = \frac{dW(t)}{dt}$$

$$P(t) = \overrightarrow{F_{net}}(t) \cdot \frac{d\overrightarrow{s_{CoM}}(t)}{dt} = \overrightarrow{F_{net}} \cdot \overrightarrow{v_{CoM}}$$

Net mechanical work was finally calculated as the area under the power-time curve.

We designed a MATLAB code to automatically calculate all parameters from the data extracted from the SRF curve obtained by force plate measurements (Fig. 2C).

Center of mass height gain and velocity at takeoff CoM displacement during push-off is equal to the distance over which the SRF is applied to create the mechanical work required to launch the animal into the jump. We identified the CoM displacement during push-off and the velocity of the CoM at TO by using the Bobbert et al. (2014) definition of push-off as lasting from the moment when mass-specific mechanical power surpasses 2 W kg^{-1} to when the SRF drops to zero. The predicted jump height was corrected for the jumps from poles (i.e., the pole height above the flat ground has been added to the height, to make estimates comparable).

Scaling biomechanical outputs To adjust for variation in body size among the squirrel individuals and make our data more easily comparable to previously collected data on other jumping mammals, we scaled the SRF (in N) to the measured body weight of the individuals (i.e., body mass [in kg] multiplied by 9.81 m s^{-2}, gravitational acceleration). We provide performance metric per unit of overall body mass or per unit of hindlimb muscle mass: we scaled the average power (P, in W), maximal power (P, in W), and work (W, in J) of the CoM using either the measured body mass (in kg) of the individuals or the hindlimb muscle mass (in kg) calculated from the mass of the hip extensors, hip adductors, knee extensors, and ankle plantarflexors (right and left hindlimbs combined).

Available data on primate species and comparisons between species Heights reached during vertical jumping were available for *C. jacchus* (Bobbert et al., 2014), *M. murinus* (Legreneur et al., 2010), *G. senegalensis* (Aerts, 1998), *Pan paniscus* (Scholz et al., 2006), and *H. sapiens* (Bobbert et al., 2008). Leg muscle masses and peak CoM powers expressed either per kilogram of body mass or leg muscle mass were available for *C. jacchus*, *G. senegalensis*, *P. paniscus,* and *H. sapiens* from Bobbert et al. (2014), who calculated those parameters from original data (Aerts, 1998; Scholz et al., 2006; Bobbert et al., 2008, 2014). The TO velocity was available for *C. jacchus* (Bobbert et al., 2014) and *M. murinus* (Legreneur et al., 2010). For *G. senegalensis* (Aerts, 1998), *P. paniscus* (Scholz et al., 2006), and *H. sapiens* (Bobbert et al., 2008), we estimated the TO velocity according to the law of conservation of energy (applied to kinetic and potential energies). For all species (including *S. carolinensis*, this study), we scaled the jump height to either the cube root of body mass or the hindlimb length (i.e., sum of femur, tibia, distal calcaneal, cuboid, and 4th metatarsal lengths). Additionally, we calculated dimensionless TO velocity using hindlimb lengths as a measure of size, following the formula of Hof (1996).

2.7. Statistical analysis

We used linear mixed-effect model (LMM) regression analysis to investigate the association between force-based estimates of maximal jump height and video-based measures of the actual height achieved, specifying video-based height as the dependent variable, force-based height as the independent variable, and individual animal a random effect. The coefficient of determination (i.e., r^2) for this model was estimated using the method of Nakagawa and Schielzeth (2013).

To investigate potential determinants of TO velocity, we combined the data collected from jumps resulting in different heights and fit an LMM with the TO velocity as the dependent variable, peak vertical SRF magnitude and CoM displacement during push-off as fixed independent variables, and individual as a random effect. We used analyses of variance (ANOVAs; type III) to test the statistical significance of each fixed term in the fitted model. Dependent and fixed variables were scaled and centered (i.e., converted to z-scores) prior to analysis, to calculate standardized regression coefficients for the model (i.e., β-weights). Standardized regression coefficients are measures of effect size, permitting direct comparison of the strength of different predictors in a multiple regression model regardless of the original scale of the variables (Quinn and Keough, 2002; Druelle et al., 2018).

We tested the effect of the substrate type on jumping strategy by comparing the ground reaction forces and CoM displacements on the flat ground versus three different pole sizes, specifying TO velocity as a covariate. Basically, this model addresses the hypothesis that squirrels may use different biomechanical strategies (i.e., force

versus displacement) to achieve the same performance outcome (TO velocity) on different types of supports. We fit two LMMs with either the peak SRF magnitude (scaled to body weight) or the CoM displacement during push-off as the dependent variable, the TO velocity and the type of substrate as fixed independent variables, and individual as a random effect. We used ANOVAs (type III) to test the statistical significance of each fixed term in the fitted models. We performed post hoc analyses by comparing estimated marginal means (EMMs, 'emmeans' package v. 1.8.4–1 for RStudio v. 1.2.5001; RStudio, Inc., 2019; Lenth, 2020), testing pairwise comparisons between the four different substrate types. To control type I error rates (i.e., alpha inflation), p-values for pairwise comparisons were adjusted using the false discovery rate method (Benjamini and Hochberg, 1995), a method that mitigates experiment-wise error rates while minimizing the loss of statistical power.

We tested whether substrate type affects the jumping performance by fitting an LMM with the TO velocity as the dependent variable, the type of substrate as a fixed independent variable, and individual as a random effect. We used ANOVA (type III), followed by post hoc analyses (EMMs), to conduct pairwise comparisons between the four different types of substrates. We carried out the same analytical steps to test the effect of the substrate type on the jump height (i.e., vertical displacement of the body CoM during the floating ballistic phase of the jump).

We tested the effect of the diameter of the branchlike substrates on the squirrels' foot position (on the poles) before jumping by fitting an LMM with the angle between the vertical axis of the substrate and the foot (i.e., central point of the part in contact with the substrate) as the dependent variable, pole diameter as a fixed independent variable, and individual as a random effect. We used ANOVA (type III) followed by post hoc analyses (EMMs) to conduct pairwise comparisons between the three different sizes of poles. In addition, we fit an LMM to test whether the squirrels' foot position affects TO velocity, with the TO velocity as the dependent variable, pole diameter as a fixed independent variable, and individual as a random effect. We used ANOVA (type III) to test the statistical significance of each fixed term in the fitted model. All statistics were performed using the software RStudio (v. 1.2.5001; RStudio, Inc., 2019) and an α-level of 0.05.

3. Results

3.1. Summary of squirrel jumping performance

Mean, maxima, and minima of the different mechanical outputs calculated from the measured vertical SRF are provided in Tables 1 and 2. Data scaled to body mass are provided in Table 1. Data scaled to hindlimb muscle mass are provided in Table 2. Raw data are provided in Table 3. Linear mixed-effect model regression indicated that video-based estimates of actual jump heights averaged only 82% of the total height gain predicted from SRF analysis (95% confidence interval: 74.9–88.8%; r^2: 0.76), suggesting that squirrels generally produced more mechanical work than strictly required to reach their target jump heights.

3.2. Determinants of jumping performance: Force production and center of mass displacement

When combining data collected during jumping from the ground to the two different target heights, linear models indicated that TO velocity (i.e., jumping performance) increased significantly with both force production (β-weight: 0.636; $F_{1,188} = 1885.5$; $p < 0.0001$) and CoM displacement (β-weight: 0.589; $F_{1,188} = 1990.5$; $p < 0.0001$; Fig. 3). Though β-weights were greater for force production than for CoM displacement, 95% confidence intervals on these estimates overlapped (i.e., force β-weight: 0.6072–0.6636; CoM displacement β-weight: 0.5060–0.6170), indicating that the two predictors were equally important in explaining variation in jumping performance.

3.3. Determinants of jumping performance: Differing strategies according to substrate type

Linear models of jumping from the ground (experimental condition) and the various poles (wide, intermediate, and narrow) detected that the squirrels increased TO velocity via increase in both force production (model 1: $F_{1,352} = 111.31$; $p < 0.0001$) and CoM displacement (model 2: $F_{1,352} = 463.93$; $p < 0.0001$) with a significant effect of the type of substrate on both metrics (model 1: $F_{3,350} = 65.46$; $p < 0.0001$; model 2: $F_{3,350} = 62.76$; $p < 0.0001$). Post hoc comparisons based on EMMs (i.e., least-squares means) revealed that squirrels emphasized force production in the ground condition versus CoM displacement on poles. Post hoc tests showed that squirrels produced significantly greater maximal forces during the ground condition versus the three pole conditions (ground vs. wide pole: $t[351] = 11.34$, $p < 0.0001$; ground vs. intermediate pole: $t[351] = 11.75$, $p < 0.0001$; ground vs. narrow pole: $t[350] = 10.96$, $p < 0.0001$), with no significant differences in force production among the pole conditions (see Fig. 4). In contrast, squirrels showed significantly greater CoM displacements on the poles versus the ground (ground vs. wide pole: $t[351] = -11.99$, $p < 0.0001$; ground vs. intermediate pole: $t[350] = -11.41$, $p < 0.0001$; ground vs. narrow pole: $t[350] = -9.46$, $p < 0.0001$); comparison between the wide and intermediate pole conditions showed no significant difference, while wide versus narrow poles ($t[351] = 3.87$, $p = 0.0002$) and intermediate versus narrow poles were significantly different ($t[351] = 2.39$, $p = 0.02$; Fig. 4).

Table 1
Mechanical output scaled to body mass during jumping in gray squirrels ($n = 3$).

Substrate	Target	n trials	SRF (% BW)			Average power (W/kg)			Maximal power (W/kg)			CoM work (J/kg)		
			Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min
Ground	Low	99	455 ± 54	647	326	36 ± 7	64	23	84 ± 17	139	44	3.95 ± 0.75	6.25	1.83
Ground	High	94	547 ± 36	635	467	57 ± 6	69	41	134 ± 12	159	100	6.00 ± 0.59	7.19	4.59
⌀ 9.1 cm	High	130	471 ± 35	579	387	43 ± 7	67	31	102 ± 14	138	64	5.05 ± 0.76	7.66	2.93
⌀ 4.9 cm	High	117	490 ± 30	575	420	47 ± 6	63	36	115 ± 12	149	80	5.69 ± 0.62	7.47	4.12
⌀ 3.5 cm	High	128	501 ± 30	566	405	47 ± 6	59	31	119 ± 13	153	84	5.83 ± 0.67	7.94	4.15

Abbreviations: ⌀ = diameter of the poles; Max = maximum; Min = minimum.
The individuals jumped from different substrates (i.e., flat ground and poles of three different diameters) to different heights (low = 56 cm and high = 86 cm). Force plates measured the substrate reaction force (SRF) during push-off, and other measures of mechanical output were calculated from SRF measurement and individual body mass using a custom MATLAB program. The SRF (in N) has been scaled by the body weight (BW; i.e., body mass, in kg, multiplied by gravitational acceleration [≈ 9.81 m s^{-2}]). The mechanical power (P, in W) and work (in J) of the center of mass (CoM) have been scaled by body mass. Mean values are provided with standard deviation (means ± SD).

Table 2
Mechanical output scaled to hindlimb muscle mass during jumping in gray squirrels ($n = 3$).

Substrate	Target	*n* trials	Average power (W/kg)			Maximal power (W/kg)			CoM work (J/kg)		
			Mean	Max	Min	Mean	Max	Min	Mean	Max	Min
Ground	Low	99	286 ± 60	507	180	671 ± 136	1108	349	31 ± 6	50	14
Ground	High	94	453 ± 49	550	330	1065 ± 98	1266	792	48 ± 5	57	36
⌀ 9.1 cm	High	130	339 ± 58	531	250	813 ± 110	1095	509	40 ± 6	61	23
⌀ 4.9 cm	High	117	375 ± 46	505	284	913 ± 99	1187	640	45 ± 5	59	33
⌀ 3.5 cm	High	128	378 ± 50	471	250	950 ± 101	1219	665	46 ± 5	63	33

Abbreviations: ⌀ = diameter of the poles; Max = maximum; Min = minimum.
The individuals jumped from different substrates (i.e., flat ground and poles of three different diameters) to different heights (low = 56 cm and high = 86 cm). Force plates measured the substrate reaction force (SRF) during push-off, and other measures of mechanical output were calculated from that measurement and individual body mass using a custom MATLAB program. The mechanical power (P, in W) and work (in J) of the center of mass (CoM) have been scaled to the hindlimb muscle mass calculated from the mass of the hip extensors, hip adductors, knee extensors, and ankle plantarflexors (i.e., both legs, data available from a previously dissected specimen of the same species). Mean values are provided with standard deviation (means ± SD).

Table 3
Vertical displacement of the body center of mass (CoM) during push-off and the airborne phase (i.e., jump height) during jumping in gray squirrels ($n = 3$).

Substrate	Target	*n* trials	CoM displacement push-off (cm)			Jump height (cm)		
			Mean	Max	Min	Mean	Max	Min
Ground	Low	99	13.10 ± 2.14	17.58	6.69	27.29 ± 6.08	46.68	11.97
Ground	High	94	15.59 ± 1.47	18.14	11.90	45.98 ± 4.76	56.09	33.26
⌀ 9.1 cm	High	130	15.82 ± 2.06	20.27	9.94	47.43 ± 6.45	67.93	29.81
⌀ 4.9 cm	High	117	16.89 ± 1.78	20.76	11.27	48.85 ± 5.75	66.54	35.67
⌀ 3.5 cm	High	128	16.80 ± 1.97	22.25	11.89	49.22 ± 6.27	70.17	33.21

Abbreviations: ⌀ = diameter of the poles; Max = maximum; Min = minimum.
The individuals jumped from different substrates (i.e., flat ground and poles of 3 different diameters) to different heights (low = 56 cm and high = 86 cm). Force plates measured the substrate reaction force (SRF) during push-off, and push-off displacement and jump height were calculated from that measurement and individual body mass using standard ballistics equations in MATLAB. The predicted jump height was corrected for the jumps realized on poles (i.e., the pole height above the flat ground has been added to the height, to make estimates comparable). Mean values are provided with standard deviation (means ± SD).

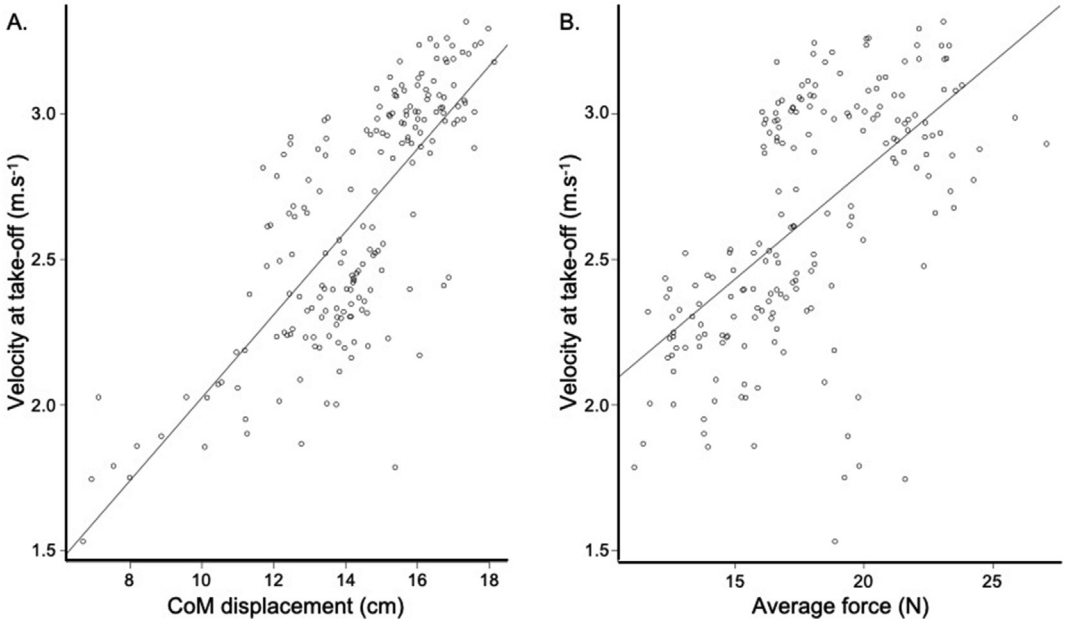

Figure 3. Plots of the relation between the velocity at takeoff—used as a measure of leaping performance—and the displacement of the body center of mass (CoM) during the push-off phase (A) and the average force produced (i.e., substrate reaction force) during vertical leaping in gray squirrels (B; $n = 3$). Trend lines indicate linear mixed-effect regression fits to the data.

3.4. Jumping performance according to substrate type

Linear modeling detected a significant effect of the substrate type (i.e., flat ground, and three different pole diameters: 9.1 cm, 4.9 cm, and 3.5 cm) on the TO velocity ($F_{3,351} = 44.65$; $p < 0.0001$). Post hoc comparisons based on EMMs revealed (1) the TO velocity to be the highest when jumping from the ground, (2) no difference between the two smallest diameters of pole, and (3) the TO velocity to be the lowest when jumping from the large pole. Post hoc tests showed a statistically significant difference between the ground condition and the wide and intermediate pole conditions but not with the narrow pole (ground vs. wide pole: t[351] = 10.89,

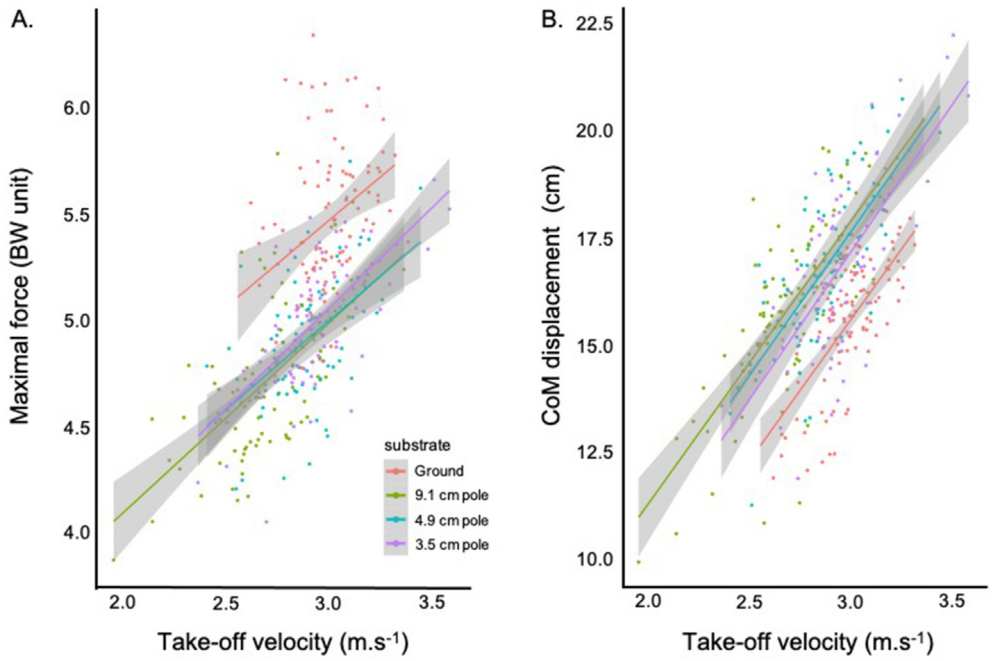

Figure 4. Plots of the relations between takeoff velocity (i.e., proxy of leaping performance), the maximal force produced (A; substrate reaction force), and the displacement of the body center of mass (B; CoM displacement) during the push-off phase of vertical leaping in gray squirrels ($n = 3$) according to different substrate types. The individuals jumped from four different substrates: a flat ground and poles of three different diameters (9.1 cm, 4.9 cm, and 3.5 cm). The figure illustrates differing strategies according to the type of substrate with emphasized force production in the ground condition versus CoM displacement on the poles. All comparisons between the ground condition and the three pole conditions are significant at $p < 0.0001$. Shaded bands indicate 95% confidence intervals on the linear mixed-effect regressions. Abbreviation: BW = body weight. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

$p < 0.0001$; ground vs. intermediate pole: $t[351] = 4.05$, $p = 0.0004$; ground vs. narrow pole: $t[351] = 1.91$, $p = 0.23$); comparisons between the large pole and the two smaller pole conditions showed significant differences (wide vs. intermediate pole: $t[351] = -6.45$, $p < 0.0001$; wide vs. narrow pole: $t[351] = -8.87$, $p < 0.0001$). There was no significant difference between intermediate and narrow poles ($t[351] = -2.17$, $p = 0.13$; Fig. 5).

Moreover, linear modeling detected a significant effect of substrate type on the jump height (i.e., vertical displacement of the body CoM) as well ($F_{3,351} = 5.95$; $p = 0.00057$). Post hoc comparisons based on EMMs revealed the vertical displacement to be the highest when jumping from the two narrower poles and the lowest when jumping from the flat ground. Post hoc tests showed no significant difference between the ground and the large pole conditions ($t[351] = -2.004$, $p = 0.19$) but showed significant differences with the two smaller diameters (ground vs. intermediate pole: $t[351] = -3.21$, $p = 0.008$; ground vs. narrow pole: $t[351] = -3.91$, $p = 0.0006$). The other three comparisons between pole conditions showed no significant differences (see Fig. 5).

3.5. Squirrels' foot position according to substrate type and relationship with takeoff velocity

Linear modeling detected a significant effect of the substrate diameter (among the three different pole diameters: 9.1 cm, 4.9 cm, and 3.5 cm) on the squirrels' foot position on the poles ($F_{2,158} = 24.34$; $p < 0.0001$). Post hoc comparisons (EMMs) showed that the three pole conditions were significantly different from each other (wide vs. intermediate pole: $t[158] = -2.46$, $p = 0.0399$; wide vs. narrow pole: $t[159] = -6.76$, $p < 0.0001$; intermediate vs. narrow pole: $t[158] = -4.89$, $p < 0.0001$), with the angle between the vertical axis of the substrate and the foot (i.e., central point of the part in contact with the substrate) increasing with smaller diameters (see Fig. 6). In other words, on the large pole, the feet were placed more on the top of the pole, whereas on thinner poles (i.e., intermediate and narrow poles), the feet were placed more laterally, contacting the sides of the poles. However, linear modeling indicated that squirrels' foot position was not significantly associated with TO velocity ($F_{1,157} = 0.71$; $p = 0.4$).

3.6. Comparisons of squirrel and primate jumping performance, relative muscle mass, and relative hindlimb length

In Table 4, we provide comparative data on vertical performance in different primate species. It should be noted that only Legreneur et al. (2010) assessed submaximal jumping performance; in the other primate studies, the animals were not required to reach a near-maximal level of performance. Thus, comparisons of these results must be made with caution. To facilitate size-adjusted comparisons among these animals, we scaled metrics of jumping mechanical output using body mass, hindlimb length, or hindlimb muscle mass. Marmosets show similarities to gray squirrels regarding both morphological traits—relative hindlimb length and extensor muscle mass—and dimensionless TO velocity. However, the peak power generated by squirrels is remarkably higher than in primate species, other than the highly specialized galagos.

4. Discussion

In this study, we investigated the jumping performance (i.e., mechanical output during vertical jumping) of Eastern gray squirrels in different substrate conditions, with the purpose of comparing the performance of these small arboreal rodents with primates. We quantified jumping performance in Eastern gray squirrels as the CoM velocity at TO and the maximal height reached during the airborne phase, using standard ballistic equations

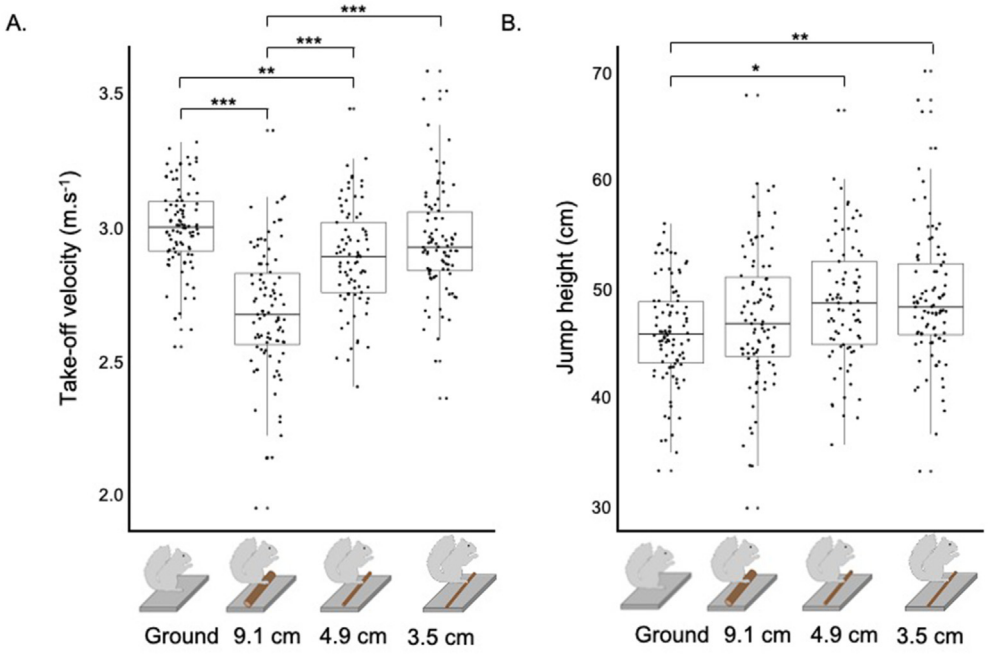

Figure 5. Box plots of the velocity at takeoff (A) and of the vertical displacement of the body center of mass (CoM)—i.e., jump height— (B) according to the substrate type during jumping in gray squirrels ($n = 3$). The individuals jumped from four different substrates: a flat ground and poles of three different diameters (9.1 cm, 4.9 cm, and 3.5 cm). The predicted jump height was corrected for the jumps realized on poles (i.e., the pole height above the ground has been added to raw jump height to make estimates more comparable). Triple asterisks indicate very high significance ($p < 0.0001$), double asterisks indicate high significance ($p < 0.001$), and single asterisks indicate significance ($p < 0.01$). The box plots are made of a vector containing the 1st quartile (Q1, box lower 'hinge'), the median (bold horizontal line), the 3rd quartile (Q3, box upper 'hinge'), and the adjacent values (whiskers). The length of the whiskers is calculated from the interquartile range (IQR = Q3 − Q1): Q1 − 1.5*IQR (lower whisker), Q3 + 1.5*IQR (upper whisker). Superimposed markers overlying each box plot show individual data points in the distribution.

calculated from the vertical SRF history. When jumping from the flat force plates, the TO velocity of the CoM was on average 3 ± 0.15 m s^{-1}. The maximal TO velocity recorded (3.31 m s^{-1}) allowed the animal to achieve an airborne distance of 56 cm.

Our predictions (1) and (2) stated that squirrels' jumping performance would be jointly determined by maximal force production and CoM displacement during TO. We also predicted that jumping strategy would differ among substrate types, given the complex and discontinuous nature of the arboreal habitat and the resulting need to reduce the magnitude of forces imparted to the substrate (Schmitt, 1999; Young, 2009).

Our results validated our predictions. When investigating the mechanical output during jumping from a flat platform to different heights, we found that squirrels increased TO velocity (i.e., jumping performance) via increases in both force production and CoM displacement. However, modulation of these strategies was affected by the type of substrate; squirrels showed divergent mechanical strategies on the two different substrate types, prioritizing force production on the flat substrate versus CoM displacement on the poles. These findings suggest the possibility of divergent mechanisms to maximize jumping performance depending on the substrate type. Several studies have noted a reduction in force magnitudes when quadrupedal mammals transition from flat substrates to narrow, branchlike supports (Schmitt, 1998; Wallace and Demes, 2008; Young, 2009; Schmidt and Fischer, 2010). These trends have been interpreted as a means of limiting balance disruptions on narrow supports. It could be that similar concerns characterize jumping as well. Additionally, though the poles in our experimental conditions varied only in diameter but not in compliance, diameter and compliance are tightly coupled in natural supports (Gilman and Irschick, 2013; van Casteren et al., 2013; Dunham et al., 2018). Compliant substrates generally compromise jumping performance by absorbing some of the mechanical work that could be used to accelerate the CoM into the jump. Reducing branch loading and increasing CoM displacement prior to TO both mitigate potential energy losses when jumping from compliant supports (Astley et al., 2015; Reynaga et al., 2019). From an evolutionary perspective, jumping on small compliant arboreal substrates might have driven selection for elongated hindlimb segments in primates—allowing the CoM to be accelerated on a longer distance—and thereby reducing the need for high SRFs. It would be interesting in future work to compare the hindlimb anatomy between species like marmosets that travel mainly on trunks and large vertical substrates (Garber, 1992; Schmitt, 2003) with other primate species that mainly travel on the fine terminal and more compliant branches of trees.

At a behavioral level, tarsiers avoid energy loss due to branch flexion by actively selecting substrates of larger diameters when making long leaps (Crompton et al., 2010). In gibbons (*Nomascus leucogenys*), individuals counterbalance the effect of substrate compliance by adjusting their jumping strategies: pronograde and more rapid leaps or slower orthograde leaps, both minimizing the substrate deflection (Channon et al., 2011). In arboreal Cuban tree frogs (*Osteopilus septentrionalis*), long legs and sticky toes allow them to keep longer contact with the substrate during the recoil and thus recover part of the dissipated energy just prior to TO (Astley et al., 2015). Future research may further investigate the presence of such mechanisms in strepsirrhine and arboreal rodent species possessing integumental structures like volar pads and fluid-secreting glands that could potentially increase friction with the substrate (Haffner, 1998; Maiolino et al., 2016).

Our third prediction stated that jumping performance should decline with decreasing support diameter, given that small diameter supports potentially compromise force production. Indeed, we found an effect of substrate type, with the highest TO velocity occurring when jumping from the ground. However, TO velocity

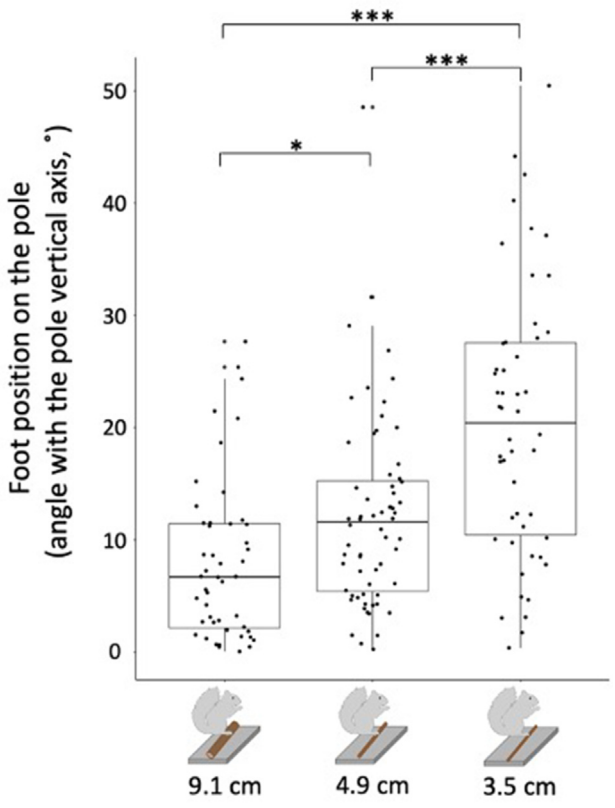

Figure 6. Box plot of the foot position on the poles according to substrate diameter before vertical jumping in gray squirrels ($n = 3$). The foot position was measured as the angle between the vertical axis of the substrate and the central point of the foot in contact with the pole. The individuals jumped from poles of three different diameters (9.1 cm, 4.9 cm, and 3.5 cm). Triple asterisks indicate very high significance ($p < 0.0001$), double asterisks indicate high significance ($p < 0.001$), and single asterisks indicate significance ($p < 0.01$). The box plots are made of a vector containing the 1st quartile (Q1, box lower 'hinge'), the median (bold horizontal line), the 3rd quartile (Q3, box upper 'hinge'), and the adjacent values (whiskers). The length of the whiskers is calculated from the interquartile range (IQR = Q3 − Q1): Q1 − 1.5*IQR (lower whisker), Q3 + 1.5*IQR (upper whisker). Superimposed markers overlying each box plot show individual data points in the distribution.

was lowest when jumping from the large pole, contrary to our expectation that TO velocity would be reduced on the two smaller pole diameters. Moreover, contradicting our hypothesis, we found the jump height (i.e., airborne maximal height) to be the lowest on the flat ground and the highest on the two smaller diameters of poles (after compensating for the height of the poles above the flat ground). In previous research on the effects of perch diameter on jumping performance, Losos and Irschick (1996) reported in *Anolis* lizards—known for grasping abilities allowing them to navigate on narrow branches (Pouydebat et al., 2023)—that substrate size had a minimal influence on jumping performance (i.e., jump distance); similar results have been shown in arboreal geckos (Grabar et al., 2016). Interestingly, we found that the position of the foot on the poles changed according to the pole diameter: for the large diameter, the feet were placed more on the top of the pole, whereas on thinner poles, the feet were placed more laterally. To further investigate the influence of foot position on jumping performance from narrow supports, it would be interesting to conduct these experiments again but include substrates with different frictional properties. Overall, our data show that—provided traction is sufficient—branch diameter per se does not negatively influence jumping performance, suggesting that specific adaptations would not be required to be a 'fine-branch leaper' in the absence of variation in compliance.

Given that tree squirrels lack primate grasping specializations for locomotion in the fine-branch arboreal environment, along with an increased dependence on jumping to navigate gaps in the canopy, we expected mechanically relevant measures of jumping performance in squirrels to be similar to previously studied small-bodied arboreal primates. Comparative jumping performance data (i.e., maximum jump height) are available in a few primate species (*G. senegalensis*: Aerts, 1998; *P. paniscus*: Scholz et al., 2006; Bobbert et al., 2008; *M. murinus*: Legreneur et al., 2010; *H. sapiens*: Bobbert and Casius, 2005; Bobbert, 2013; *C. jacchus*: Bobbert et al., 2014). To facilitate size-adjusted comparisons among these animals, we scaled metrics of jumping mechanical output using body mass, hindlimb length, or hindlimb muscle mass (Table 4). It should be noted that in most of these previous studies on jumping performance, individuals were not required to perform a jump near their

Table 4
Comparative data of leaping performance in gray squirrels and various primate species.

Species	Body mass (g)	Relative HL extensor muscle mass	HL length scaled to body mass	Jump height (cm)	Jump height (scaled to HL length)	Jump height (scaled to cube root of body mass)	TO velocity (m/s)	Froude number	Peak power (W/kg) scaled to body mass	Peak power (W/kg) scaled to muscle mass
Sciurus carolinensis[a]	529	0.13	1.75	56	3.96	6.92	3.31	2.81	160	1266
Callithrix jacchus[a,b]	365	0.12	1.66	46	3.87	6.44	3.00	2.78	118	970
Microcebus murinus[c]	97		1.80	33	4.00	7.18	3.23	3.59		
Galago senegalensis[d,e,f]	279	0.25	2.30	174	11.55	26.63	5.84	4.81	797	3187
Pan paniscus[f,g]	38,000	0.14	1.89	78	1.23	2.32	3.91	1.56	83	520
Homo sapiens[e,f,h]	76,700	0.17	2.38	43	0.42	1.01	2.9	0.92	49	332

Abbreviation: HL = hindlimb.
The velocity at takeoff (TO) and the height reached by the animals' centers of mass during the airborne phase (i.e., jump height) were calculated according to ballistic equations using the substrate reaction force (SRF) profiles.
[a] Substrate reaction force profiles measured by force plates.
[b] Data from Bobbert et al. (2014).
[c] Data from Legreneur et al. (2010). Jump height was estimated from Newtonian equations using video-based measures of velocity data (i.e., using high-speed X-ray films).
[d] Data from Aerts (1998).
[e] Jump height was calculated according to ballistic equations (i.e., SRF measured using force plates).
[f] We estimated the TO velocity according to the law of conservation of energy (applied to kinetic and potential energies). We scaled the jump height to the cube root of body mass and hindlimb length (i.e., sum of femur, tibia, distal calcaneal, cuboid, and 4th metatarsal lengths). Additionally, we calculated dimensionless takeoff velocity (i.e., Froude number) using HL lengths as a measure of size. Hindlimb measurements were taken from μCT scans of specimens downloaded from Morphosource.org, published data sources (Ward et al., 2011; Boyer et al., 2013; Prang, 2019; this study), or directly measured. Femur and tibia lengths for *Pan paniscus* and *Homo sapiens* were taken from Zihlman et al. (2007) and Aitken (2021), respectively. Peak CoM powers are expressed per kilogram of body mass or leg muscle mass. Modified with permission from Bobbert et al. (2014) who calculated those parameters from original data for *Callithrix jacchus* (Bobbert et al., 2014), *Galago senegalensis* (Aerts, 1998), *Pan paniscus* (Scholz et al., 2006), and *Homo sapiens* (Bobbert et al., 2008).
[g] Data from Scholz et al. (2006). Jump height was calculated according to the flight time method (i.e., flight time was determined from high-speed video recordings).
[h] Data from Bobbert et al. (2008).

maximal-level performance, requiring careful comparison of these results. Data from Legreneur et al. (2010) of submaximal jumping performance in mouse lemurs—who are not typically classified as specialized jumpers—showed that the scaled and absolute TO velocities of these small arboreal primates were greater than those of the squirrels in this study, even if the highest jump height they achieved (i.e., 33 cm) was lower than that reached by the squirrels. However, mouse lemurs were not asked to perform a vertical jump (strictly speaking), but rather a more diagonally oriented jump. This is still indicative of maximal performance, but not precisely the same task as in the other studies in our comparative dataset. In the study by Bobbert et al. (2014) on common marmosets, individuals were asked to reach a perch 70 cm high. Absolute and scaled TO velocities were lower than those in the squirrels. However, the target the marmosets were asked to reach was close but lower than the highest target reached by squirrels, and the study by Bobbert et al. (2014) was not assessing maximal performance. In fact, the authors reported that 70 cm was not the highest height marmosets could reach (Bobbert et al., 2014). When adjusting for body size, all the 'small-bodied' taxa in our comparative sample (i.e., *Sciurus, Microcebus, Callithrix,* and *Galago*) achieved greater jump heights and TO velocities than large-bodied hominids (i.e., *Pan* and *Homo*). Finally, *Galago* outperformed all other taxa on every metric of jumping performance, reflecting this species' well-known extreme adaptation for superior jumping performance (Hall-Craggs, 1965; Aerts, 1998). Overall, however, existing data do not allow us to properly assess our prediction, stating that jumping performance would be similar in squirrels than in previously studied arboreal primates of similar size (Aerts, 1998; Bobbert and Casius, 2005; Scholz et al., 2006; Bobbert et al., 2008, 2014; Legreneur et al., 2010; Bobbert, 2013). To be able to compare the mechanical output of jumping between species, we stress the importance of assessing near-maximal levels of jumping performance, using similar methods. Additionally, this study, which is the first of its kind, focused on vertical jumping performance and vertical forces. This is an important step in a comparative analysis of leaping mechanics and the effects of substrate on the underlying biomechanical strategies. Horizontal forces and CoM trajectories are also important and are a logical next step in this research. It is expected that similar patterns and strategies would obtain for more horizontally oriented leaps as well.

5. Conclusions

The height attained when jumping is dependent on the animal's CoM velocity at TO, which can be increased by pushing harder against the substrate (i.e., increase the SRF magnitude) and/or more fully extending the hindlimb joints (i.e., increase the distance over which the SRF is applied). By using jumping propensity as a proxy for performance (i.e., assuming that species that jump frequently would also have heightened jumping performance), previous studies highlighted several morphological features that may indicate increased jumping ability, not only in primates but also in kangaroos, frogs, and bipedal rodents (Emerson, 1985; Marsh, 1994), namely, species that jump more frequently tend to have longer hind feet and hindlimbs overall (Burr et al., 1982; Connour et al., 2000; Polk et al., 2000; Boyer et al., 2013; Boulinguez-Ambroise et al., 2019). As noted by Dagosto (2007: p. 509), a long limb permits "the propulsive force to act over a longer distance and therefore for a longer time, enabling a longer (or higher) jump for a given amount of muscle mass". Additionally, a long hindlimb can be used as a brake to absorb landing forces (Preuschoft et al., 1995).

Interestingly, we found the peak power generated by squirrels to be remarkably higher than in the primate species that have been thus far studied—though still less than the power generated by the highly specialized galagos. This discrepancy between squirrels and primates may be indicative of different jumping strategies. Potentially, squirrels might have evolved physiological traits that permit power (i.e., more work per unit time) in lieu of the elongated segments characteristic of extant primate leapers and many Eocene stem primates as well (i.e., *Notharctus* and omomyids; Gregory, 1920; Napier and Walker, 1967; Szalay and Dagosto, 1980; Dagosto, 2007; Boyer et al., 2013; Boyer et al., 2017). For further research, the next logical step would be to investigate the morphological correlates of jumping performance across extant primates and other arboreal mammals, particularly focusing on associations between relative hindlimb length and jumping mechanics.

Though tree squirrels lack certain 'primatelike' features, they frequently move and forage on the fine terminal branches of trees, making them a viable extant model for an early stage of primate locomotor evolution. In this vein, we found that tree squirrels display divergent mechanical jumping strategies according to the type of substrate, prioritizing force production on flat ground versus CoM displacement on poles. Again, this finding points to a possible explanation for the elongated hindlimb segments of primate leapers. As jumping represents a significant part of the locomotor behavior of most primates, jumping from small (and, in nature, compliant) arboreal substrates may have been a potential driver of the selection on elongated hindlimb's segments in primates, allowing the CoM to be accelerated on a longer distance—and thereby reducing the need for high SRFs. For future research, we stress the necessity to be able to compare jumping performance across arboreal mammals, which will require assessing near-maximal levels of performance. By identifying morphological correlates of jumping performance for a behaviorally and phylogenetically diverse sample, we can facilitate a more robust understanding of the selective role of jumping behaviors during primate locomotor evolution.

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