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Cognitive Biomechanics of Arboreal Locomotion

By

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Professor Robert Dudley
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Abstract

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The interaction between cognitive control and biomechanics has enabled animal locomotion capabilities that far surpass state of the art mobile robot performance. But there has been little research focusing on the interaction of the cognitive processes, like learning and decision making, with the biomechanics of the animal coupled to the mechanical properties of the environment. Understanding the cognitive biomechanical strategies, specifically how cognitive processes may work synergistically with the unique mechanical properties of the organism in its environment, is likely to inspire future generations of bioinspired search-and-rescue and environmental monitoring robots. In this dissertation, two model organisms were used to study the cognitive biomechanics of arboreal locomotion. First, high speed branch locomotion was examined using the American cockroach, *Periplaneta americana*. This cockroach is one of the fastest runners relative to its body length. This hexapedal animal uses an alternating tripod to run up to 1.5 meters per second, becoming bipedal at the fastest speeds. Second, the Fox squirrel, *Sciurus niger* was studied. This arboreal specialist exhibits high performance climbing, branch navigation, and gap crossing via targeted leaping. Fox squirrels demonstrated learning to improve targeted leaping performance, a novel parkour-like wall jumping behavior, and decisions on when to leap that was dependent on the mechanical behavior of the branch and geometric properties of the gap to cross. These discoveries give new insights into the cognitive biomechanics of arboreal locomotion, and represent a promising path towards a principled understanding of canopy navigation.

To my family

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Chapter 1

Introduction and Summary

1.1 Introduction

Arboreal Locomotion Performance

Cognitive biomechanics, the interaction between cognitive control processes and mechanical properties of the animal, is an exciting area of research because it can address scientific questions that cannot be answered by either biomechanics or cognitive science alone. The canopy presents good environment for investigating cognitive biomechanics. Canopies have complex geometries spanning three dimensional volumes to a large degree, within which principles of cognitive biomechanics may be discovered. Branches and stems form substrates with wide ranging diameters and compliances at all orientation angles (van Casteren et al., 2013). Irregular surfaces with outcroppings and invaginations provide affordances for adherence *via* toes or claws (Cartmill, 1974; Gladun & Gorb, 2007). Small diameters pose stability challenges (Astley & Jayne, 2007; A. Schmidt & Fischer, 2010). Branch compliance precipitates deflections during leaping, affecting the speed, angle, and initial position of the animal's center-of-mass at the initial aerial phase (Gilman, Bartlett, Gillis, & Irschick, 2012). Gaps between branches require aerial maneuvers, such as leaping, to locomote across the canopy. Despite these challenges, many scansorial and arboreal animals can navigate the canopy with impressive speed and agility. The variability and creativity inherent in high performance arboreal locomotion is rich for investigating the interaction of biomechanics with cognitive processes like learning and decision making.

Model Organisms

The American cockroach, *Periplaneta americana* (Figure 1.1), has long been a model organism in high speed locomotion biomechanics studies. These cockroaches are about 4 cm long, weigh 850 mg, and can run up to 1.5 meters per second, about 50 body lengths per second (Full & Tu, 1991). They have long thin legs and complex foot/leg contact structures such as a claw, euplantulae (friction pad), arolia (adhesive glands) and collapsible spines along their tibia (Spagna, Goldman, Lin, Koditschek, & Full, 2007). *Periplaneta americana* are sexually dimorphic, (only adult males were used in these studies). The American cockroach is an exceptional scansorial animal for studying high performance arboreal locomotion as it can run uphill (Full & Tullis, 1990) and rapidly along branches of various diameters.

Figure 1.1

Figure 1.1: Introduction to the American cockroach (*Periplaneta americana*). Photograph of an adult male American cockroach. Due to their propensity to, and excellent ability for climbing, they may be classified as scansorial animals. American cockroaches have six complex legs with multiple structural components. Their long, slender (low-inertia) legs take long strides at high frequencies to achieve rapid locomotion on many types substrates. Multi-structured, distributed feet enable multiple modes of generating adhesion and substrate reaction forces. This species has been an important model organism for many years of biomechanics research investigating principles of high-performance locomotion (Full & Tu, 1991; Goldman, Chen, Dudek, & Full, 2006; Simon Sponberg, Spence, Mullens, & Full, 2011; Ting, Blickhan, & Full, 1994).

The Fox squirrel, S*ciurus niger* (Figure 1.2), is an arboreal specialist, and an excellent model organism for cognitive biomechanics. These squirrels have long lives, complex cognition, athletic biomechanical capabilities and are highly trainable (Waisman & Jacobs, 2008). They are 45-70 cm long including the tail, which is approximately 20-33 cm. They weigh approximately 500-1000 grams. They are not sexually dimorphic. The have large hind limb extensors which enable them to leap many multiples of their body length. Their feet are capable of hind-foot reversal, and all feet have friction pads, long flexible toes and sharp claws that aid in attachment and force generation on bark. They are food caching animals with great memory capacity, helping them to bury and retrieve nuts. The combination of their strong biomechanical and cognitive abilities make them well suited for cognitive biomechanics research.

Figure 1.2

Figure 1.2: Introduction to the Fox squirrel (*Sciurus niger*). Photograph of an adult male Fox squirrel. Fox squirrels are arboreal animals, nesting foraging and spending most of their time in trees. Fox squirrels have large powerful muscles in their hind-limbs which enable them to leap across gaps many times their own body length. Long flexible toes terminate in very sharp claws, facilitating adhesion and generation of substrate reaction forces. Fox squirrels have a high arboreal agility and maneuverability enabling high-speed chasing competitions during mating seasons, and escape from predators such as hawks, owls, bobcats, dogs, etc. (Burde & Feldhamer, 2005).

Importance of Discovering Arboreal Locomotion Principles

Arboreal locomotion requires integration of biomechanical and cognitive components of motor control. The challenges posed by navigating the canopy, and the abilities of arboreal animals to meet those challenges to successfully navigate canopies suggest the presence of arboreal locomotion principles that may be discovered through cognitive biomechanics investigation. One challenge of legged locomotion in arboreal habitats is maintaining stability on branches with different diameters (F A Jenkins, 1974; Lammers & Biknevicius, 2004; A. Schmidt & Fischer, 2010; Witte, Preuschoft, & Fischer, 2002) while still achieving high velocities (Losos & Sinervo, 1989; Losos, Walton, & Bennett, 1993; Sinervo & Losos, 1991). Another challenge faced in an arboreal habitat is deciding how to balance various costs and benefits, such as energetics, risk, and different foot rewards that may be present (Pyke, 1984; Hanson, 2016). Further investigations into how arboreal animals exploit both motor memory (Ashe, Lungu, Basford, & Lu, 2006; Krakauer & Shadmehr, 2006; R Shadmehr & Holcomb, 1997) and motor planning processes (C. Harris & Wolpert, 1998; Kawato, 1999) to navigate the complex three-dimensional substrate will lead to new principles on the use of internal models and memory for control. Principles of arboreal locomotion are likely to generalize to adaptive locomotion in complex environments. Principles of arboreal locomotion will also inspire arboreal robots with new capabilities for search and rescue, or environmental monitoring of forests.

1.2 Summary

Chapter 2 investigates the performance and stability of the American cockroach running along branches of different diameters. By triggering escape responses of these animal on rods of different diameters, it was discovered that their ability to roll underneath the rod as the diameter decreased, and thereby maintain velocity using an inverted running gait. Modeling control of this behavior suggests a complete lack of balancing control or decision making, unless presented with aversive stimulus underneath the rod.

Chapter 3 examines the role of learning in the performance of leaping from a novel compliant beam across a gap to a small target. By training free-ranging Fox squirrels to leap from a compliant beam to a perch, a complex learning process was quantified that resulted in error reduction over five trials of leaping experience. Although biomechanical changes producing improvement were highly variable, and performance changes were not monotonically increasing, it was discovered that squirrels primarily increased takeoff velocity to reduce errors.

Chapter 4 describes a novel, dynamic behavior for gap crossing during which Fox squirrels leap to an intermediate vertical surface, rotate their body 180 degrees along the anteroposterior axis, then jump off the vertical wall creating reaction forces to redirect their body's trajectory to land on a perch. Squirrels used the wall-jump maneuver to cross longer gaps, even though they are capable of leaping directly to the perch at those distances. The choice to use the wall jump was unaffected by changes of ±20 cm in height. But, changes in height of the landing perch affected the way squirrels generated reaction impulses from the wall.

Chapter 5 examines the role of branch compliance and gap distance in deciding when to leap from a compliant branch across a gap to a target. By training squirrels to cross a gap partially spanned by rods that varied in compliance properties, the dependence of takeoff-position-choice on gap length and branch compliance was quantified. Both gap distance and branch compliance affected the choice of takeoff position. Squirrels choose a takeoff position to balance the natural tradeoff between gap length and compliance that they experience using cantilevered branches to cross gaps in the canopy.

Chapter 2

Stability of High Speed Branch Running

2.1 Introduction

Types of Stability

Stability is thought to be critical for locomotion. Stability can be defined in many ways, but typically captures a notion of persistence and resistance to perturbations. In locomotion, stability is closely related to balance, using legs and feet to keep the body off the ground during a gait or standing posture. For a cockroach that runs with an alternating-tripod leg-coordination pattern, stability may be quantified as keeping the center of mass above the triangular base of support (Ting, Blickhan, & Full, 1994). But if stability for locomotion is generally defined as maintaining a locomotion in the face of perturbations or variable substrate conditions, then this constraint may be too strict. Keeping the center of mass above a region of support is sufficient for locomotion static or quasi-static stability, but during faster moving gaits may be unnecessary. During slow moving gaits, stability can be quantified using a quasi-static assumption. Since there is very little momentum at any point in time, stability is well approximated by considering the body in a static state. But, using the quasi-static assumption under-estimates stability for faster gaits, where the momentum of the body can carry the center of mass outside the base of support, keeping it off the ground until the next step. A less stringent constraint for stability in fast gaits is generating a net vertical impulse to counter gravity and keep the center of mass from falling. This notion of dynamic stability can be captured using a technique from dynamical systems theory (Full, Kubow, Schmitt, Holmes, & Koditschek, 2002; Holmes, Full, Koditschek, & Guckenheimer, 2006; J. Seipel & Holmes, 2006). First, model the gait cycle as a trajectory in state space. Then, define a surface that is orthogonal to the gait trajectory at the point of intersection. Perturbations to the gait cycle will cause the state space trajectory to intersect that surface at different points. Using either an analytical model, or data, one can define a map that determines how intersections with the plane change from one gait cycle to the next. A maximum eigenvalue on that map less than one indicates dynamic stability, whereas a value greater than one indicates instability. This technique has been used to quantify stability of dynamic gaits in both animal (Ting et al., 1994) and robot locomotion (Garcia, Chatterjee, Ruina, & Coleman, 1998). These techniques can classify gait in a binary way, as either stable or unstable. But, the presence of noise requires an extended notion of stability.

Stochastic dynamical systems, i.e. systems evolving under the effects of noise, cannot always be classified as either stable or unstable. Animal gait cycles are affected by exogenous (Spagna et al., 2007; S Sponberg & Full, 2008) and endogenous sources (C. Harris & Wolpert, 1998) of noise and variability. This variability can accumulate and carry the state of the animal outside its region of stability, and transition it into another, e.g. a fall region. The time it takes to transition from locomotion to a fall depends on the restoring forces that counter perturbations, the size of the basin of stability, and the noise level or perturbation magnitudes. Therefore, when considering a stochastic locomotion system, it is often more valuable to quantify how stable, instead of asking only whether the gait is stable or unstable. One way to quantify how stable a legged system is uses the expected number of steps until an animal has transitioned to a fall state (Byl & Tedrake, 2009; Cowan et al., 2014). The expected number of steps before a fall may be very small. For example, a newly walking human toddler may be expected to fall approximately every 10 steps (Adolph et al., 2012). Or, for an exceptionally stable animal, the expected number of steps before a fall may be much greater. By explicitly modeling the stochastic contributions to the dynamics, new and possibly more useful quantifications of stability become possible.

Mechanical Self-Stabilization in the Horizontal Plane

It is generally thought that stability is an essential ingredient of legged locomotion, but there is an apparent neuromechanical challenge in producing a movement that is both fast and stable. Fast running animals with high stride frequencies show a disparity between the short duration of a movement and the characteristic times of feedback stabilizing mechanisms. Feedback control delays include delays in sensory transduction (Schlag & Schlag-rey, 2002), interneuron signal transformations, neural conduction (Hoffmeister, Jänig, & Lisney, 1991), and muscle force generation (Norman & Komi, 1979). The conduction delay scales with an animal's size - generally taking up a longer portion of stance phase for larger animals (More et al., 2010). These delay sources add up to a lower bound on the duration that a sensory signal takes to propagate through the neuromechanical system and affect the evolving dynamics of a fast running animal. Cognitive delays, such as making decisions about which path or action to take in the current environmental context can also contribute to the global sensorimotor delay. When the animal is presented with multiple pathways, the additional latency due to making the decision of which path to follow increases with the number and similarity of alternatives (Fairweather & Hutt, 1978; Rosenbaum, Barnes, & Slotta, 1988). In a fast running animal with a high frequency gait, total sensorimotor feedback latency approaches or exceeds the stride duration. For example, during high speed running the American cockroach may take only 20 milliseconds to complete a full step (at 50 Hz), yet one of the fastest known sensorimotor reactions, the wind-evoked escape response, takes 58 milliseconds (Camhi & Tom, 1978). The cumulative sensory motor delay challenges feedback stabilization of fast movements in complex environments. The abilities of animals to run fast in these environments demonstrate a gap in our understanding that can be partially filled by the phenomenon of mechanical stabilization.

The presence of sensory feedback control in regulating slow movements is established for invertebrates (Bartling & Schmitz, 2000; Büschges, 2005; Cruse, Dürr, & Schmitz, 2007; Pearson, 2004) and vertebrates (Donelan & Pearson, 2004; Libby et al., 2012). Passive mechanical properties of a cockroach leg can eliminate perturbations in less than a swing duration (Dudek & Full, 2007). Evidence is accumulating for mechanical feedback stabilization strategies, but a neuromechanical synthesis toward a theory of morphological computation remains a challenge (Hauser, Ijspeert, Füchslin, Pfeifer, & Maass, 2012; Hauser, Sumioka, Füchslin, & Pfeifer, 2013; Holmes et al., 2006). For example, in running, a feedforward leg retraction strategy stabilizes a sagittal-plane template-model (Seyfarth, Geyer, & Herr, 2003). For fast movements, stabilizing mechanisms like mechanical feedback (G. Loeb, Brown, & Cheng, 1999) contribute to stabilization (Kubow & Full, 1999; Schmitt, Garcia, Razo, Holmes, & Full, 2002; Schmitt & Holmes, 2000; J. E. Seipel, Holmes, & Full, 2004). A template model (Full & Koditschek, 1999) of running in the lateral plane called the Lateral Leg Spring model (LLS) predicts rapid passive mechanical perturbation rejection during running (Schmitt et al., 2002). In response to perturbations, the LLS model exhibits neutral stability in heading and velocity, and asymptotic stability in orientation and rotational velocity. Animal experiments to test this model demonstrate that rapid recovery after perturbations from an impulse (Jindrich & Full, 2002) or lateral ground translation

(Revzen, Burden, & Moore, 2013) happen in less than 10 milliseconds – faster than the fastest neural reflexes (Camhi & Tom, 1978).

There are many possibilities for testing the role of posture on stability in the horizontal plane. One is by natural experiment, comparing the dynamics across species that naturally adopt different degrees of sprawled posture (Manton, 1952). Another way is to build a physical model that can adjust sprawl and compare the dynamics (Komsuoglu, Sohn, Full, & Koditschek, 2008). A third way to test the role of posture is to manipulate it *via* direct experiment. Here, it is hypothesized that systematic manipulation of posture of a running animal in a direct experiment can be achieved by changing surface curvature of the ground. This was investigated by studying the high-speed running escape response of *Periplaneta ame*ricana on rods with a range of diameters.

Branch Locomotion, Attachment, Stability and Performance

Small animals use a diversity of attachment and force production strategies to maintain stability and locomotion performance. Slow moving insects attach to rods using diverse passive and active foot/leg structures and kinematic strategies (Gladun & Gorb, 2007). Insects have complex legs with many diverse morphological structures. Various foot structures are better at producing forces in different directions. For example, arolia can produce larger maximal forces during pulling, rather than pushing, and euplantulae producing greater maximal pushing forces compared to pulling forces (Clemente & Federle, 2008).

Lateral forces are altered in climbing compared to running. In running, both cockroaches (Goldman et al., 2006) and geckos push outward (Autumn et al., 2006), generating inward directed ground reaction forces. During climbing, both cockroaches (Goldman et al., 2006) and geckos pull inward (Autumn et al., 2006), producing outward directed ground reaction forces. Lateral forces are also altered during branch running as the diameter changes. Rats' mediolateral reaction forces switch from lateral on terrestrial substrate to medial on branches (Schmidt & Fischer, 2010). Animals capable of gripping the branch may produce moments to counteract displacements of the center of mass away from the center of the rod. Animals with opposing digits grasp the rod and balance from step to step with by producing substrate reaction torques (Lammers & Gauntner, 2008; Larson & Stern, 2006). Performance of small animals running is also affected by the diameter of the branch. Speed of small rodents and lizards decreases on small rods (Hyams, Jayne, & Cameron, 2012; Losos & Sinervo, 1989; Sinervo & Losos, 1991)

Experimental manipulation of posture, by requiring animals to run on rods of decreasing diameter, is predicted to reduce both their static and dynamic stability by decreasing their base of support and dynamic basin of stability. Passive dynamic stability should be disrupted as animals are forced to move their leg attachment points closer to the midline of their bodies. This imposed adjustment in posture is likely to alter passive dynamic stabilizing lateral ground reaction forces, and thereby the momentum trading that leads to stability. Examining a rapid escape behavior reduces the time available for a neural reflex control response and increases the likelihood that mechanical feedback must play a dominant role. Predictions from previous studies lead to either instability and catastrophic failure, or to a decision to reduce speed, so as to exert the forces and torques necessary for stabilization. Surprisingly, results showed a transition to a newly stabilized behavior, inverted running, that demonstrated minimal performance decrement. Adding an aversive stimulus below the rod showed that animals could decide to remain on top.

2.2 Methods

Animal Preparation

We used adult male *Periplaneta americana* (Carolina Biological Supply, Burlington, NC, USA) from a single population. Our sample included 36 animals with a mass of 0.76 ± 0.13 g (mean ± standard deviation). The cockroaches were housed in plastic cages at 27 degrees Celsius, kept on cycles of 12 hours light / 12 hours dark, and provided rat food and water *ad libitum*. 36 adult male cockroaches were selected from the population and randomly assigned them to one of 6 treatment groups without replacement so that each treatment group comprised 6 animals.

The cockroaches were cold anesthetized by placing them in a refrigerator for 15 minutes. Both pairs of wings were clipped. A single drop of cyanoacrylate was placed on the center backpack (described subsequently) and was attached to the center of the animal’s thorax. Then, the animal was placed back into a cage to rest for 30 minutes before the first trial. The backpack served two purposes. First, the backpack was used to hold the animal in a precise initial condition at the start of the escape response, (Figure 2.1 and Figure 2.2). Second, three retroreflective markers were placed on the backpack for tracking cockroach pose during the escape response, however this data proved too noisy and unusable.

Figure 2.1

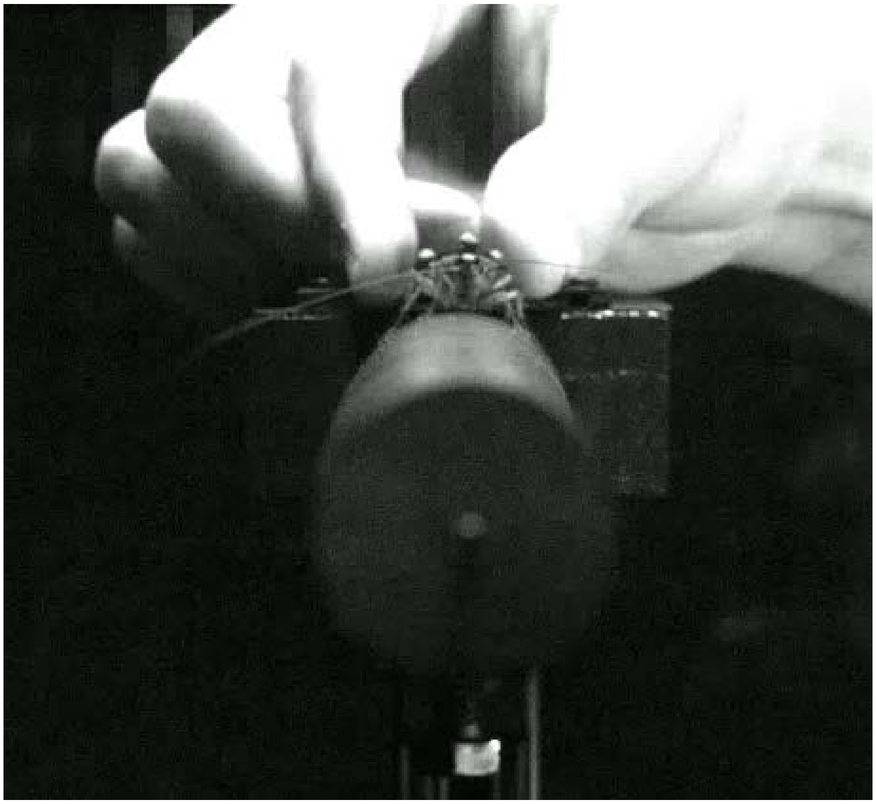

Figure 2.1: Single frame taken from a high-speed video. Frontal plane view of experiment initial conditions. Cockroach was held directly above and at one end of a large rod. Releasing the animal in this position elicited escape responses of rapid running along the length of the rod.

Figure 2.2

Figure 2.2: Sagittal plane view of the experiment initial condition. Cockroach was held above a medium diameter rod in the initial condition before the escape response is initiated.

Branch Running Apparatus

To systematically vary the ground curvature, cylindrical wooden dowel rods were selected to represent a branch-like structure. The branches were made of maple and spray painted mat black to reduce reflections. The selected branch diameters were 0.32, 0.64, 1.27, 1.91, 2.54, and 3.81 ± 0.038 cm (McMaster-Carr, Los Angeles, CA). To mount each branch, a ¼ inch hole was drilled in each end and inserted ¼ inch steel dowel. Branches were mounted horizontally to rigid aluminum framework (80/20 Inc., Columbia City, IN). One end of the branch was mounted directly to the rigid aluminum framework. The steel dowel on the opposite end was mounted to a hole drilled in a sheet of clear acrylic. Mounting one end of the dowel to an acrylic sheet allowed recording of video through the clear acrylic, down the long axis of the branch, capturing movement in the running animals' frontal (coronal) plane. In all trials the cockroach ran in the direction towards the frontal plane camera (Figure 2.3).

Figure 2.3

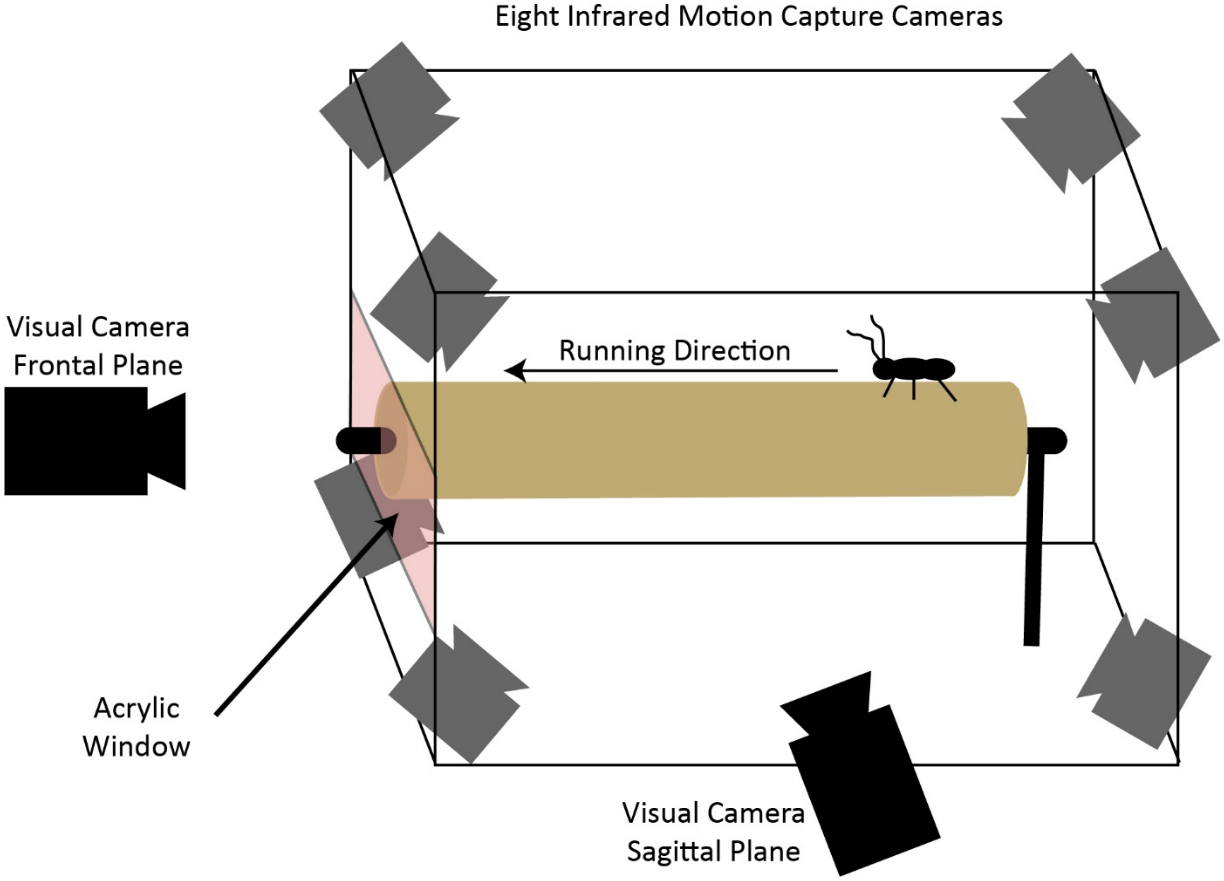

Figure 2.3: Diagram shows the rod running apparatus geometry. Two high speed visual cameras are shown in black. Eight infrared motion capture cameras are shown in grey. The wooden rod is mounted to aluminum framing on one side, and a clear acrylic window on the other.

Cockroaches were outfitted with a T-shaped backpack made of 1/32” thickness laser cut birch with 3 retro-reflective markers attached (B&L Engineering, Santa Ana, CA) Infrared markers were tracked using eight infrared high speed cameras (Optitrack, NaturalPoint, Corvallis, OR) synchronized with the high speed visual spectrum cameras (Phantom, Vision Research Inc., Wayne, NJ). The infrared marker trajectories were not of sufficient quality, and are not included in these results. Control trials show no difference in the transition trajectories of animals with and without backpacks.

Kinematic Data Collection

The arena was lit from the top and sides using six halogen flood lamps (Designer’s Edge, Waukegan, Illinois), and from the bottom using two double goose-neck lights (Dolan-Jenner Industries, Boxborough, Massachusetts). The lighting was arranged to provide consistent light coming from all directions and to eliminate any shadows around the branch.

We recorded the cockroaches running down the long axis of the branches using two high speed cameras (Phantom, Vision Research Inc., Wayne, NJ) placed orthogonally relative to the arena. One camera recorded video in the sagittal plane, and another recorded video through the acrylic sheet in the frontal plane (Figure 2.3). The framerate of both cameras was set to 360 Hz and synchronized frame by frame using an external clock signal provided by the infrared camera system.

The center of mass (COM) was manually tracked in the frontal and sagittal planes using a custom program (MATLAB, Mathworks, Natick, MA). The synchronized COM data from the two orthogonal planes was combined and projected onto the cylindrical branch. All resultant trajectories are in 2D cylindrical coordinates. The coordinate θ is the angle of the COM relative to the branch with $\theta = 0$ being vertical (Figure 2.4, B). The z coordinate is distance of the COM along the branch with the positive direction being the direction of running, and $z = 0$ representing the initial position of the animal’s COM (Figure 2.4, B).

Branch Running Protocol

Cockroaches were placed in a standing position directly on the top of the branch at the end supported by the aluminum framework. Escape responses were initiated by brushing the animals' cerci with a finger so that the animal would run down the long axis of the branch towards the acrylic sheet and the frontal plane camera. Videos were recorded into a circular buffer in the cameras and triggered with a post-trigger signal from the experimenter. Trials were discarded if the cockroach immediately jumped off the branch when the escape response was initiated. Trials were discarded if the cockroach did not run at least 25 cm without pausing or stopping. After each successful trial, cockroaches were returned to individual cages and the video was cropped and exported from the camera to the control computer. Then, the temperature of the arena was recorded using a thermometer (Extech Instruments, Waltham, Massachusetts) with the sensor placed at beginning of the rod. The animals were allowed to rest in an individual cage containing food and water for 10 minutes between trials. This process was repeated until three trials for each animal were obtained that complied with the above requirements. 108 trials from 18 individuals were obtained.

Branch Running Kinematic Analysis

We quantified the effect of branch diameter on the animal's posture using sprawl angle. Sprawl angle is defined as the angle from line segments connecting from one foot to the COM to the contralateral foot (Figure 2.4, A). The COM and the foot contacts on a representative stride were digitized for each trial. The representative sprawl angle for each animal was quantified as the mean of the sprawl angle over its three trials. A one-way between-subjects ANOVA was conducted to compare the effect of rod diameter on sprawl angle in the six rod size conditions.

A transition to the inverted orientation is defined as the animal moving below the horizontal with respect to the center of the rod. The representative transition rate for each animal was quantified as the total number of transitions divided by the number of trials. A one-way between-subjects ANOVA was conducted to compare the effects of rod diameter on transition rate across the six rod sizes.

Water Aversion Protocol

In this second experiment, animals were prepared as during branch running. The three smaller rods, (0.32, 0.64, 1.27, ± 0.038 cm), were used to determine whether the animals have the capability to use feedback control to reduce the transition frequency. To deter transitions, a body of water was placed underneath the rod with the water surface as close as possible to the bottom of the rod without touching it.

Six animals each ran five times on each of the three branch diameters. If the animal made contact with the water for more than two seconds it was pulled from the water and allowed to rest in a cage for 10 minutes.

Water Aversion Analysis

As in the first experiment, the transition was defined as the animal's COM moving below the horizontal with respect to the center of the rod. Differences in transition rates were determined by a one-way repeated measures ANOVA.

Modeling Stability

A quasi-static basin of stability was defined as an angular range around the vertical position for each rod. The limits of the stability basin were determined geometrically as the angles in which the outer leg was vertical. The stable region of the model is determined quasi-statically. From a simple geometric argument, these limits depend solely on the sprawl angle the animal adopts on each rod (Figure 2.4, A).

Figure 2.4

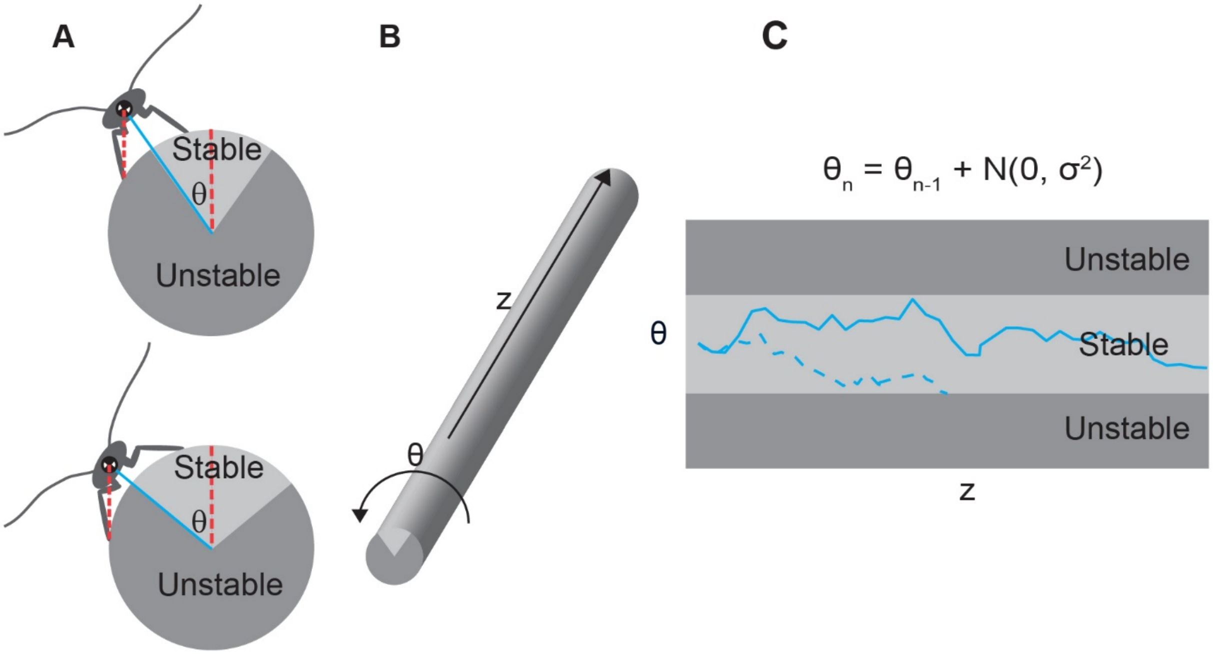

Figure 2.4: Modeling cockroach stability. **A:** Range of stable upright running positions is determined from the animals' posture. The stable region is the maximum possible angular deviation from vertical that satisfies the constraint that the center of mass is within the base of support in the frontal plane. The maximum angular deviation within the stable region occurs when the center of mass is directly above the lowest ground contact point. This quasi-static assumption leads to the upright stable region being completely determined by the sprawl angle of the animal. **B:** Cylindrical coordinate system for quantifying cockroach COM position. θ is the angle of the cockroach on the rod with θ=0 representing the vertical orientation. Z is the longitudinal dimension, increasing in the direction of running. **C:** Baseline diffusion model of cockroach trajectories. Diffusion model describes cockroach trajectories as the accumulation of random angular deviations on each step. Forward progress in Z is modeled as constant speed. The baseline model predicts a cockroach transition if the diffusion trajectory exits the stable region as shown by the dashed line. The model predicts an upright escape response if the trajectory remains within the stable region, as shown by the solid line.

Stochastic modeling has a long history of being used to capture variability in biological systems and can generate predictions that are qualitatively different than their deterministic counterparts (Delbrück, 1940; Watson & Galton, 1875). Here, the cockroaches' motion of the branch is modeled as a discrete-time stochastic process. The dynamics are modeled as a constant forward speed combined with a controlled diffusion process within a quasi-statically defined basin of stability in the frontal plane (Figure 2.4, C). Feedback-control balancing models of increasing complexity, beginning with the simplest no balancing model were examined.

The stochastic portion of all considered balancing models consisted of a difference equation. This difference equation predicts the angle of the animal on the next step as a function of the animals' angle on the current step plus a Gaussian noise term (Figure 2.4, C).

$$\theta_{n+1} = \theta_n + N(0, \sigma)$$

The variable θ_n is the angle of the cockroaches' center-of-mass on the current step, and the variable θ_{n+1} is the angle on the next step. The parameter σ of the Gaussian diffusion model for each branch size was determined from the data. The standard deviation of the Gaussian noise term *N* was taken empirically from the step-to-step COM variability separately on each rod diameter. The diffusion coefficients were determined using data where the animal was inside the nominal basin of stability. The model produced a gait transition to the inverted state if the diffusion of the angle brought the angle outside of 90 degrees from vertical (Figure 2.4, C).

Beginning with the simplest model and progressing towards the more and more complex, models were subjected to statistical hypothesis testing, attempting to reject simple models in favor of the next level of complexity (Figure 2.5).

Figure 2.5

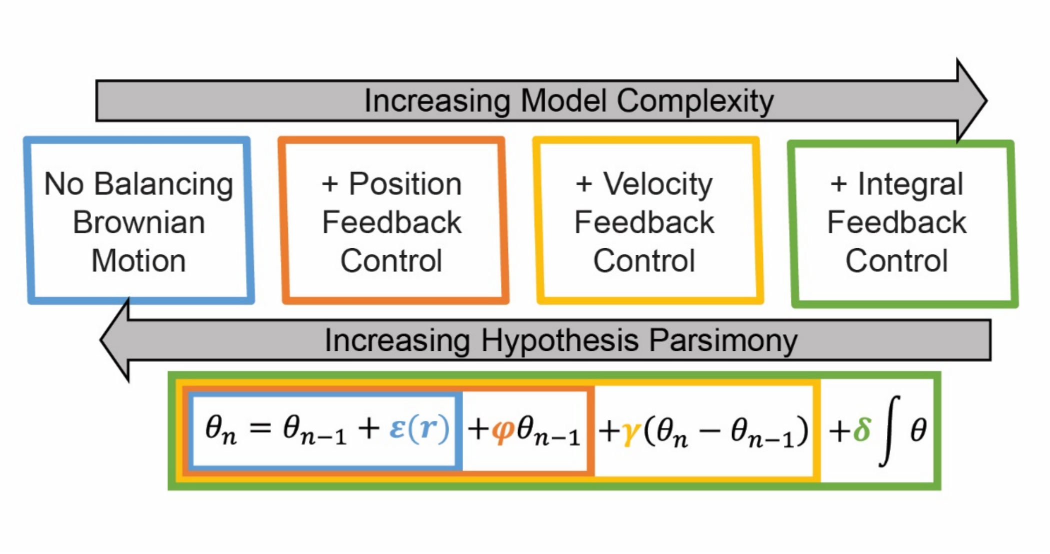

Figure 2.5: Iteratively testing more complex control-theoretic models of cockroach balancing behavior. No Balancing Brownian Motion model was taken as the baseline. Each additional level of complexity is represented by a coefficient, e.g., phi represents the coefficient for the position feedback control model. Evaluation of more complex models was done iteratively by testing if the distribution of the associated coefficient was significantly different from zero.

For future work, another model based on a Markov-chain will be useful. Markov chain Monte Carlo approaches have been used to model animal paths over large areas (Benhamou, 2007; Blackwell, 1997; de Jager, Weissing, Herman, Nolet, & van de Koppel, 2011; Mcclintock, King, Matthiopoulos, Mcconnell, & Morales, 2012; Smouse et al., 2010), transitions between different behaviors (C. Li et al., 2015), and kinematics (Ankarali, Tutkun Sen, De, Okamura, & Cowan, 2014). A much larger data set will generate lower variance estimates of the probability parameters for low probability transitions, finer discretization of the state space over smaller angular ranges and allow consideration of higher order Markov chains.

2.3 Results and Discussion

Branch Diameter Changed Posture

It was hypothesized that varying rod diameter would systematically manipulate the animal's posture. Posture was quantified by measuring the sprawl angle, defined as the angle made from one foot contact, to the COM, to the contralateral foot contact. Sprawl angle increased with increasing rod diameter (p = 6.03e-25, F=347.69). Pairwise comparisons, done with Tukey's honestly significant difference criterion, and showed that the posture for each rod diameter was significantly different from the posture on every other rod diameter (Figure 2.6). This confirmed the hypothesis that different substrate curvatures strongly affected the resulting posture.

Figure 2.6

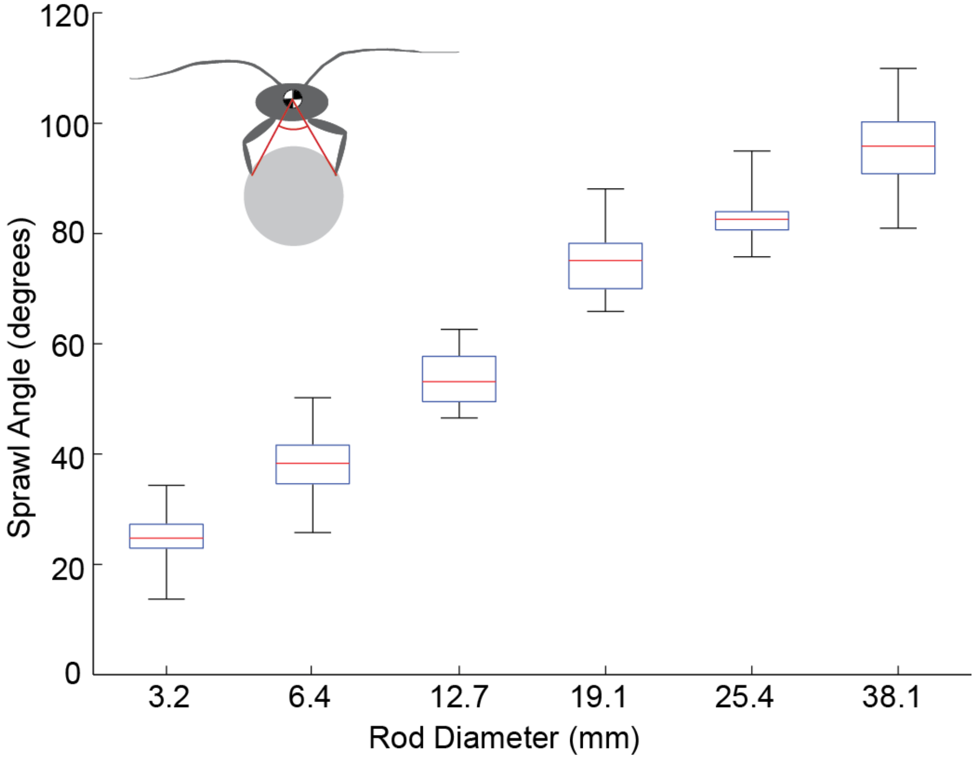

Figure 2.6: Box-plot shows the sprawl angle of the animal while running grouped by rod diameter. Sprawl angle is defined as the angle made from one foot contact, to the center of mass, to the contralateral foot contact (shown in red). The band inside the box indicates the median (2nd quartile) sprawl angle, while the upper and lower edges of the box indicate the 1st and 3rd quartile. Whiskers indicate the range. Significant differences were found between the sprawl angle for each rod diameter and every other diameter using ANOVA and Tukey post-hoc tests.

Manipulation of posture is a highly effective way to perform systematic manipulations of posture in a direct experiment (Figure 2.6). The increasing sprawl angle resulting from increasing rod diameters should asymptote as the substrate gets closer to the infinite curvature of flat ground. As the rod diameter is decreased, sprawl angle will approach zero. It was observed that cockroaches were able to locomote on a very thin copper wire, albeit slowly. Within the range of diameters in this experiment there was a clear monotonic effect of variations in rod diameter on sprawl angle, making it an effective tool for direct studies of posture differences while running, complementing natural experimental methods, (Manton, 1952), and the use of physical models (Komsuoglu et al., 2008).

Smaller Branch Diameters Increased Transition Probabilities

It was hypothesized that smaller diameter rods would lead to reduced stability and an increased probability of animals falling from the branch. Surprisingly, animals never fell, even from the smallest rod. Instead, the animals executed a rolling inversion from an upright running gait to an inverted running gait while continuing to run at high speed. The probability of transition increased as the rod diameter decreased (Figure 2.9). A one-way ANOVA found an effect of rod diameter on the transition probability (p = 4.94e-11, F=31.21). Pairwise comparisons were done with Tukey's honestly significant difference criterion. Significant differences between transition probabilities on different rod diameters are indicated by p-values for pairwise comparisons in Table 1. Decreases in the rod diameter caused increases in the probability that the cockroach will execute a rolling inversion into an inverted running gait. All tracked body trajectories are shown in Figure 2.7 and Figure 2.9.

The leg kinematic strategy of reaching around the rod and making contact on the top surface on smaller rods may simplify attachment. Making contact on top of the rod allows the cockroach to support its weight by pushing into the surface, creating ground reaction forces that point upward, away from the substrate surface. If instead the cockroach were to place its feet on the bottom surface of the rod it would have to attach and pull on the substrate to support its center-of-mass, creating ground reaction forces directed into the surface and then detach for the leg to enter swing phase. This would require precise temporal coordination between attachment/detachment of the feet with adduction/abduction of the limbs. While cockroaches can indeed attach to the underside of a surface, this strategy may create difficulties in foot-leg coordination that aren't seen in attachment strategies for slower moving insects (Gladun & Gorb, 2007)s. Making contact on the top side of the rod enables the leg to attach to the rod with simple friction and detach without coordination with the claw engagement. Future work will determine how these animals use their foot structures to achieve this behavior.

The inverted position is passively stabilized due to pendulum-like dynamics. Any angular deviations from the inverted position will be countered by a force equal to bodyweight multiplied by the sine of the body angle. For the American cockroach, this passive stabilization negates the necessity of stabilizing branch locomotion seen in other animals (F A Jenkins, 1974; Lammers & Biknevicius, 2004; A. Schmidt & Fischer, 2010; Witte et al., 2002).

Table 1. Comparison of transition probabilities across rod diameters: Tukey's honestly significant difference test p-values

Rod Diameter (cm)	3.2	6.4	12.7	19.1	25.4	38.1
3.2	-					
6.4	1	-				
12.7	0.57	0.57	-			
19.1	0.03*	0.03*	0.57	-		
25.4	0.00***	0.00***	0.00***	0.00**	-	
38.1	0.00***	0.00***	0.00***	0.00***	0.4	-

One star signifies significant differences at the 0.05 threshold, two stars at the 0.01 threshold, and three stars at the 0.001 threshold.

Figure 2.7

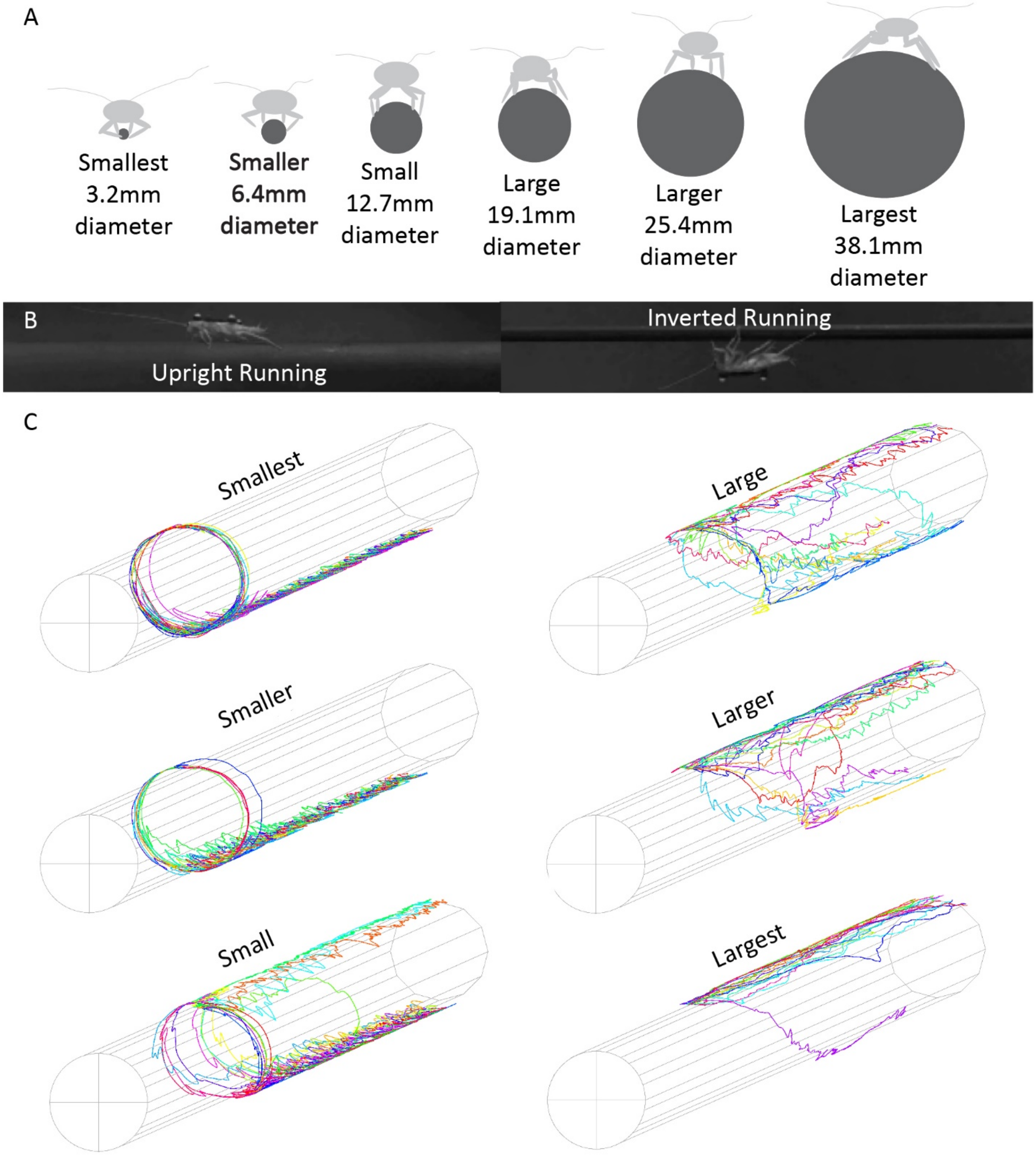

Figure 2.7: Trajectories followed by cockroaches during escape responses on 6 distinct sized rods. **A:** Diagram shows the relative size between the cockroach and the different rod sizes in the frontal plane. **B:** Photos show the cockroach during an

escape response in the sagittal plane view. The first photo shows a representative upright running position, and the second photo shows the posture of the animal after transitioning to inverted running. **C:** Figure shows the trajectories of all cockroaches on all rods. Different colors specify different trials. Initial position at the initiation of the escape response is always on top of the rod. As the rod diameter becomes smaller, more trajectories go to the inverted orientation.

Feedback Control Model Supports No-Balancing Hypothesis

The proportional position feedback control model consists of the no-balancing diffusion model with an additional term, resulting in one free parameter representing a proportional balancing strength coefficient (Figure 2.5). Fitting this free parameter of the proportional feedback control balance model to each measured trajectory resulted in a distribution of balance control coefficients (Figure 2.8). Using the Sign Test it was found that the distribution of balance control coefficients were not significantly different from 0. Thus, a simpler no-balancing diffusion model could not be rejected. This negated testing of the balancing models of greater complexity. Based on this analysis a no-balancing diffusion model was used to generate model trajectories and predict the transition probability and expected transition position as a function of rod diameter.

In many behaviors, stability can be a critical feature of locomotion. Tasks that severely challenge stability, such as running along small stems, may force animals to slow down to allow feedback control processes time to affect the unfolding dynamics. This creates a speed/stability tradeoff. The American cockroach bypasses this tradeoff by transitioning to inverted running. The capability to use a rolling maneuver to transition while running from upright to inverted orientation eliminates the need for the cockroach to exercise feedback control to balance above the rod. Based on the predictive power of a simple diffusion model, it appears that cockroaches do not control balance above the rod. Instead they allow random side-to-side deviations to accumulate, leading them to the inverted orientation. Furthermore, the inverted running capability allows the cockroach to take advantage of the passively stabilized pendulum dynamics afforded by positioning the body’s center-of-mass below the branch. This is another example of this high running speed animal foregoing control and relying on passive mechanical stabilization. Although, in this case, passive mechanical stabilization is conferred by the orientation of the animal in relation to the branch instead of, for example, tuning the nonlinear compliance of a limb (Dudek & Full, 2007) or horizontal plane ground reaction forces (Kubow & Full, 1999; Schmitt et al., 2002; Schmitt & Holmes, 2000; J. E. Seipel et al., 2004). This passive mechanical stabilization is likely to be the determining factor for the cockroaches' high speed rod running capability. Unlike its quadrupedal counterparts, whose speed decreases on smaller rods (Hyams et al., 2012; Losos & Sinervo, 1989; Losos et al., 1993; Sinervo & Losos, 1991)s, American cockroaches maintain similarly high speed when running atop a large diameter rod, and running beneath a small diameter rod.

Figure 2.8

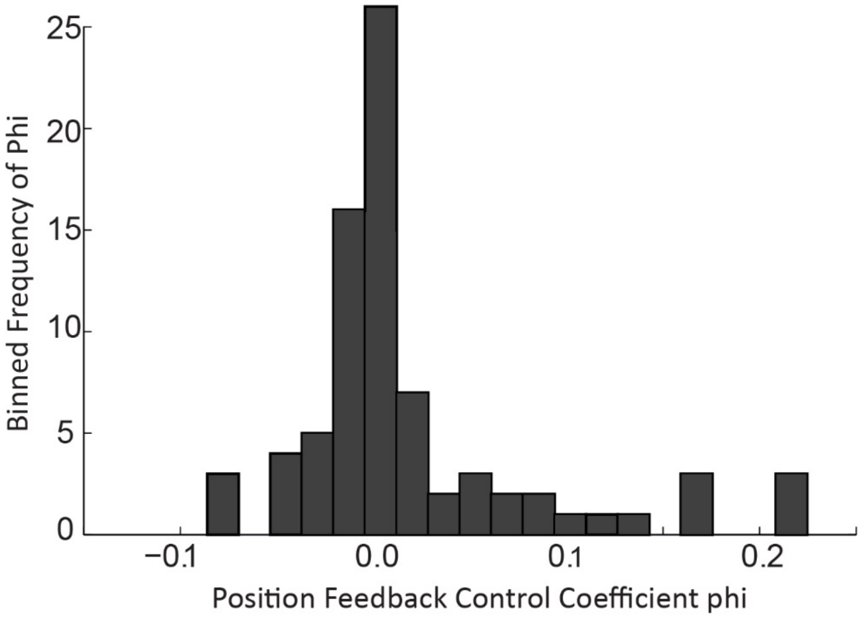

Figure 2.8: Fitting a position feedback controller to each cockroach trajectory gives a distribution of position feedback coefficients. Sign test demonstrates that this distribution of position feedback control coefficients is not significantly different from zero (p = 1.0), indicating a simple diffusion model is sufficient.

No-Balancing Diffusion Model Predicts Transition Probability but not Position of Transition

The no-balancing diffusion model is simple. It estimates all parameters directly from tracked data (Figure 2.9). There were no free fitting parameters in the model. The no-balancing model predicts transition probability as a function of rod diameter. This model reproduces the nonlinear relationship between rod diameter and transition probability, i.e. inverse sigmoidal shape (Figure 2.10). In addition, the no-balancing diffusion model generates a highly accurate prediction of the transition probability for each rod diameter with a Mean Absolute Error of 0.09%.

The no-balancing diffusion model also makes a prediction for the expected transition position for the subset of trajectories that do transition within the length of an escape response. This prediction captures the qualitative trend that cockroaches run further before transitioning on larger rods, but it does not predict the position well with a Mean Absolute Error of 10.4 cm (Figure 2.11).

In these experiments, all the animals started in an upright position. The probability of the transition varied inversely in a nonlinear way as a function of rod diameter (Figure 2.10). The sigmoidal shape of this transition was predicted well by a simple model. In this model, the trajectory of the cockroach was represented as the accumulation of random angular deviations with each step that it took. This random diffusion happened within a quasi-static region of stability defined by the posture that the animals adopted at each rod diameter. This suggests that the animals are not balancing as they run along the rod. To complement this model, a balancing feedback control model (proportional controller) was fit to each measured cockroach trajectory, and the distribution of control term coefficients did not differ significantly from zero. These 2 results indicate a lack of motivation to control the body's position relative to gravity. It appears that the existence of a highly effective transition and inverted running gait eliminates the repercussions of angular deviations and loss of stability.

Stochastic modeling is useful in modeling cockroach running because there is a great deal of variability that can be incorporated in a model *via* probability distributions in the dynamics. The importance of predictive models that include variability can arise in many scenarios. For example, the optimal choice of behavior in a deterministic system may no longer be optimal in a system that is equivalent except for the addition of a stochastic term. If the objective function is nonlinear and asymmetric, and if there is noise, then variations in different directions from the optimal choice can have different costs and effect the optimal operating point in a stochastic system (Laine Martin & Huey, 2008). Thus, it is important to quantify the variability in a locomotion system to properly account for the benefit and size of a safety-margin that may tradeoff against other objectives. It is also important to model the variability to understand how robust the locomotion system is to changes in magnitude of variability, and what strategies may be used to ameliorate costs of deviations. Furthermore, stochastic modeling is important for modeling stability. In a system with multiple stable states, like various running states and a fall state, stochastic modeling can predict transition times between those states.

Stochastic models can make qualitatively different predictions than their deterministic counterparts (Kubow & Full, 1999; Schmitt et al., 2002; Schmitt &

Holmes, 2000; J. E. Seipel et al., 2004). This is true in the current experiment. Without a noise term, the model would either predict that the animal would remain on top of the rod every time if it was stable, or would transition every time if it was unstable. The stochastic term is critical in predicting the gradual change in the transition probability that results from changes in the rod diameter Figure 2.10.

One promising stochastic modeling approach is to use Markov chain modeling to predict stability under different rod diameters and aversive stimuli. This approach discretizes the space of possible body states, and models the dynamics via probabilities for transitions between neighboring states. A diagram of how Markov chain modeling applies to this data set is shown in Figure 2.9. This model is capable of predicting a probability distribution of falls over time, and estimating the time until a fall as the Mean First Passage Time (Figure 2.10). In the future a larger data set to produce low-variance estimates of these transition probabilities and calculate Mean First Passage Times (Byl & Tedrake, 2009; Saglam & Byl, 2014)s for running on rods of various sizes. In addition, Markov chain modeling can be used to study rates of transitions between multiple kinematic states and multiple behaviors (Kelso, 2012). This type of modeling has potential to unify kinematic descriptions with path predictions to estimate a distribution of time spent in different regions of an arboreal habitat. As such, Markov chain modeling may be able to make testable predictions about how locomotion behavior depends on consideration of energetics, risk and distribution of food (Pyke, 1984; Hanson, 2016).

Figure 2.9

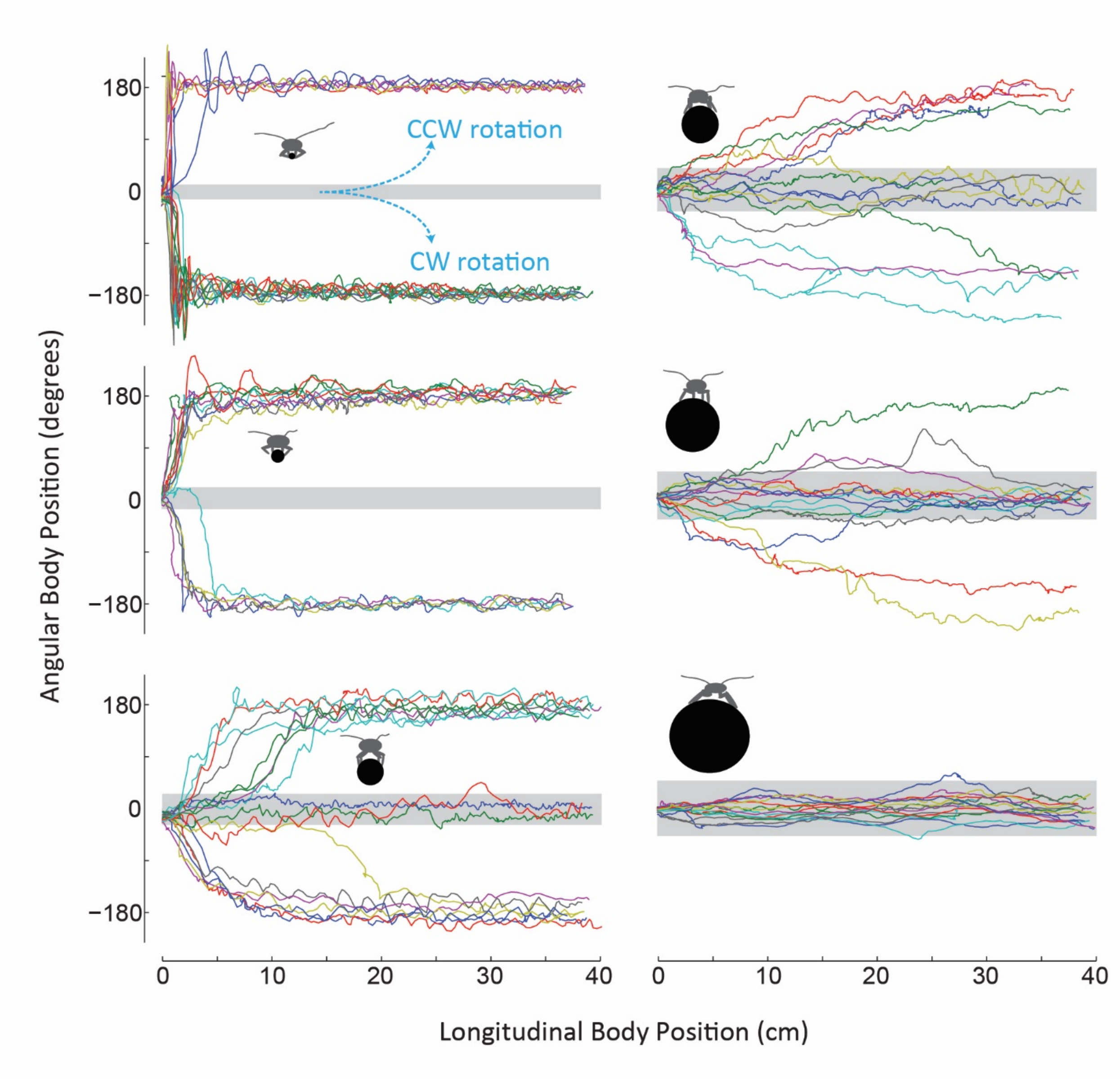

Figure 2.9: Tracked cockroach trajectories compared to model predictions. **A:** Figures show the tracked positions, angle vs longitudinal position, of all trials grouped by rod diameter. As the rod diameter decreases a greater proportion of trajectories show transition to inverted running during the escape response. Gray bands show the stable region as predicted from the quasi-static stability analysis based on variations in sprawl angle.

Figure 2.10

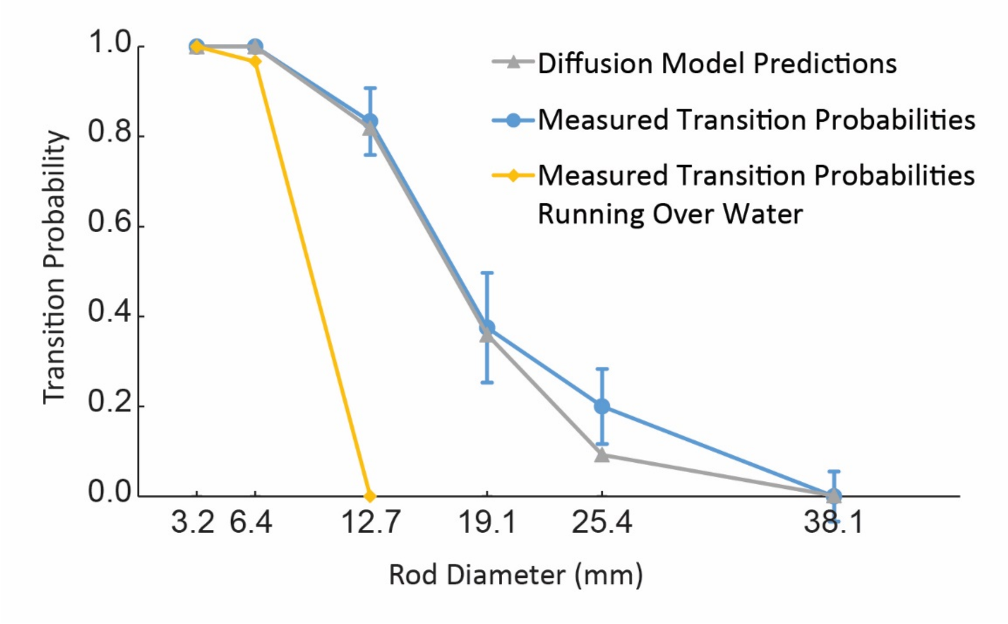

Figure 2.10: Transition probability as a function of rod diameter. Simple diffusion model of cockroach angular position that includes no free parameters predicts the transition probability across all diameters. The transition probability as a function of rod diameter is shown from the tracked cockroach trajectories, as well as from the trials in which the cockroach was running over water. There was a strong effect of the additional water deterrent on the 12.7 mm diameter rod. 100% of the cockroaches remained upright on the water trials. When there was no water, the cockroaches remained upright in 17% of the trials. **C:** Transition position is defined as the point where the cockroach angular trajectory crosses from the stable to the unstable region.

Figure 2.11

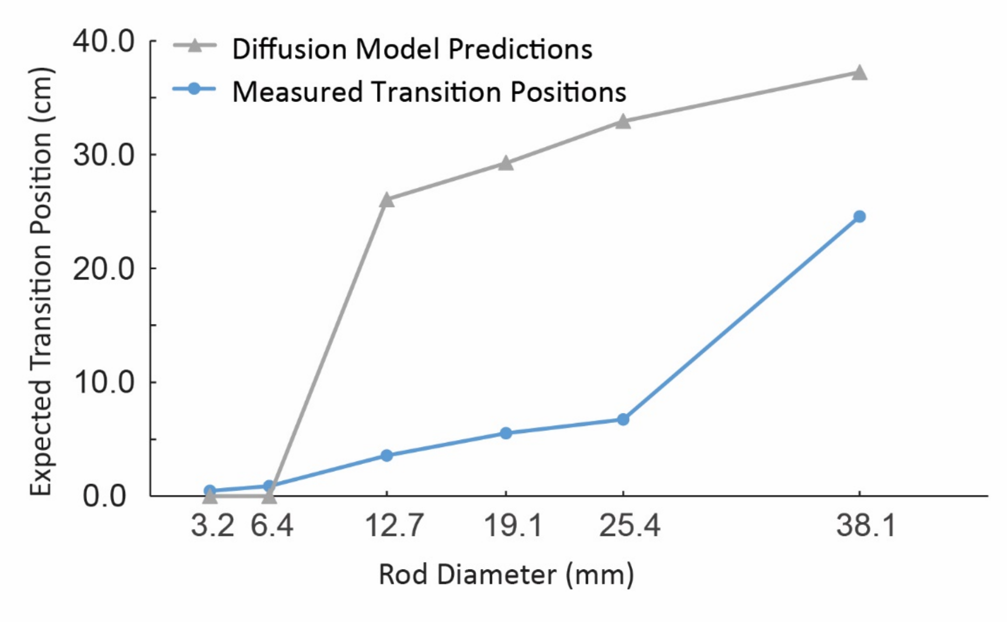

Figure 2.11: shows the predictions of expected transition position as a function of rod diameter from the simple diffusion model versus the measured transition probabilities in the tracked data.

Cockroaches Can Remain Upright if Motivated by an Aversive Stimulus

Following the previous result, that simple random diffusion predicts cockroach transition frequencies, an additional experiment was conducted to determine if cockroaches can selectively employ stabilizing control while running on the 3 smallest rods. Based on previous experience working with *Periplaneta americana*, the fact that these animals tend to avoid pools of water was exploited to add an aversive stimulus to deter the animals from executing their rolling transition maneuver. For the 2 smallest rods, no difference was found in the transition probabilities – the animals transitioned every trial. But, on the 12.7 mm diameter rod there was a very strong effect of the aversive stimulus (Figure 2.8, B). When no water was present on the 12.7 mm rod, cockroaches transitioned 83% of the time. With the addition of the aversive water stimulus, cockroach transitioned 0% of the time. Cockroaches are strongly deterred from falling into the water, and on the larger 12.7 mm diameter rod are capable of balancing to prevent a rolling inversion, and maintaining upright running at this diameter.

Adding repercussions to angular deviations, by including an aversive water stimulus beneath the rod had a large effect on the propensity to transition to an inverted posture. The diffusion model, and the feedback control model both suggest that cockroaches are not controlling their angular position on the rod, and they let random angular variations accumulate until they passively transition to inverted running. But it's possible that they can choose to balance if maintaining an upright position becomes valuable. This is what was found by including a body of water underneath the rod. The presence of water on the small 12.7 mm diameter rod leads to a drastic change in transition probability from 0.83 to 0.00. At the even smaller rod diameters of 6.4 and 3.2 mm however, the cockroaches were apparently unable to balance and their transition probabilities matched those without the water deterrent. One outstanding question is, is there a tradeoff between the strength of balancing control, and other objectives such as speed. It may be the case that cockroaches can selectively engage balancing feedback control of different strengths to balance the relative requirements and priority of maintaining upright, and running fast. Future work will investigate the role of deterrents and motivation on transition probabilities and branch running performance.

2.3 Conclusions

In this study, it was found that posture, as quantified by sprawl angle, could be effectively manipulated by varying the curvature of the substrate. This effect was strong, changing sprawl angle from less than 20 to over 100 degrees. Systematically varying substrate curvature is an experimental manipulation that can be used to generate large or small differences in posture, since small changes in rod diameter led to small but significant differences in sprawl angle. Horizontal forces are likely reduced due to reductions in sprawled posture, since ground reaction forces are typically directed along the length of the limb towards the center-of-mass. Therefore, reductions in sprawl posture are likely to limit passive dynamic stability.

The rapid escape response exhibited by the cockroach running along the rod reduces the time available for a neural feedback-control response compared to slower branch locomotion. Cockroaches transitioned during rod running, rolling around the rod and running in an inverted orientation. Passive mechanical stabilization due to the pendulum-like dynamics of running beneath the rod allowed a rapid escape response without feedback-control stabilization. But, when an aversive stimulus was presented beneath the rod, cockroaches made a choice to implement stabilizing feedback-control to remain on top of the rod.

Future work on cognitive biomechanics of branch running will examine decision making as it related to performance and stability. Effects of different branch diameters, and tradeoffs between speed, balance and body orientation will be investigated. Also, the small-diameter limit for upright locomotion and its causes will be determined. On a broader scale, investigations will examine how animals choose to use multiple gaits to navigate the complex terrain of branches and stems. These questions are important towards a larger goal of building a systems level understanding of arboreal locomotion, advancing a principled understanding of how animals accomplish fast, and agile, yet stable movements in complex environments. These studies will discover principles that can potentially improve state of the art search-and-rescue or environmental-monitoring robotic systems.

Chapter 3

Learning Targeted Leaping from a Compliant Substrate

3.1 Introduction

Cognitive biomechanics explores the interaction of the mechanics of the animal and environment with cognitive control processes, such as decision making and motor learning. Motor learning consists of many simultaneous processes that can affect biomechanical performance (Lior Shmuelof & Krakauer, 2011). From the perspective of classical motor control theory, action selection, or sequence learning can allow animals to determine what actions to take in what context. Error based motor learning or motor adaptation is learning to recalibrate a task controller in the face of a systematic perturbation (Izawa, Rane, Donchin, & Shadmehr, 2008; Reza Shadmehr, Smith, & Krakauer, 2010). Skill learning is a slower process in which the motor control system learns to improve maximal performance (Lior Shmuelof, Krakauer, & Mazzoni, 2012). Maximal performance on a task can be defined by a performance tradeoff function, e.g. speed/accuracy tradeoff which describes how the maximum accuracy of a movement depends on the speed of execution. Fitt's Law, and empirical model of a tradeoff between movement duration and movement difficulty has been refined to quantitatively model the tradeoff between speed and accuracy (Fitts & Peterson, 1964). A proposed physiological mechanics for explaining the speed-accuracy tradeoff is signal-dependent noise. Signal-dependent noise is a linear relationship between magnitude of force produced by a muscle and the standard deviation of that force (R. A. Schmidt, Zelaznik, Frank, & Stelmach, 1978), but see nonlinear refinements and extensions to this model (Carlton & Newell, 1993; Christou, Grossman, & Carlton, 2002; Sherwood & Schmidt, 1980). A model of targeted movements which hypothesizes that the motor control system attempts to minimize end-point variance in the face of signal-dependent noise predicts experimentally recorded trajectories of eye saccades and arm reaching movements, and predicts Fitt's Law (C. Harris & Wolpert, 1998). But, signal-dependent noise suggests a more general impulse/accuracy tradeoff that applies to eye saccades and targeted reaching, but also to more dynamic maneuvers like targeted leaping. Skill learning in this context is characterized by a shift in the speed/accuracy tradeoff function (Lior Shmuelof & Krakauer, 2011). In addition, motor performance can also depend on learning explicit information (Stanley & Krakauer, 2013). In the current research project, the effects of motor learning on targeted leaping performance were determined.

Targeted leaping from a compliant beam represents a model system for cognitive biomechanics, because the biomechanics of leaping from a compliant beam has been studied in a few diverse species. Gibbons leap from a compliant beam using different postures to achieve jumps at different takeoff speeds (Channon et al., 2011). Also, green anoles leap from perches of various compliance in the wild, and these perches have different effects on leaping kinematics. Moreover, the recoil of the branch often strikes the tail of lizard, altering their body pitch during the aerial phase (Gilman et al., 2012). Animals may execute different pre-leaping patterns to carry momentum into the leap (Brigitte Demes, Franz, & Carlson, 2005). With cognitive biomechanics, we attempt to extend understanding of arboreal locomotion by combining the well-studied mechanics of leaping from a compliant beam with results on learning and decision making processes.

Free ranging squirrels were used as a model organism for cognitive biomechanics. One benefit of using free ranging animals is that they have a life history embedded within a complex environment, and they may have developed motor skills that might allow for greater performance than caged animals of the same species. Differences in the size, dimensionality, and propensity of cues present during an animals development can affect locomotion strategies, and how those strategies are integrated into navigational abilities (Jacobs & Menzel, 2014). This is also supported by findings of reduced mushroom bodies in caged honeybees compared to their outdoor foraging conspecifics (Withers, Day, Talbot, Dobson, & Wallace, 2008). In another example, captive mountain chickadees have reduced hippocampal volume compared to their wild conspecifics (LaDage, Roth Ii, Fox, & Pravosudov, 2009). Using free-ranging animals may allow discovery of principles for interaction between biomechanics and complex cognitive processes.

Fox squirrels were chosen as model organisms for cognitive biomechanics because they are cognitively complex, and have highly dynamic gaits and maneuvers. Fox squirrels use complex decision making processes to consider multiple factors when taking actions in the natural environment (Delgado, Nicholas, Petrie, & Jacobs, 2014). Squirrels have dynamic biomechanical capabilities, such as using dynamic gaits on compliant branches (Figure 3.1), and making leaps across gaps spanning many times its own body length (Figure 3.2).

Figure 3.1

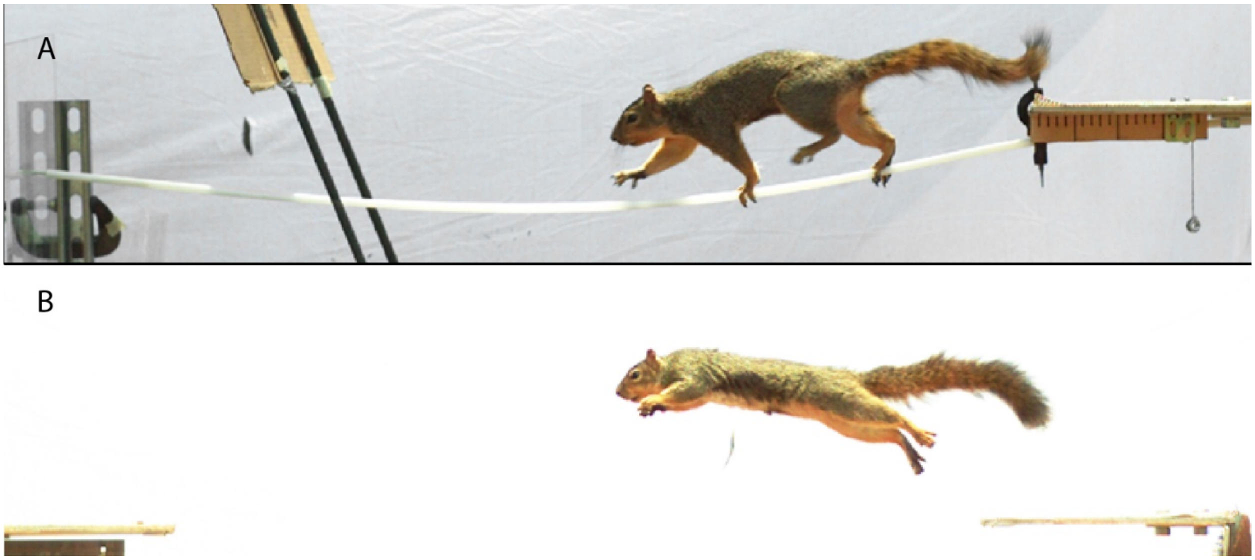

Figure 3.1: Fox squirrels exhibit dynamic gaits running on compliant branches. **A:** Fox squirrel walking across a highly compliant acrylic rod. **B:** Squirrel leaping across a gap three times its body length.

In this experiment, three hypotheses were tested: 1) beam compliance causes greater initial landing errors compared to leaping from a rigid beam, 2) landing errors decrease with experience and 3) greater beam compliance increases the learning time.

3.2 Methods

Study Subjects and Location

Fox squirrels in this study came from one of three known wild populations of squirrels on the University of California, Berkeley campus. The chosen population resided within a small fragmented forest on the west side of campus called the Eucalyptus grove/Grinnell Nature area. The study site consisted predominately of coast live oak (*Quercus agrifolia*), redwood (*Sequoia sempervirens*), and bluegum eucalyptus (*Eucalyptus globulus*) which bordered on Strawberry creek. Experiments were conducted three times a week between the hours of 1400-1700 from September 2014 to March 2015.

The study site consisted of 23 known individuals, each marked with a unique, black fur dye (Nyanzol D) pattern. Squirrels from this population were reliably found in the study area daily. From this population, we drew five adult squirrels to test, three males and two females, ranging between 750-985g (Figure 3.2).

Figure 3.2

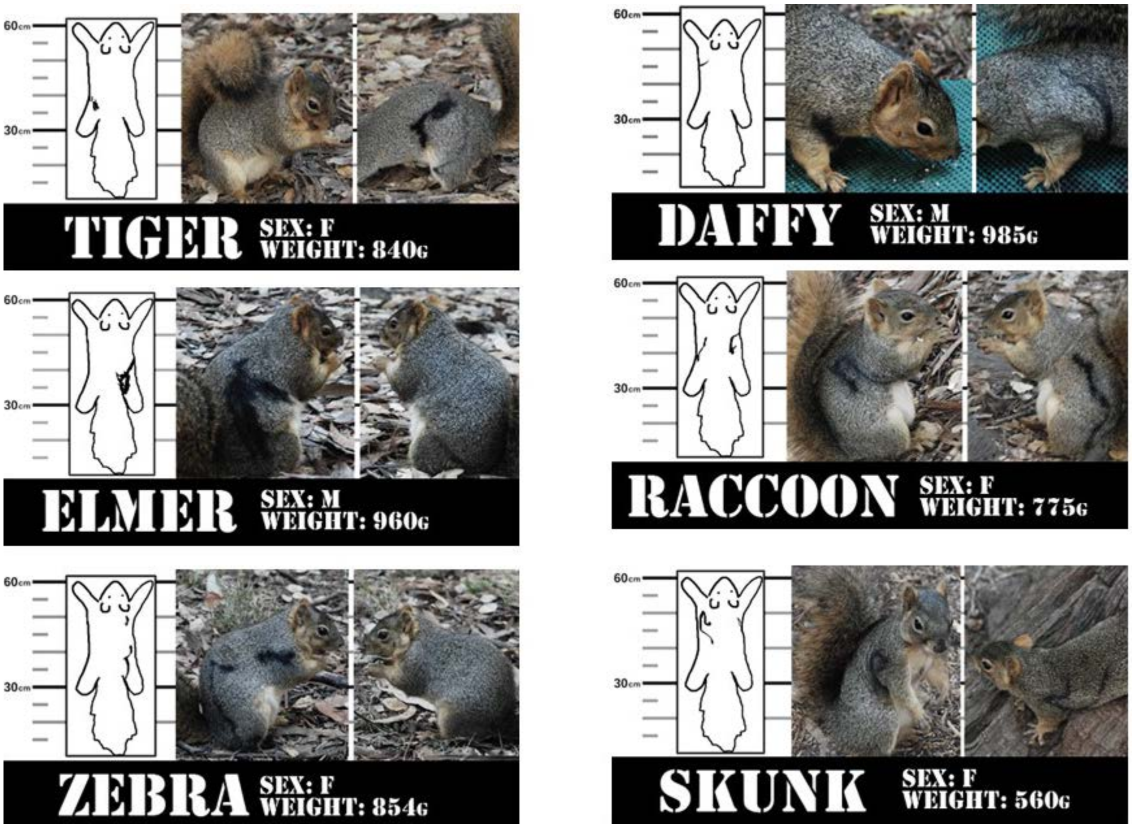

Figure 3.2: Squirrel identification and morphometric data. Photos show experimenter-applied squirrel markings. Diagrams show the recording of squirrel markings for continued identification across multiple sessions. Sex and mass were determined and memorable names given for each animal.

Apparatus

The main face of the apparatus was a 72” x 48”, 16-gauge steel sheet, mounted using VHB tape (3M, 4941) to a frame of 2”x4”s. Two 2”x4” A-frames served as legs to hold the steel frame vertically, resulting in a standing height of 60”. The steel was coated with a corrosion inhibitor (Rust-oleum primer) before being painted white to increase contrast between the background and squirrels for data analysis. The apparatus was referred to as “the wall” (Figure 3.3).

The steel sheet served as a magnetic surface for modular devices to be attached. 2” x ¼” x 1/8” neodymium magnets were used to secure devices to the board. A jumping platform measuring 12”x12” was made of two interconnected L-brackets created with 2”x4”s. It was spray painted blue (Krylon oxford blue, satin) to provide further contrast from the white wall. Acrylic backing was laser cut to provide wells in which magnets could be secured with epoxy. 3”x3” acrylic square with well-space for magnets was then glued to the top surface of each L-bracket along the distal ends. A 36” x 3”, 11-gauge steel sheet was laid on top of the magnets to the top of the jumping platform to create a 60 cm overhanging beam which was 9” from the wall. Using a standard cantilevered beam compliance model, (Beer et al., 1972), beam compliance at the endpoint was estimated to be 0.030 meters per Newton. The 60 cm overhang was wrapped in athletic tape to give squirrels traction.

For training and tests where a rigid beam was required, we created a wood bracket with a 45 degree angle. The backing was created with a 12” section of 2”x4” and a 17” segment of wood was attached at 45 degrees pointing upwards in a V-shape, where the end contacted with the overhanging steel beam to prevent it from bending. This was also mounted painted blue and embedded with neodymium magnets to attach to the wall.

A landing perch was made from a 1/2” diameter, 19” long dowel. A hole was drilled into two overlapping 12” sections of 2”x4” which served as an anchor for the dowel to sit perpendicularly to the steel board. The dowel was attached with epoxy to the boards. To increase traction, the dowel was wrapped in athletic tape. A small cup was inserted over the end of the dowel to hold food rewards. The completed landing perch and food receptacle were then spray painted the same color blue as the other devices and outfitted with neodymium magnets.

To prevent squirrels from finding other jumping points than the provided platform, baffles were created. Baffles were made of blue card stock paper. Blocks of wood with smaller neodymium magnets were attached to the card stock using rubber bands and staples. A single baffle was placed approximately 5 cm from the end of the beam. Its width extended 9” from the wall, such that it did not obstruct the beam. This baffle served to discourage squirrels from using the wall was an accessory to help them leap to the landing perch. No other baffles were placed in the direction of travel besides this first baffle. Other baffles were placed on the apparatus as necessary to stop squirrels from climbing onto the wall.

The wall and all modular pieces were moved outside each experiment day to the Eucalyptus grove and placed between the creek and Grinnell pathway, facing due north to prevent casting of harsh shadows onto the face of the wall. A level was used to ensure the wall face was perpendicular to the ground. We then leveled the jumping platform and attached beam on the walls such that squirrels always had a flat surface to jump from.

Figure 3.3

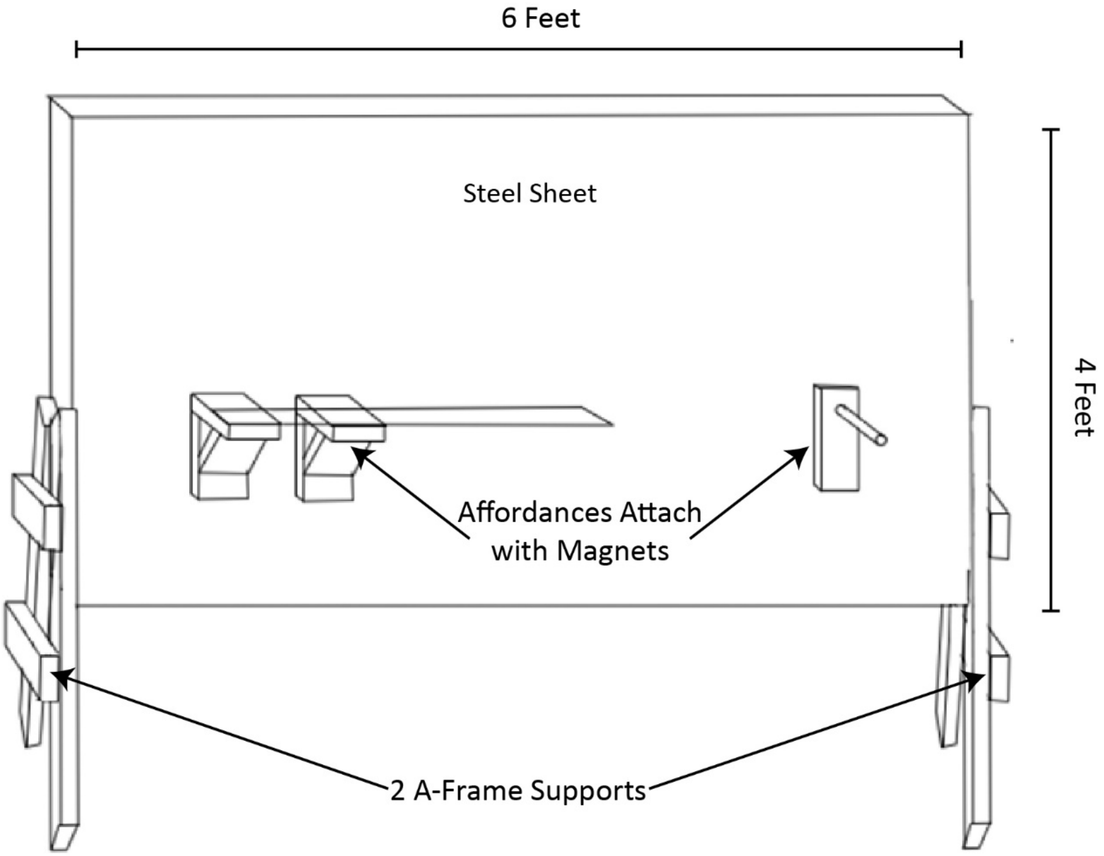

Figure 3.3: Diagram of wall apparatus. Front surface of wall is a sheet of 16-gauge steel (0.0598” thick) that was cut to 4 feet high by 6 feet long. The sheet of steel was framed in with 2”x4” wooden boards, and supported off the ground by A-frames on each side. A-frames were designed with a single bolt attachment at each point where boards were adjoined. This allowed A-frames to pivot and the wall could be aligned with gravity despite uneven ground. Affordances, such as the compliant beam and the landing perch shown, were made with embedded neodymium magnets. The embedded magnets allow the affordances to be precisely placed on the wall to produce gap geometries prescribed by the experimenter. The compliant beam affordance consisted of a rectangular sheet of steel cantilevered from two wooden supports. The perch affordance consisted of a dowel mounted into a 2x4 board.

Training

A 6’ 2”x4” board with shelf liner laid on top to provide traction was leaned against the left A-frame to provide a ramp for squirrels. The jumping platform was placed on the left side of the wall next to the ramp. Small pieces of peanuts were placed on top of the ramp leading onto the jumping platform and beam. The supporting bracket was placed beneath the beam to provide a rigid surface to walk on during training. The landing perch was placed at the end of the beam, such that squirrels would initially only have to walk onto the perch from the beam to receive a half of a peanut from the reward cup.

For each experiment, an individual was chosen at random which had not previously encountered the wall. Other squirrels were kept away by discouraging their attempts to climb the wall or fed *ad lib* on the ground. Naïve squirrels were first habituated to the apparatus by being fed near the wall. They were gradually led towards the baited ramp and allowed to eat peanuts until they were comfortably retrieving food from the reward cup without hesitation. Squirrels generally habituated to the wall within ten minutes.

Once squirrels were habituated to the apparatus, the perch was gradually pulled farther away from the beam until leaping was required to reach the food reward. The position of the perch was kept parallel to the beam by using a level placed on a meter long 2”x4” which spanned from the beam to the perch each time the perch was moved. This process continued until the jumping distance reached approximately 50 cm. Training was considered complete when squirrels were jumping without hesitation. Reaching training criterion took approximately 30 minutes. (Figure 3.4)

Testing

Once training was complete, squirrels were tested on jumping from a rigid and compliant beam to the landing perch. Initially the landing perch was 75 cm away and the compliant beam was calculated to have a compliance of 0.014 meters per Newton. Leaps from this beam caused deflections of approximately nine cm. But this gap distance/compliance combination was determined to be too easy for the squirrels as they eliminated the error after only one or two leaps (Figure 3.10). To make the leaping task more difficult, a landing perch was placed 65 cm away from the end of the compliant beam, and the length of the cantilever was extended to double beam compliance to 0.030 meters per Newton. Leaps from this beam caused deflections of approximately 13 cm. In addition, the landing platform was substituted with a landing perch. By requiring the squirrels to land on a perch, bot negative and positive landing error could be quantified. To balance the data, squirrels were randomly assigned an initial condition. In the rigid jump condition, the supporting bracket remained in place and the perch was placed 65 cm from the end of the beam at the same level. An extra baffle was placed on the beam to block the landing perch from sight. Once the squirrel was on the jumping platform and facing the landing perch to the right, the baffle was removed. Squirrels then leapt from the jumping platform to the landing perch to receive a peanut. Occasional coaxing from an experimenter by waving a peanut over the landing perch was used to encourage the squirrel to leap. Squirrels were then coaxed to leap back to the start platform and kept occupied with a peanut, the baffle was replaced, and trials were saved to the computer. This process was repeated up to five times for each squirrel. In the compliant condition, the supporting bracket was simply removed and the perch was set slightly lower to match the level of the end of the compliant beam. The squirrels then leaped five times to the perch using the previously described methods. Each squirrel was then tested on the opposite condition at a later date. Of five squirrels, one squirrel failed to complete both conditions and performed only two of the five rigid trials.

Recording

All trials were recorded with a high-speed camera (Phantom, Vision Research Inc., Wayne, NJ). The camera was placed such that it had a lateral view of squirrels, and bisected the distance jumped by the squirrel during tests. It was also level with the jumping platform and framed such that only the overhanging beam and the landing perch were in frame. Squirrels were filmed at 200 fps. Uncompressed .avi files were saves to the camera control computer.

Figure 3.4

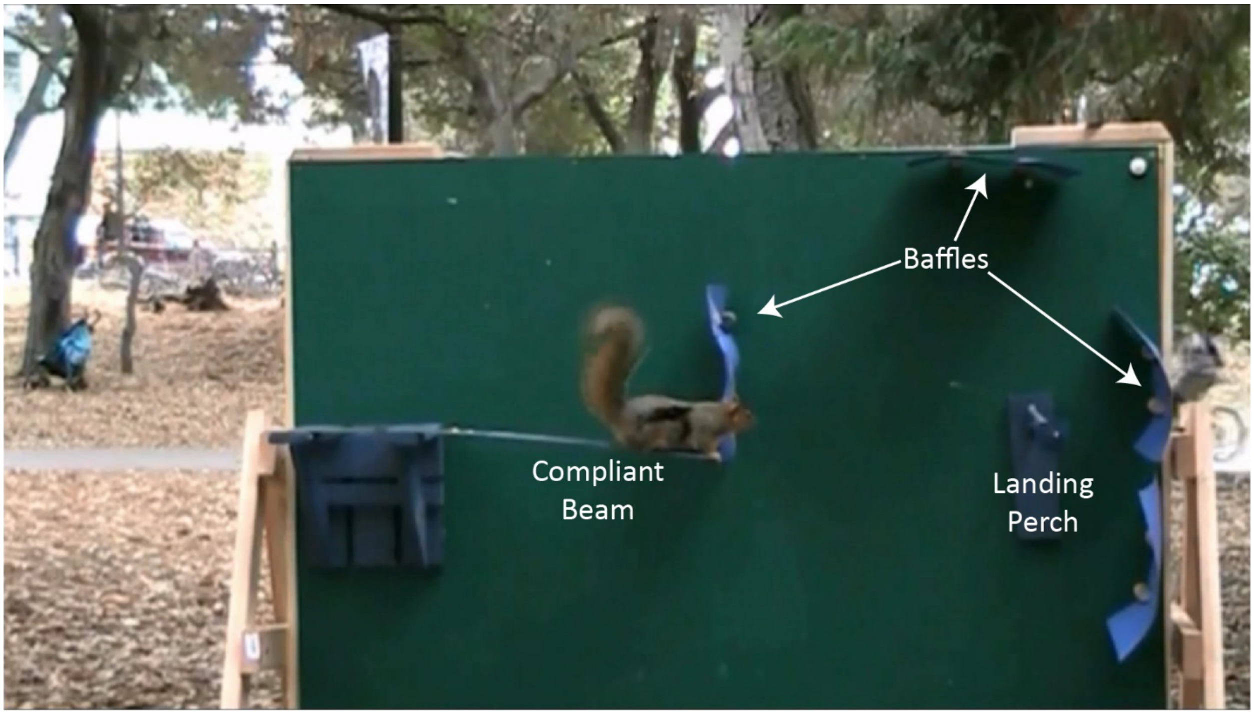

Figure 3.4: Training free-ranging squirrels with peanuts. Photograph shows wall apparatus with a squirrel that is being trained by an experimenter with peanuts to leap across the gap. Shaping training procedures were used where the squirrel was initially rewarded for climbing onto the apparatus, then stepping directly to the perch, then leaping across gaps to the perch. The gap was progressively lengthened until the squirrel was trained to jump the full length of the gap prescribed in the protocol. Baffles were used to prevent the squirrel from taking alternative paths to the landing perch.

Body Curvature and Center of Mass Determination

We used a standardized method to estimate the center of mass (COM) position in each video frame of a squirrel’s jump (Figure 3.5). First, the rostrum of the squirrel and the base of the tail were hand-tracked in a custom MATLAB program. The program fit a line between these two points (anterior-posterior line), which was then bisected by a line which represents the transverse plane of the squirrel’s body. On the transverse line, the points intersecting the dorsal and ventral sides of the animal were then tracked. A line segment (dorsal-ventral line) connected the two points, and the midpoint was found. This dorsal-ventral midpoint was then translated to the origin, with all other features also translated respective to it. All features were then rotated around the origin such that the anterior-posterior line was parallel to the x-axis of the coordinate plane. A quadratic function was fit using the anterior point, dorsal-ventral midpoint, and posterior point. The curve of the squirrel’s body was recorded as the coefficient of the quadratic fit. More negative coefficients represented a greater arching of the squirrel’s back. The center of mass was designated as the point where 60% of the total length of the fitted quadratic line lay from the anterior point. This value of 60% was determined by balancing a squirrel specimen on a knife edge that had been frozen in a leaping posture. Finally, all estimated features were then translated and rotated to the original positions in the frame, along with the newly calculated features. The center of mass point was then recorded according to its true position in the image frame. (Figure 3.5)

Figure 3.5

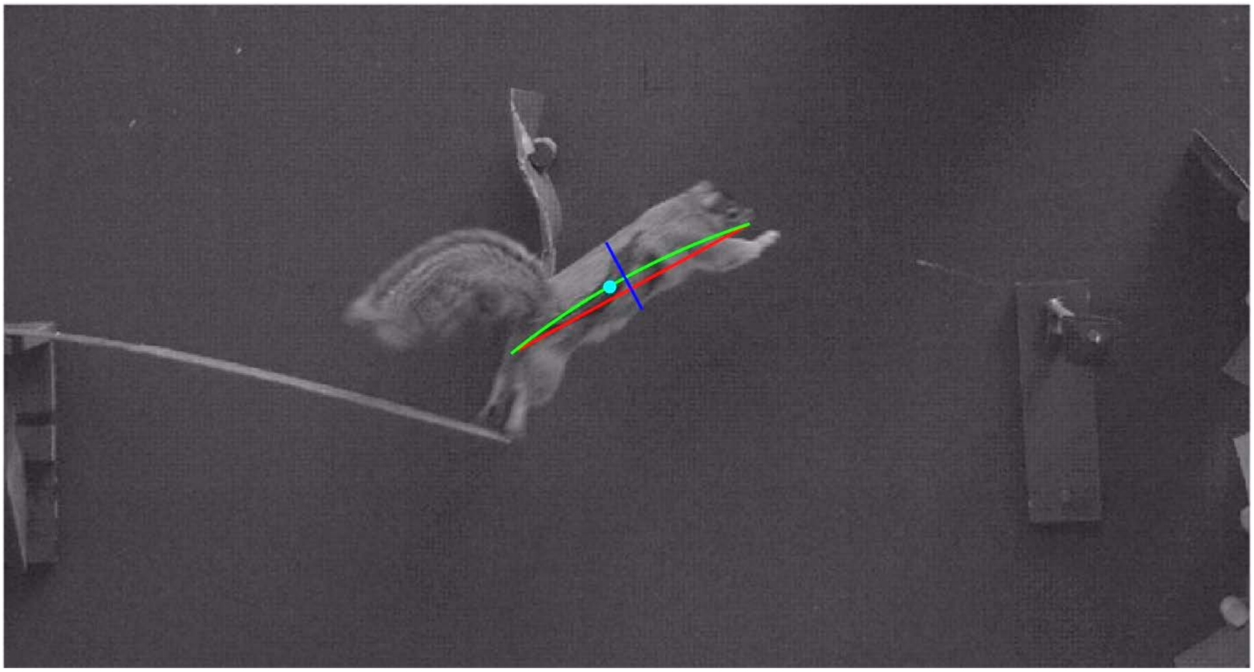

Figure 3.5: Identification of the center of mass in each high-speed video frame. A proxy point for the center of mass was determined on each frame of the video using custom MATLAB code. The tip of the nose and the center of the hind torso was chosen. A construction line connecting (red) these points and another that bisected this line at the midpoint were displayed (blue). The points where the bisecting line intersected the dorsal and ventral surfaces were chosen. A body curve (green) was fit from the tip of the nose, to the center of the blue bisecting line, to the hind torso. 60% of the distance from the nose to the hind torso along the curve is indicated by a cyan dot in the photograph, representing the calculated center of mass proxy.

Leap Angle, Velocity and Landing Error

The magnitude of initial leap angle and velocity was calculated by tracking the center of mass as the squirrel leapt from the jumping platform and using the first three frames of the aerial phase. Using the tracked COM trajectory over the entire aerial phase, a quadratic formula was fit to estimate the parabolic trajectory. Landing error is characterized by the vertical offset from the landing perch predicted by the extrapolated quadratic fit intersecting the vertical line through the perch location. The theoretical justification for choosing this definition of landing error is that, under this definition, a landing error of zero will be one where the extrapolated COM trajectory intersects the landing perch and does not require any torque to be produced to stabilize landing.

Figure 3.6

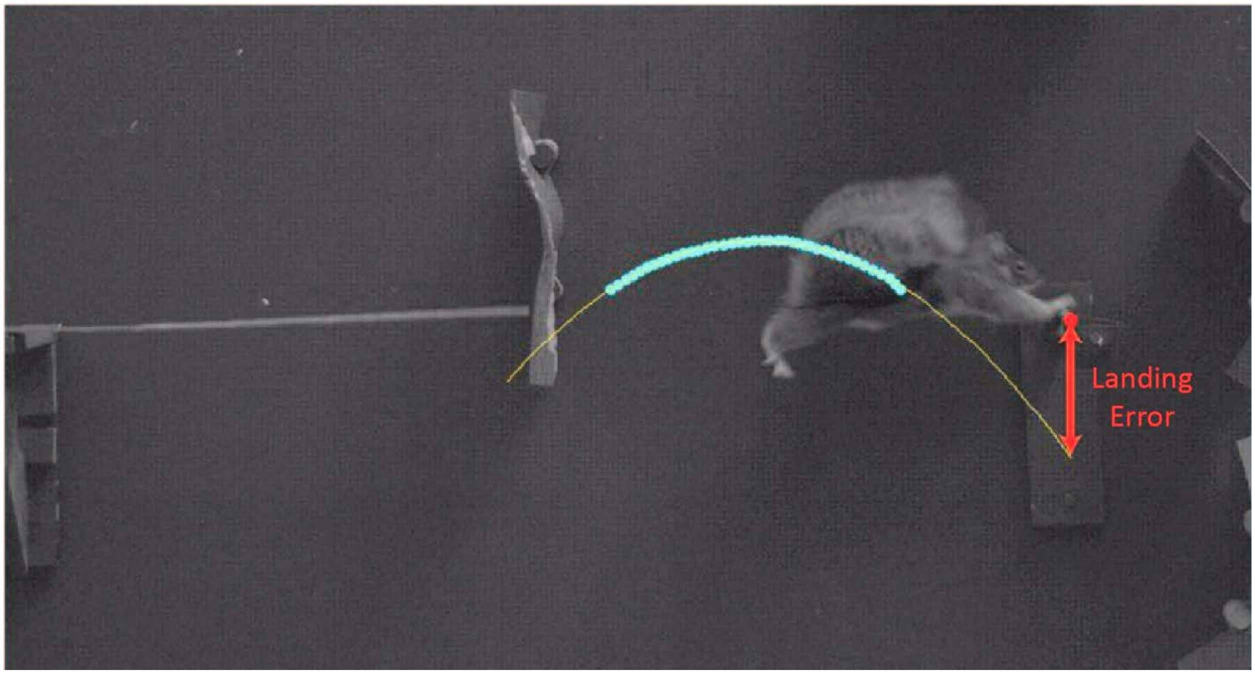

Figure 3.6: Quantifying landing error. Sequence of cyan dots show the squirrel's center of mass at successive frames from the high-speed video. Yellow line shows a quadratic fit to the center of mass data. Extrapolating the center of mass trajectory shows that it does not intersect with the landing perch. Landing error was quantified as the vertical distance between the perch and the extrapolated center of mass at the full horizontal gap distance. This metric is used for all further characterizations of landing error.

Analysis

All data recorded by the program (MATLAB) were then transferred to a spreadsheet (Microsoft Excel, 2013). Averages of body curvature, initial angle, initial speed, and landing error were calculated for trials 1-5 for each condition. Student's t-tests were used to compare trial 1 to trial 5 in each condition for initial angle, initial speed, and body curvature. Landing error analysis was calculated using a two-way within-subjects ANOVA in R. Missing data for one squirrel on the compliant beam were substituted by averaging the other landing error values for the respective trial. We compared differences across trials and between beam type.

3.3 Results and Discussion

Landing Differences After Leaping from the Rigid versus Compliant Beam

Fox squirrels had very stereotypic behavior when leaping from a rigid platform. Their forelimbs left the leaping platform first, followed by their hindlimbs. Landing reversed the foot fall pattern – they made initial contact with the landing perch with both forelimbs followed by both hindlimbs (Figure 3.7, A). It was observed that introducing compliance to the leaping platform led the squirrels to undershoot the rod in a very stereotyped way. The pattern of limbs leaving the compliant platform for the leap was the same as what was observed for the rigid platform. However, upon landing the squirrels made contact with their forelimbs, but not with their hindlimbs. This caused them to swing from their forefeet with their body swinging beneath the perch (Figure 3.7, B). From that position, they pulled their body above the rod while placing their hindlimbs on the rod. This difference in landing footfall patterns held true for every trial from the rigid and compliant beams.

Arboreal animals have various maneuvers to control landings and reduce the landing forces (B Demes, Fleagle, & Jungers, 1999). For example, geckos can re-orient the body with tail movement, (Jusufi, Goldman, Revzen, & Full, 2008). Colugos create aerodynamic forces to reduce landing substrate reaction forces (Byrnes, Lim, & Spence, 2008). The landing maneuver exhibited here by squirrels after leaping from the compliant beam, (Figure 3.7, B), involves a brief forelimb suspension behavior as commonly seen in primates (Hunt et al., 1996) with a swing maneuver to get on top that appears to have pendulum-like dynamics, similar to brachiation (Bertram, Ruina, Cannon, Chang, & Coleman, 1999).

Figure 3.7

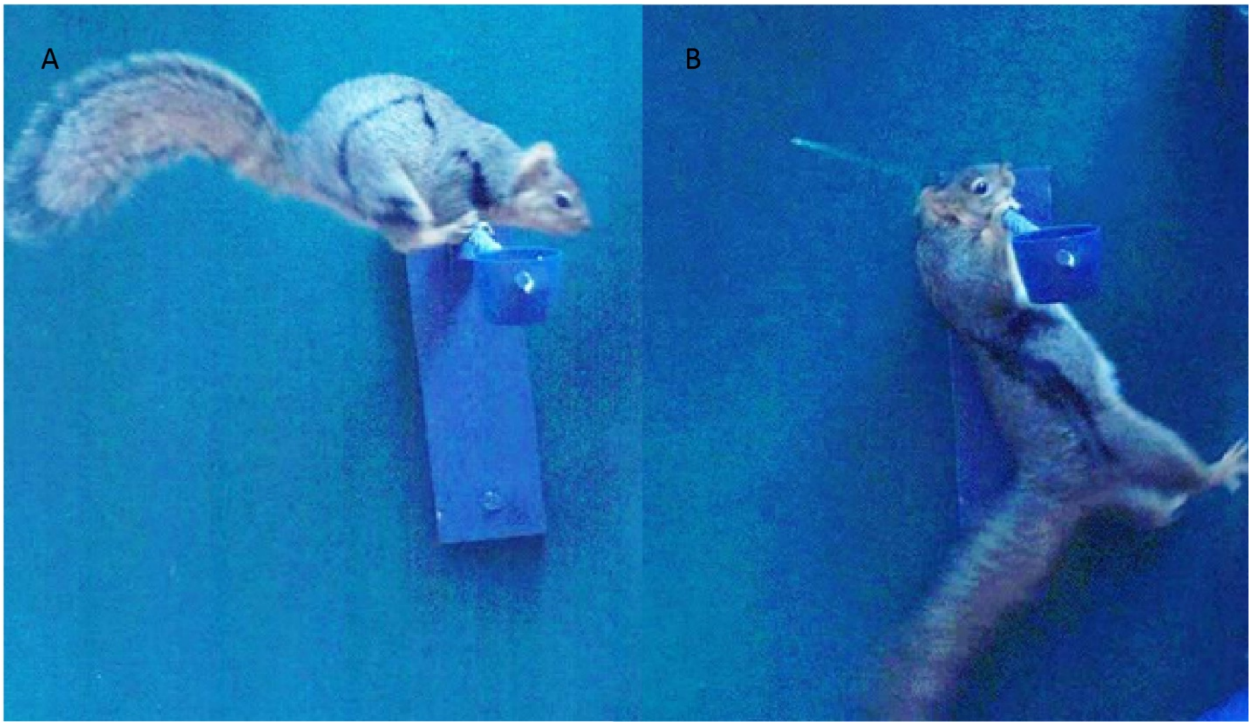

Figure 3.7: Squirrels had different landing patterns after leaping from a rigid beam versus after leaping from a compliant beam. The two landings in the above photographs are representative of every rigid or compliant leaping trial, respectively. **A:** After leaping from a rigid beam the squirrel lands with forelimbs and then hindlimbs. **B:** After leaping from a compliant beam the squirrel lands with forelimbs but hindlimbs swing under the landing perch.

Large and Small Landing Errors After Leaping from the Compliant Beam

A large landing error, characteristic for the first leap from the compliant beam is shown in Figure 3.8. The largest of these landing errors were approximately half the body-length (not including tail) of the squirrel. The trajectory producing these large landing errors required the squirrel to extend the front legs to near-maximal range in order to catch the perch. But no animals fell during any of the trials.

Figure 3.8

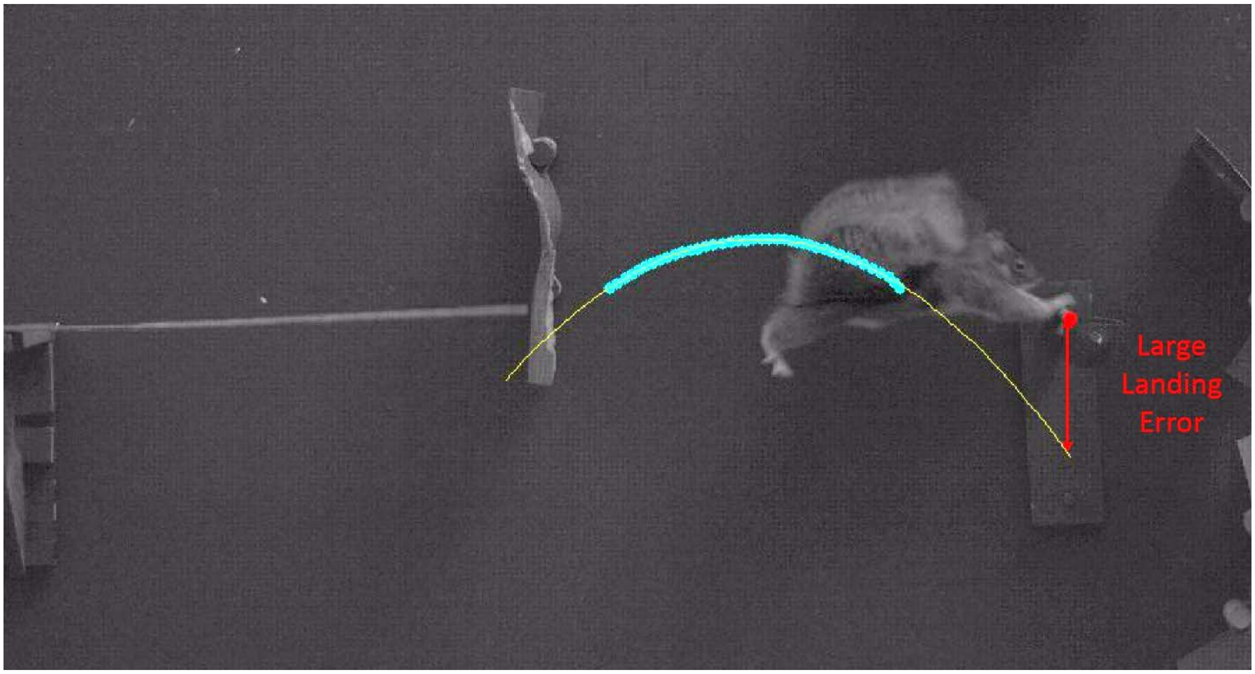

Figure 3.8: Typical high landing error exhibited on the first compliant beam leaping trial. The Fox squirrel's extrapolated center of mass trajectory undershoots the landing perch.

Figure 3.9

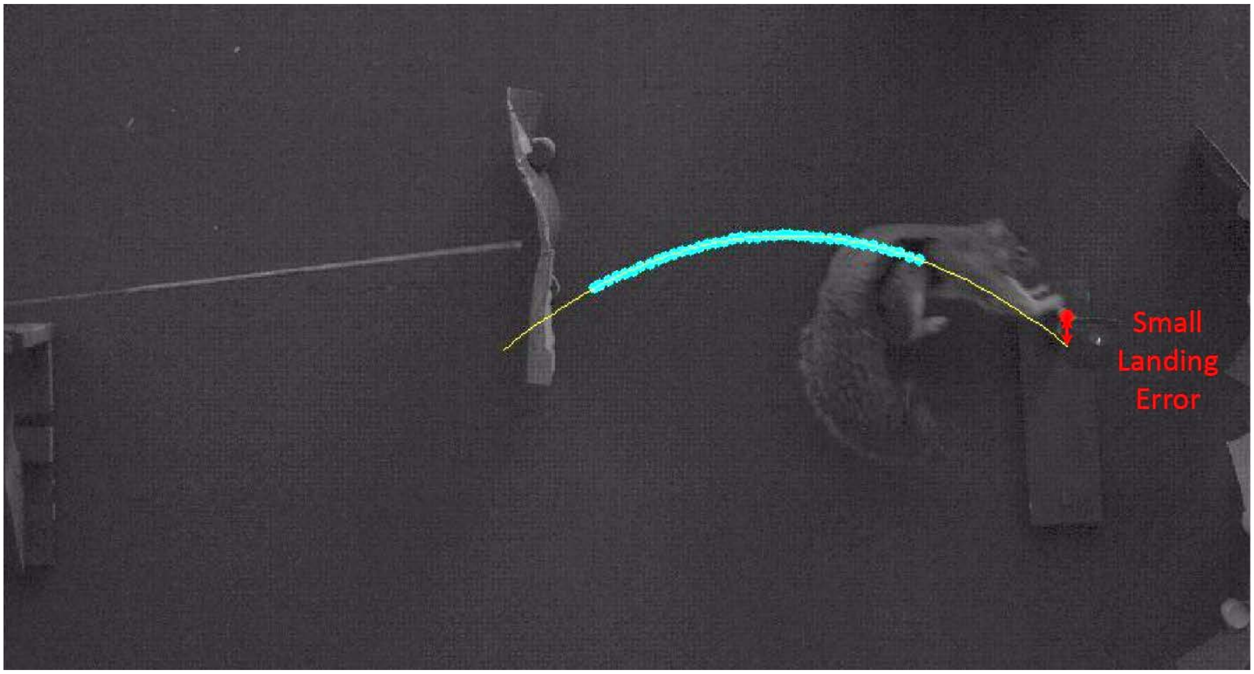

Figure 3.9: Typical small landing error exhibited on the fifth compliant beam leaping trial. The squirrel's extrapolated center of mass trajectory nearly intersects with the landing perch.

Rapid Learning on Initial Gap/Compliance Combination

Our initial choice of a 75 cm gap distance and a beam compliance of 0.014 meters per newton led to rapid learning. Of the eight squirrels tested at this leaping task combination, three converged on low-error landings after two or three jumps, and two individuals had low-error landings on their initial jump (Figure 3.9). This made it difficult to examine the course of learning, so we increased the leap task difficulty by doubling the compliance. We also reduced the gap length to 65 cm.

In addition to rapid leaning, if a squirrel achieved a landing error near zero, then they repeated this performance on all subsequent leaps. This is consistent with the hypothesis that leaping errors are reduced through an error based learning process. In error based learning, the errors drive changes in behavior to reduce them. If no errors are present then this process does not alter the behavior (Izawa et al., 2008; Reza Shadmehr et al., 2010).

Figure 3.10

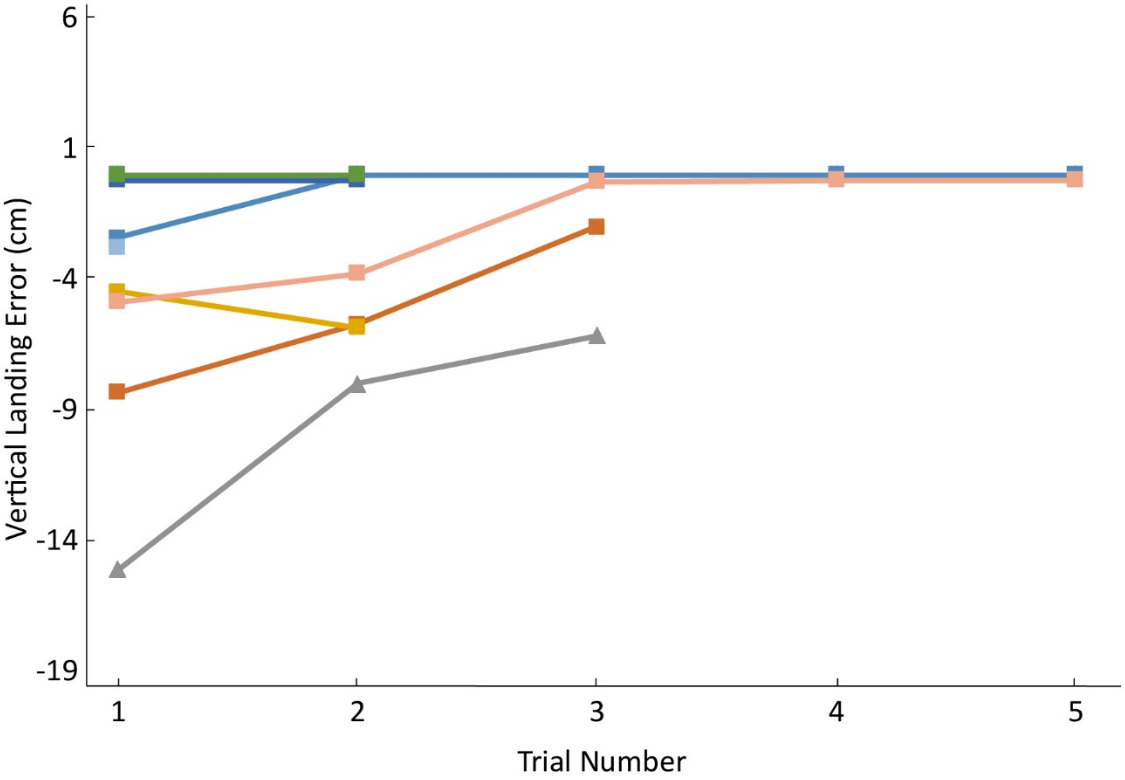

Figure 3.10: Vertical landing error versus trial number. Each color represents a different individual. With the 75 cm gap length, and 50 cm cantilever combination, some squirrels did not exhibit landing errors on the first trial. Among the squirrels that did exhibit a landing error, the error was reduced rapidly, and in some cases eliminated after one or two trials. This rapid learning led us to increase the difficulty for a second experiment.

Squirrels Learn to Increase Leap Performance by Reducing Landing Error

It was hypothesized that there would be no learning exhibited in leaping from the rigid beam due to squirrels' extensive experience with this task. Observing the trials leaping from the rigid beam, they appear to have low-error landings on all trials. The calculated landing error also indicated low-error landings for all trials. Due to apparent variation in the performance of different individuals, we used a repeated measures design instead of grouping data across individuals. A repeated-measures one-way ANOVA found no significant effect of trial number for the rigid beam trials (p=0.233), (Figure 3.11).

It is likely that that didn't show any change in performance because leaping from a rigid structure is a task squirrels do often, leaping from large tree branches to cross a gap.

Figure 3.11

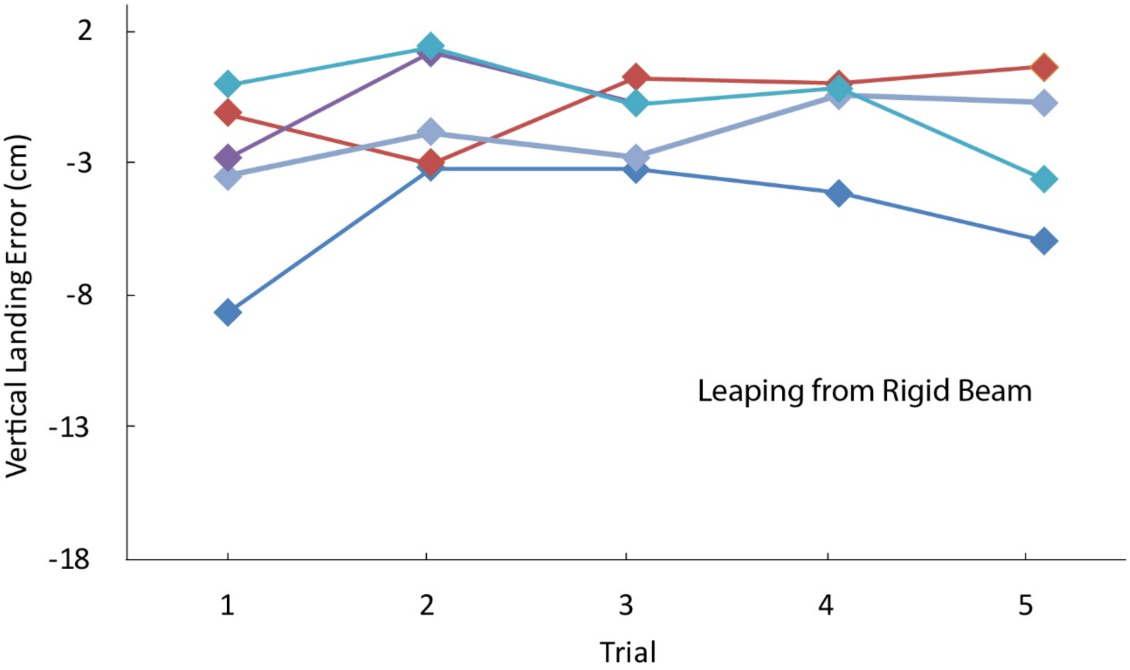

Figure 3.11: Vertical landing error versus trial number for squirrels leaping from a rigid beam across a gap of 65 cm. Each color represents a different individual.

It was hypothesized that introducing compliance to the beam would lead to an increase in the magnitude of the landing error. Note that the use of a small cylindrical landing perch as opposed to a landing platform allowed calculation of both positive and negative landing errors. A negative landing error occurs when the extrapolated COM trajectory reaches the perch distance at a point below the perch, and indicates the squirrel came up did not leap far enough. A positive landing error occurs when the extrapolated COM trajectory reaches the perch distance at a point above the perch. Large landing errors where the hindlimbs did not make contact with the landing perch were observed for all initial trials on the compliant beam (Figure 3.12). A paired t-test between landing error for the first trial on the rigid beam, and the landing error for the first trial on the compliant beam showed they were significantly different (p=0.0158).

The introduction of a highly compliant beam produced initial landing errors compared to leaping from a rigid beam. The squirrel was trained to leap from the same beam, but with a support on both ends keeping it rigid. Removal of the support caused the beam to be cantilevered, and highly compliant on the side towards the gap. This change in mechanical properties on a substrate that squirrels had already become familiar with is likely the cause. An alternative explanation is that there was a mismatch between the compliance and the expected compliance based on cues. In arboreal habitats, compliance varies positively with branch diameter (Crompton, Sellers, & Gunther, 1993). This beam was 3” wide, and much more compliant than a tree branch of similar diameter. This sensory/proprioception mismatch may have led to an error is anticipating the beams mechanical properties.

Despite landing errors that were occasionally half a body-length, squirrels never fell during a leap. Also, high landing errors did not deter the squirrel from performing another trial to get another peanut.

Increased beam compliance generated high-landing errors, but Fox squirrels were capable of recovering from those errors, and landing effectively on the perch. For the initial trials on the compliant beam, they leapt at trajectories that pushed the limits of their ability to land. On the initial leaping trial from the compliant beam squirrels had a leaping error of -12.8 cm ± 4.1 (mean, standard deviation). This is for an animal with an average body length, excluding tail, of approximately 30 cm. Squirrels appear to have a repertoire of landing recovery maneuvers that makes them robust to changes in aerial trajectories relative to their landing perch position.

Optimal control theory suggests a single optimal reference trajectory, and that deviations from that trajectory should be considered errors. But there may be a range of trajectories within which variability should not be considered equivalent to error. Variability within the range of good enough trajectories (Loeb, 2012b) may indicate exploration processes (Van Emmerik & van Wegen, 2002), or the maintenance of redundant leaping and landing solutions that confers robustness and adaptability (Stergiou, Harbourne, & Cavanaugh, 2006).

Figure 3.12

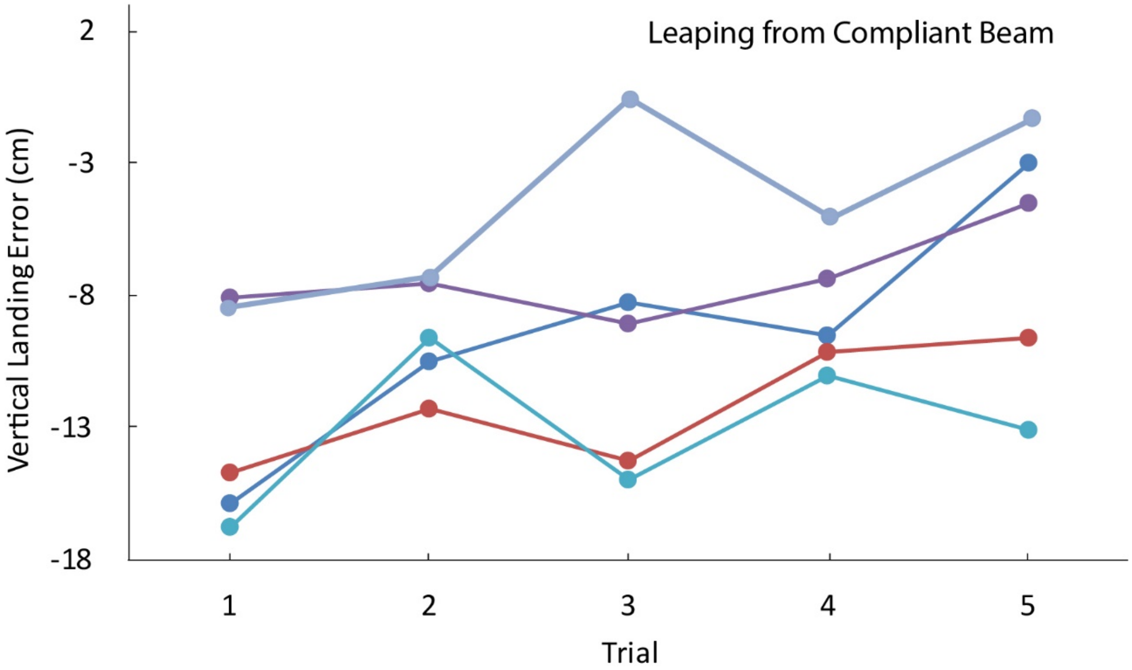

Figure 3.12: Vertical landing error versus trial number for an added difficulty leap from a compliant beam. Each color represents a different individual. Compliance was doubled from 0.014 meters per Newton to 0.03 meters per Newton. Gap length was also reduced from 75 to 65 cm.

It was hypothesized that squirrels learn to reduce landing error with experience leaping from a compliant beam. To test this hypothesis, a repeated-measures one way ANOVA was performed on the leaping errors of the compliant beam trials. Individual differences in landing errors were accounted for by using the repeated measures design. We found a significant effect of trial (p=0.0116), indicating that over five trials squirrels learn to significantly reduce their vertical landing error (Figure 3.13).

Error based learning is likely to play an important role in the performance of leaping from compliant substrates for many animals. This example illustrates the importance of considering cognitive and biomechanical factors of performance simultaneously. Leaping from compliant perches may affect performance of the leap (Gilman et al., 2012) and survival of an leaping animal (Bonser, 1999). But, the rapid learning results seen here in Fox squirrels (Figure 3.13) demonstrate a reduction in leaping error of 16 percent per trial. Within only 5 episodes of leaping from a beam with novel compliance properties, squirrels are capable of significantly altering their motor controller to compensate. Studies of substrate compliance on locomotion performance must account for the possible presence of rapid learning processes and how error-based learning may quickly ameliorate negative consequences.

Figure 3.13

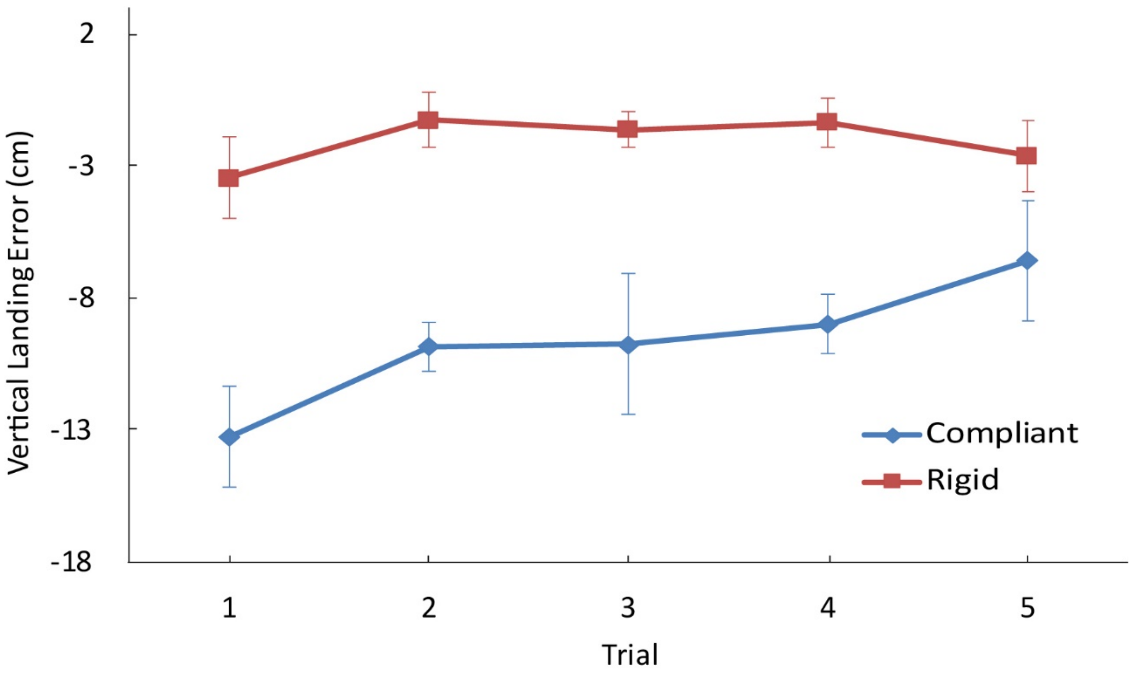

Figure 3.13: Figure shows vertical error vs trial number grouped by compliance level. Red line indicates trials leaping from a rigid beam. Blue line indicates trials leaping from a compliant beam. Error bars indicate the standard deviation of vertical error.

Modeling Squirrels Aerial Phase as a Ballistic Trajectory Suggests Four Determinants of Landing Error

The trajectory of the center of mass was modeled using ballistic trajectory equations. This model assumes that any aerodynamic forces produced during the aerial phase are negligible and the predominant force accelerating the center-of-mass is gravity, g. Thus, the position of the center of mass at any time t during the aerial phase is determined by

$$x_t = x_0 + \dot{x}_0 t$$

$$y_t = y_0 + \dot{y}_0 t + \frac{1}{2} g t^2$$

Where x_0, the initial horizontal position, $\dot{x}_0$, the initial horizontal speed, y_0, the initial vertical position, and $\dot{y}_0$, the initial vertical speed are the determinants of leaping. These initial conditions can also be fully represented by the horizontal and vertical position, the speed, and the angle of the velocity vector: [x_0, y_0, v, θ].

Changes in the four different leaping determinants have different effects on the landing error. The ballistic trajectory model was used to calculate the sensitivity of the landing error with respect to 1, 2, and 5 percent changes in each of these determinants. This sensitivity analysis suggests that to achieve the greatest reduction in landing error with the smallest change in leaping determinant, squirrels should adjust their takeoff speed (Figure 3.14).

There are several important limitations to consider when interpreting this sensitivity analysis: 1) the initial conditions are correlated and cannot be changed independently, 2) there is a manifold of initial conditions that achieve zero-error leap trajectories, and the sensitivity to changes in initial conditions depend on which initial conditions are chosen, and 3) changes to different initial conditions may impose different leaping costs on the squirrel specific to its body structure.

Figure 3.14

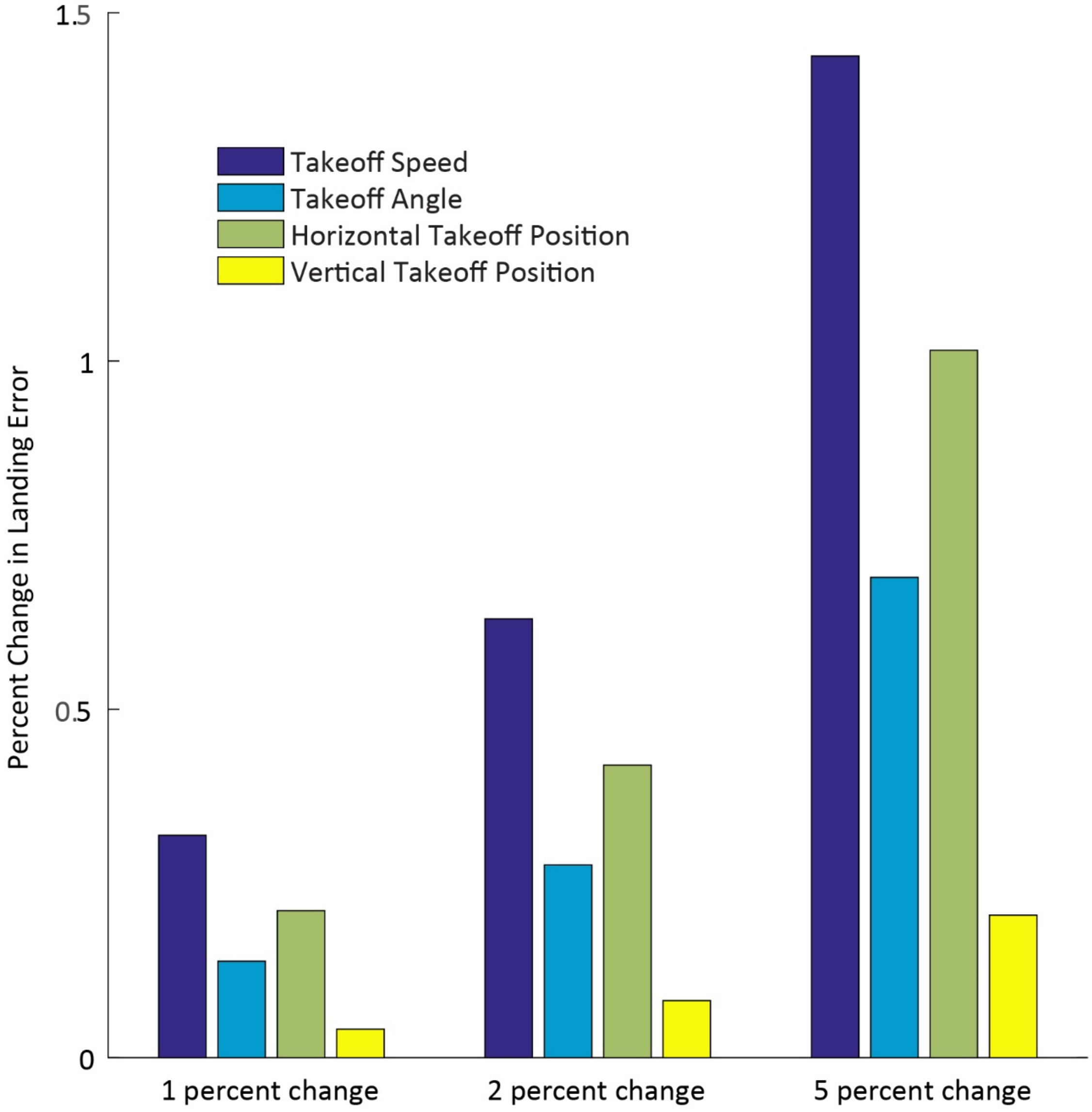

Figure 3.14: Sensitivity of landing error to 1, 2 or 5 percent change in each of the 4 determinants of leaping.

Speed Changes During Learning

Of all four determinants, the only significant change across trials was in takeoff speed. Squirrels increased their speed at the initiation of aerial phase over the five trials for the compliant condition, (F(4,16)=3.38, p=0.03). They increased their speed by 7.1 % (a 14.6 cm/s increase) from the first trial to the fifth trial (Figure 3.15). There was no change in the speed over trials for the rigid condition (p=0.57). No change in the initial angle was found (Figure 3.16). There was no significant difference between the compliant and rigid trials on the initial angle (p=0.246). There was no significant effect of trial on angle for the compliant beam trials (p=0.076) or for the rigid beam trials (p=0.391). There was a significant effect of beam type on horizontal position (p=0.011) and vertical position (p=0.003), but no effect of trial on these leaping determinants (Figures 3.18, 3.19). To account for the apparent differences between individuals, mixed effects models were used that included individual as a random factor.

The biomechanical changes that produced better landing performance over time is primarily increases in takeoff speed. Of the four determinants of leaping identified to produce changes in landing error: takeoff speed, takeoff angle, initial horizontal and initial vertical position, the only significant effect of experience was on speed. However, large variability between squirrels in these determinants suggest individual squirrels are prioritizing parameters of the leap differently. Furthermore, performance did not increase monotonically across trials indicating noise and/or purposeful exploration of the dynamics in the learning process – making identification of *what was learned* challenging. If the squirrel learns an internal representation (Kawato, 1999; Mischiati et al., 2015) of the leaping task, the structure of the representation is unlikely to be embedded in the Cartesian coordinates or typical physical parameters that experimenters find convenient for analysis. So, if squirrels are using an internal model for the task and learning new parameters of that model, those representations likely are entirely different than the determinants of leaping we identified. Although, the physics guarantee that any parameters of an internal model they vary to improve performance must affect the leaping determinants identified.

One approach to investigating how the squirrels represent and control their leap is through Principal Components Analysis (PCA). PCA determines new coordinates, called Principal Components, based on linear combinations of the determinants of leaping. The Principal Components are chosen to parsimoniously describe the variance in the original leaping determinants (Figure 3.19).

Using PCA, it was found that over 95% of the variance in four leaping determinants can be described by just three Principal Components (Figure 3.19). Speed, which is the only significantly changing leaping determinant across trials, is the second largest quantity in the first principal component and the largest quantity in the second principal component. This suggests that instead of reducing errors simply by increasing speed, squirrels may be controlling the task in some other coordinates that represent the task differently. Future work can use these types of dimension reduction techniques to investigate the internal representations used for planning and control of this targeted leaping.

Figure 3.15

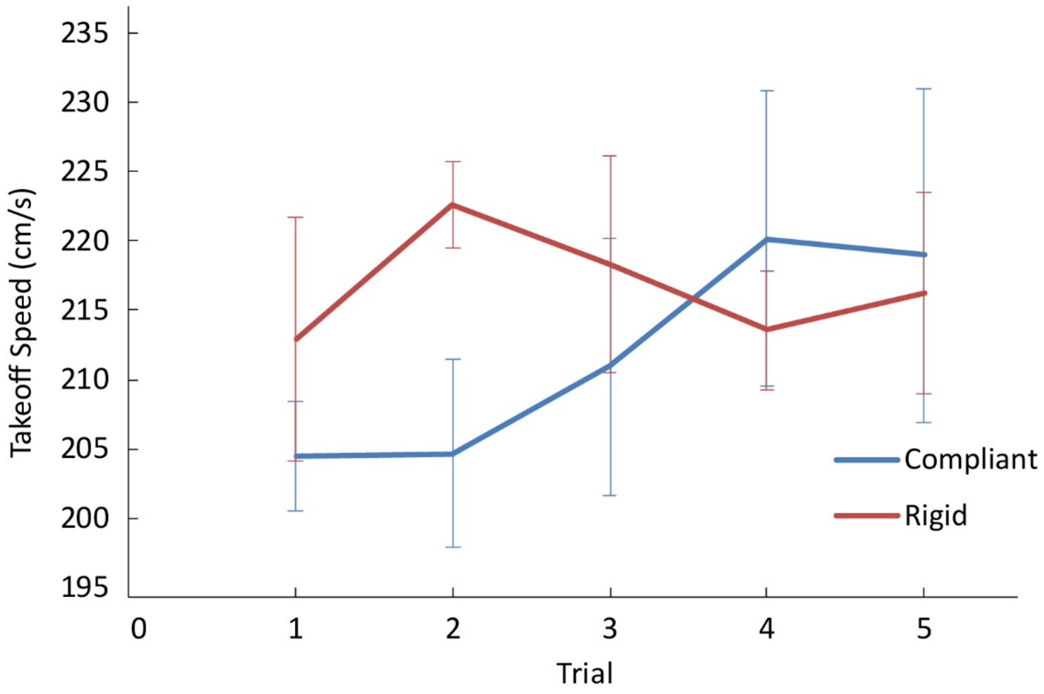

Figure 3.15: Takeoff speed plotted over five trials for both the rigid beam and compliant beam conditions. Error bars show standard error of the mean.

Figure 3.16

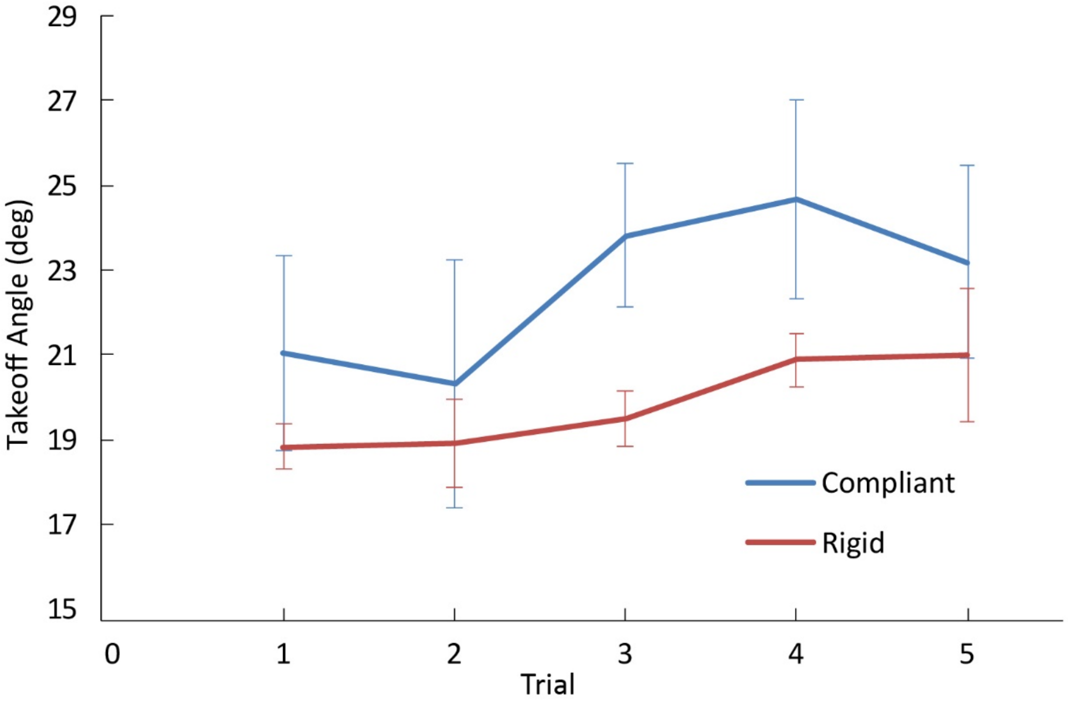

Figure 3.16: Takeoff angle plotted over five trials for both the rigid beam and compliant beam conditions. Error bars show standard error of the mean.

Figure 3.17

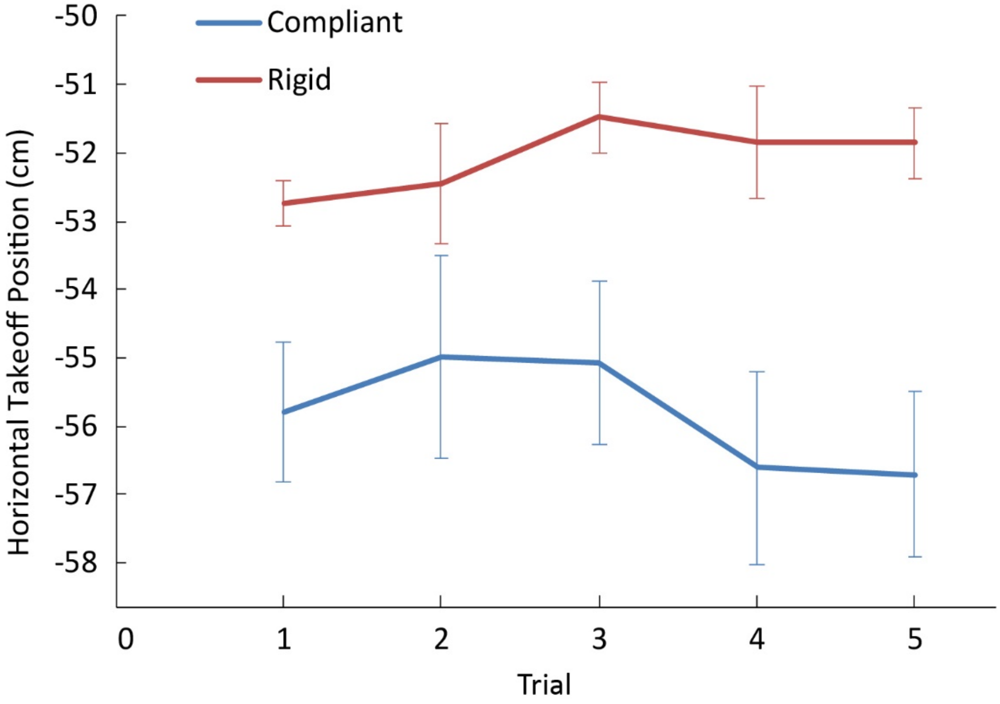

Figure 3.17: Horizontal takeoff position plotted over five trials for both the rigid beam and compliant beam conditions. Error bars show standard error of the mean.

Figure 3.18

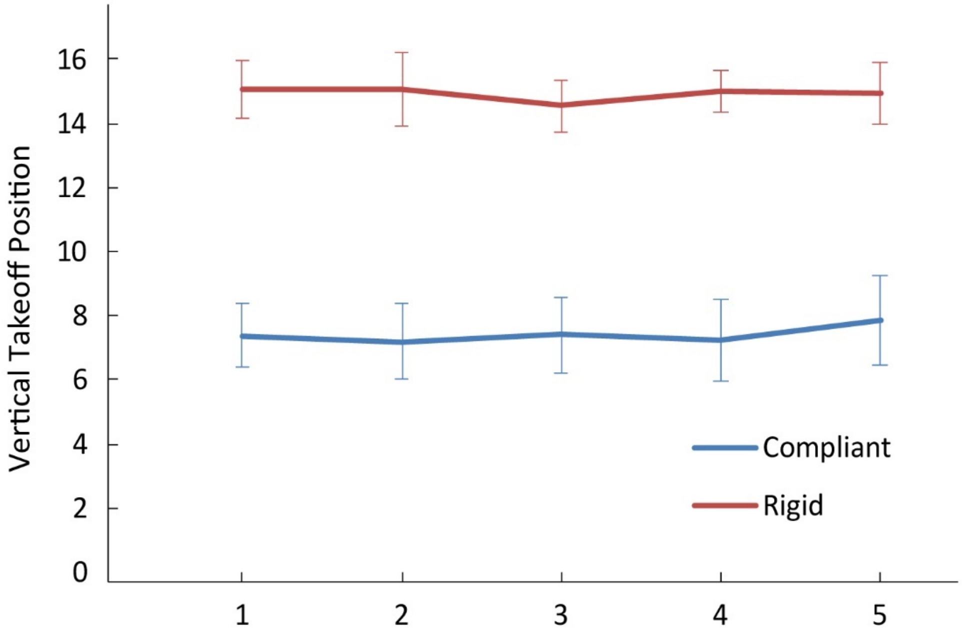

Figure 3.18: Vertical takeoff position plotted over five trials for both the rigid beam and compliant beam conditions. Error bars show standard error of the mean.

Figure 3.19

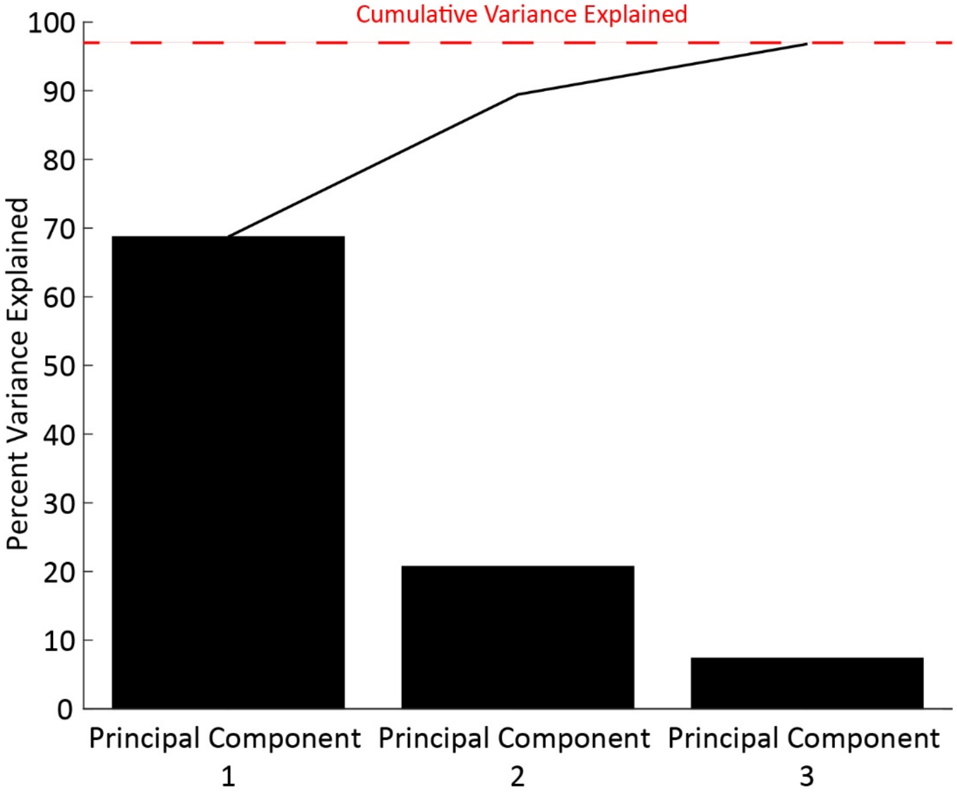

Figure 3.19: Principal component analysis of the leaping variability showed that over 95% of the variation in the four dimensional initial conditions can be explained by three principal components. Principal components are linear combinations of the initial conditions such that each principal component is orthogonal to the others. The principal components are ordered such that the first principal component has the largest possible variance, and the second has the second largest possible variance, and so on.

Individual Differences in Leaping

The five squirrels tested in this experiment exhibited inter-individual variability in their leaping determinants. The four-dimensional variation for all leaping trials and all squirrels is shown in Figure 3.20. Individual effects were evaluated by comparing a model of initial horizontal position that was dependent only on compliance to one that included a random effect of individual. Using the likelihood ratio test, including individual effects led to a model that was a significantly better fit (F(12), $p=1.43x10^{-9}$). Since there was a significant effect of individual in the initial horizontal position, mixed effects models that included individual as a random effect were used to test the effects of rod compliance level on initial conditions (Figures 3.16, 3.17, 3.18, 3.19).

Squirrels are a model system for cognitive biomechanics research into variability and performance because they exhibit high variability between individuals. There are many possible genetic, and developmental causes for variability among conspecifics. A meta-analysis of animal cognitive performance shows that it is affected by age, sex, rearing conditions and previous experience (Thornton & Lukas, 2012). There is personality variation within animals of the same species (Stamps & Groothuis, 2010) that can lead to behavioral variability (Bell, Hankison, & Laskowski, 2009; Bolnick et al., 2003). Cognitive variation can lead to behavioral differences that may cause variation in biomechanical capabilities. And variation in biomechanical capabilities is likely to affect cognitive factors, like decision making processes and risk assessment. This variation is interesting from the perspective of biomechanics and bioinspired robotics because it can clarify different strategies for a given task. But, cognitive biomechanical performance variation has ecological and evolutionary implications as well (Wolf & Weissing, 2010).

Figure 3.20

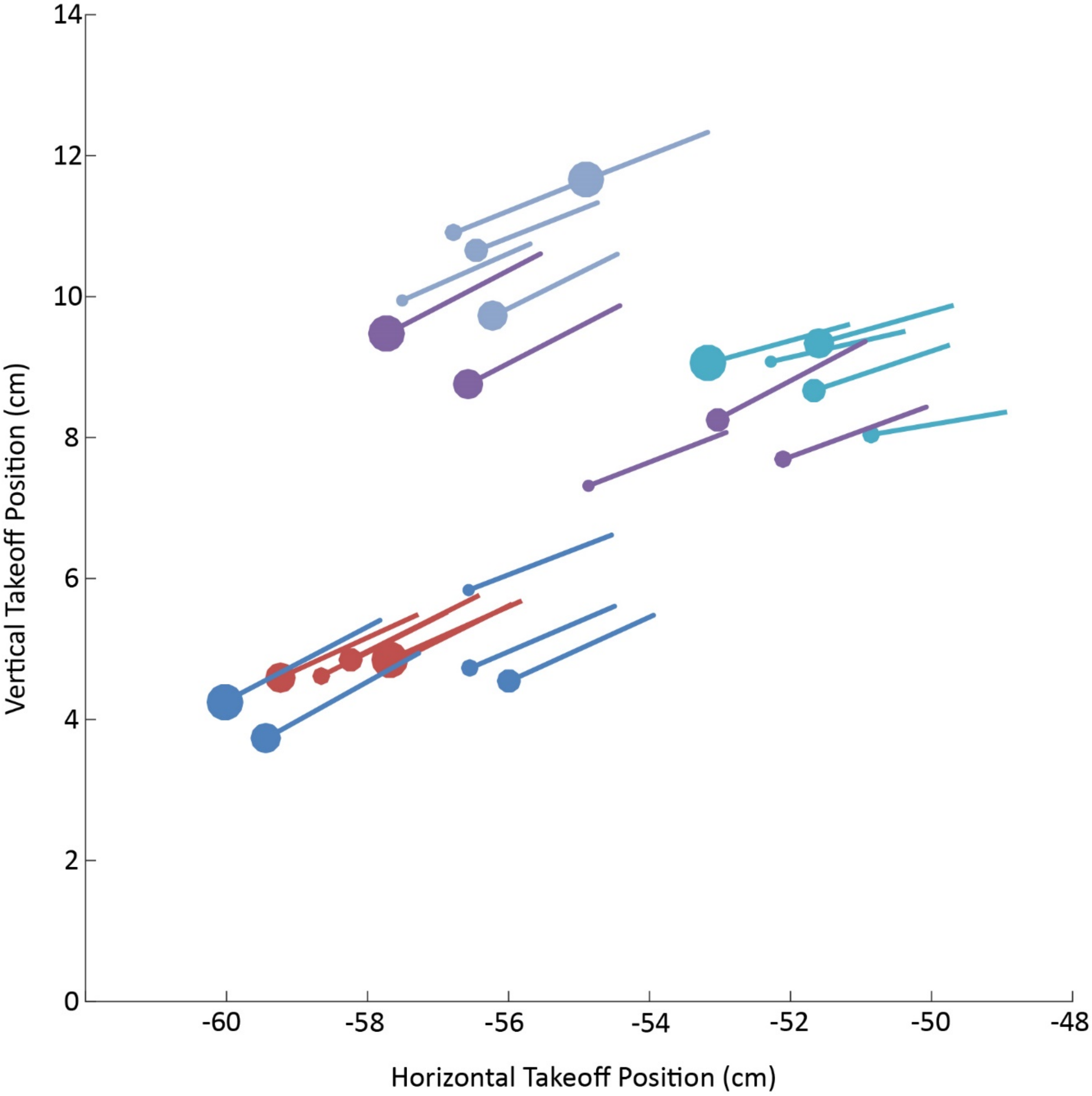

Figure 3.20: Figure showing the 4-dimensional initial condition of each squirrel for each trial. Each color represents a different squirrel leaping from the compliant beam and corresponds to the colors in Figure 3.12. The marker size indicates trial number. The smallest marker is the first trial and the largest is the fifth trial. The length of the line segment from the marker indicates takeoff speed. The angle of the line segment from the marker indicates takeoff angle. The position of the marker on the abscissa indicates the horizontal takeoff position of the squirrel's

COM. The position of the marker on the ordinate represents the vertical takeoff position of the squirrel's COM.

Body Curvature During Aerial Phase Changes During Learning

Squirrels' body curvature during aerial phase is altered by beam type and experience. At the beginning of aerial phase, squirrels have a greater body curvature on rigid beam trials than on complaint beam trials, (F(1,4)=20.57, p=0.01). Squirrels' body curvature at mid-leap changes over five trials for leaps from the compliant beam, but not for leaps from the rigid beam (Figure 24). This is indicated by a beam trial interaction (F(4,16)=8.92, p=0.0005). This result can also be seen by comparing body curvature across phase by trial for the rigid trials (Figure 3.21) versus the compliant trials (Figure 3.22). At the end of aerial phase, body curvature is greater for the compliant beams than the rigid beams (F(1,4)=31.82, p=0.005). Also, at the end of aerial phase, body curvature changes over trials for the compliant beam (F(4,16)=3.29, p=0.04), but not for the rigid beam (p=0.351).

When leaping from the rigid beam, squirrels do not change body curvature over 5 trials (Figure 3.21). Body curvature increases during the first 40% of aerial phase and then decreases to approximately no curvature on landing. Squirrels are likely to be experts at targeted leaping from a rigid substrate across gaps of a few body lengths. Low variability kinematics is characteristic of expert performance (L. Shmuelof, Krakauer, & Mazzoni, 2012).

As squirrels gain experience leaping from the compliant rod they increase their body curvature at mid-leap (Figure 3.22). Changes in body curvature don't affect the trajectory of the COM, and therefore don't affect the landing error as defined here. But changes in body curvature may affect landing dynamics. By increasing the curvature of the body during aerial phase, squirrels may be providing the same impulse required to land, but spreading that impulse out over a longer period as the body lengthens upon landing, producing lower peak landing forces.

Approximations of aerodynamic forces generated by the squirrel's body suggest aerodynamic effects of changing body curvature are not biologically significant to targeted leaping. Lift is approximately 2 orders of magnitude less than body weight. Drag is approximately 3 orders of magnitude less than body weight. Although, future experiments in a wind tunnel that include systematic variation in the posture of the Fox squirrels bushy tail may show significant aerodynamic effects.

In many animals leaping from compliant perches, the peak takeoff forces are higher than the peak landing forces (B Demes et al., 1999; Brigitte Demes et al., 2005). This has been interpreted as a biomechanical strategy to deal with beam compliance and deflection at takeoff. When leaping from a compliant substrate, some of the impulse is depleted to deflect the substrate, so greater peak forces are required to generate the required takeoff velocity to cross a gap (B. Demes, Jungers, Gross, & Fleagle, 1995). But an alternative hypothesis is that animals prefer to reduce peak landing forces when landing on unfamiliar perches. Supporting this is the result that pigeons use a slower approach for the first two landings on a novel perch and then sped up on subsequent trials (Green & Cheng, 1998). Arboreal animals that engage in gap crossing are sensitive to landing forces and employ maneuvers to reduce them (Byrnes et al., 2008). This sensitivity to landing forces may drive learning processes to increase squirrel’s body curvature as they gain experience leaping from a highly compliant beam.

Figure 3.21

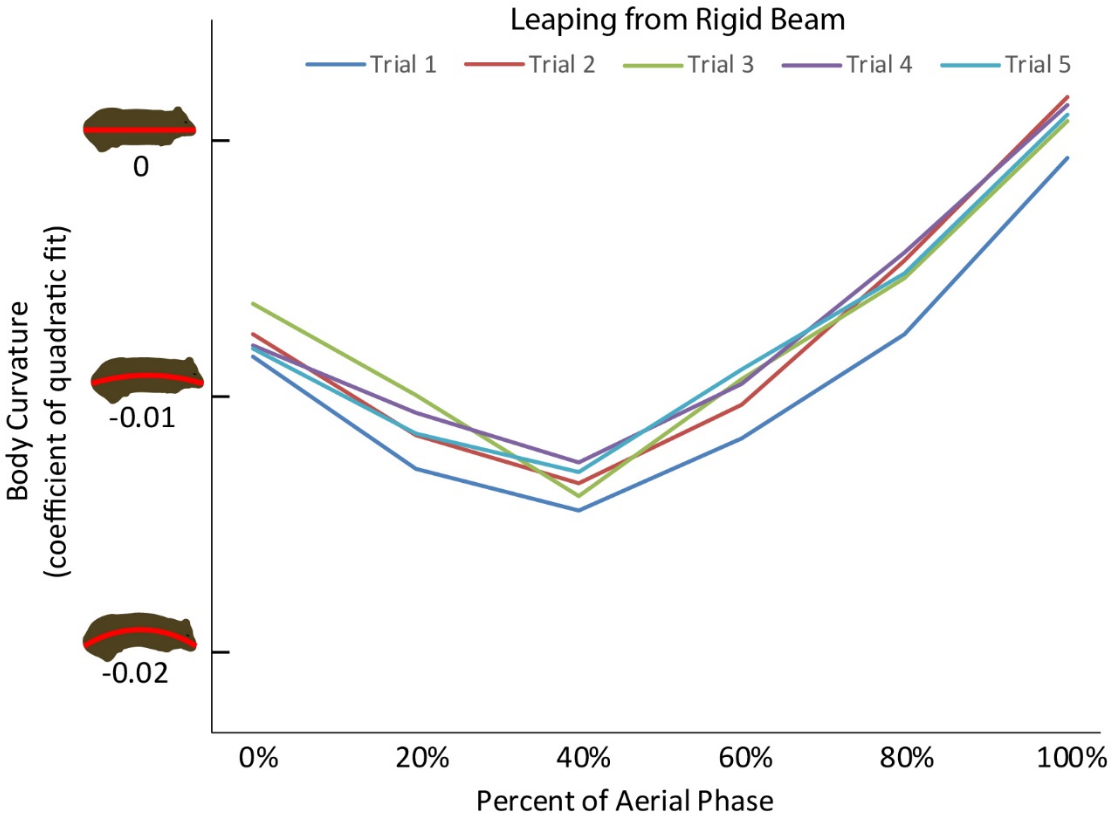

Figure 3.21: Body curvature versus percent aerial phase for leaps from the rigid beam, grouped by trial for all squirrels. Body curvature is quantified by the coefficient of a quadratic function fit to the body curve (see Figure 3.5).

Figure 3.22

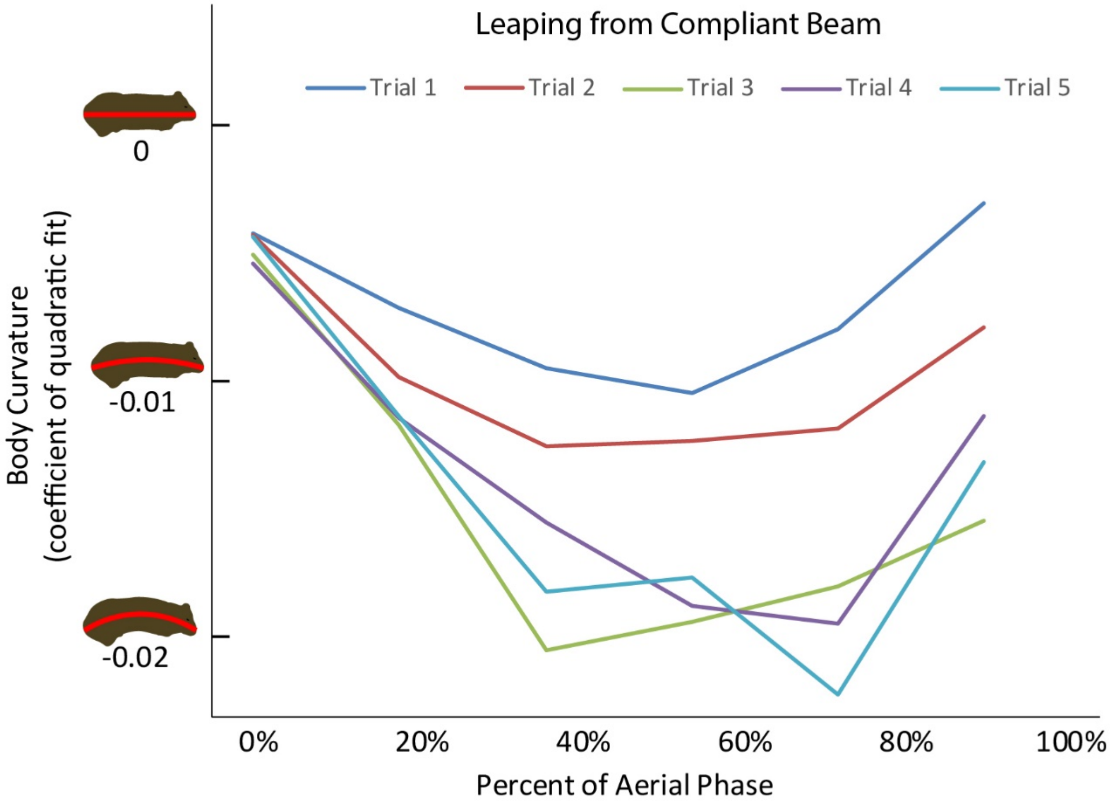

Figure 3.22: Body curvature versus percent aerial phase for leaps from the compliant beam, grouped by trial for all squirrels. Body curvature is quantified by the coefficient of a quadratic function fit to the body curve (see Figure 3.5).

Figure 3.23

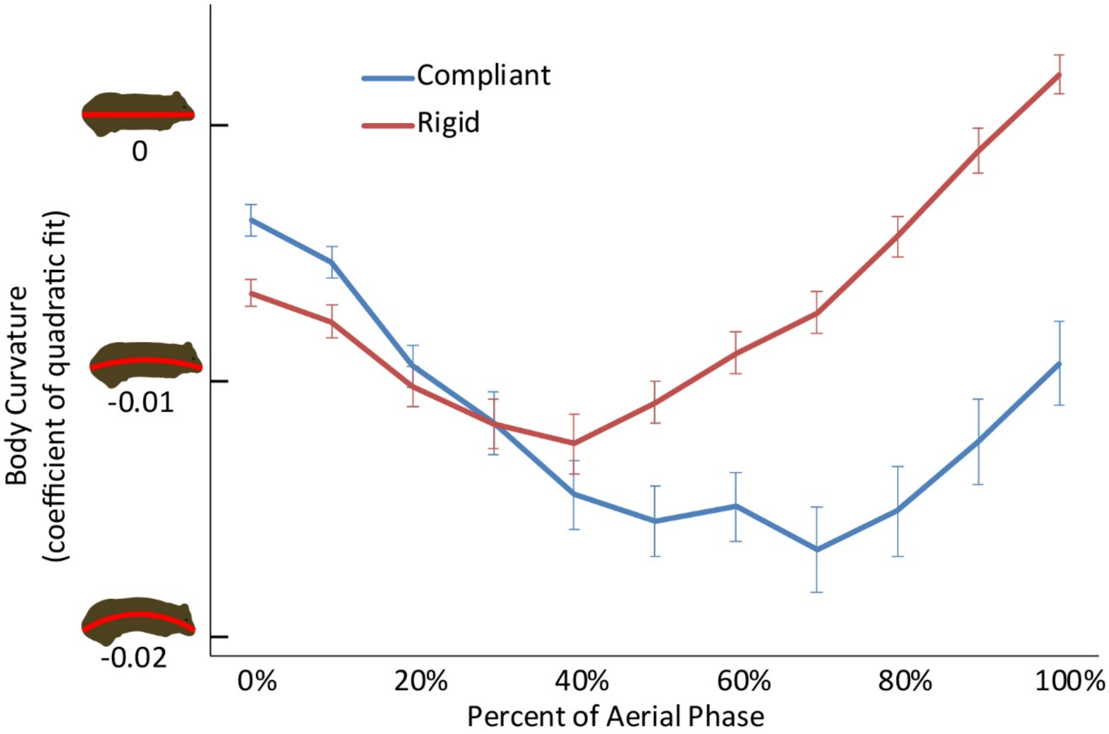

Figure 3.23: Body curvature versus percent of aerial phase. Body curvature is quantified by the coefficient of a quadratic function fit to the body curve (see Figure 3.5). Aerial phase is defined as the time when no feet are in contact with the substrate. Data are grouped by compliance level. Trials in which squirrels leap from the rigid beam are in orange, and trials in which squirrels leap from the compliant beam are in blue. Error bars represent standard error of the mean.

3.4 Conclusions

The primary purpose of this study was to investigate the role of learning processes in a highly dynamic arboreal maneuver using a cognitive biomechanics paradigm. Using free ranging Fox squirrels, the presented task was to leap from a beam across a gap and land on a target perch. It was determined that the introduction of high substrate compliance caused leaping squirrels to produce takeoff conditions which led to landing error. These landing errors were negative, indicating that the extrapolated COM trajectory did not reach the landing perch. Free ranging Fox squirrels demonstrated the ability to reduce these errors through learning. Squirrels achieved performance increases through a process of rapid error-based motor learning, reducing error by an average of 16% per trial over five trials. Error-based learning is likely to play an important role in continually recalibrating the squirrel's leaping control as it navigates its arboreal habitat. This rapid error-based learning process should be accounted for in future experimental designs and interpretations of research on the performance targeted leaping (Bonser, 1999).

Squirrels reduced landing errors by increasing takeoff speed. There were no changes over trials for takeoff angle, horizontal takeoff position or vertical takeoff position. Although, changes in the four takeoff determinants were highly variable. Squirrels also increased their body curvature over multiple trials of leaping from the compliant beam, which may have improved landing dynamics. Future manipulations and modeling may allow the prediction of objectives and costs that drive error-based motor learning for targeted leaping, and determination of the internal representations used for planning and control of this behavior.

Recent work in motor learning has shown that it consists of many distinct processes acting simultaneously (Lior Shmuelof & Krakauer, 2011). In this study, it was demonstrated that rapid error-based motor learning brought the squirrels leaping performance back towards the pre-perturbation baseline accuracy levels in a process of error-based motor learning. The baseline accuracy of the landing likely depends on the difficulty of the task, and by manipulating the difficulty of the leap, different accuracies can be generated, quantifying an accuracy/difficulty tradeoff function. Future experiments will be made to quantify the accuracy/difficulty tradeoff function through error based motor learning at leaps of various difficulty. Furthermore, skill learning will be investigated by determining if large training volumes of targeted leaping from a compliant beam over large spans of time result in upwards shifts in the accuracy/difficulty tradeoff function, elucidating the cognitive biomechanical basis of extending performance beyond baseline levels.

To perform the current study in the field with high experimental precision, a wall apparatus and associated squirrel training methods were developed. Using the steel wall with magnetic affordances allowed precise control over the geometry of the compliant beam, gap geometry and visual backdrop for planar, video-based kinematic data collection in the field. This experimental framework will support future cognitive biomechanics research into decision making, motor control, motor learning and performance of arboreal locomotion.

Chapter 4

Targeted Leaping Using a Wall-Jump Maneuver

4.1 Introduction

Canopy has been defined as "…any aboveground parts of all plant communities, temperate and tropical" (Moffett, 2000). Canopy architecture often has complex spatial arrangements (size, angle, distribution of structures) that provide the navigation substrate for many canopy organisms. Navigating and planning a path through the canopy depends on the gaits and maneuvers possessed by the animal, and the affordances provided by the interaction of those movement skills and the canopy architecture. Specific arboreal capabilities may open new route possibilities. One example, facilitated by dedicated morphology, is hind-foot reversal which allows many arboreal specialists to rotate their hind limbs 180 degrees, grip the trunk of a tree, and descend head-first (Farish A. Jenkins & McClearn, 1984). Other capabilities may rely on behavior, rather than dedicated biomechanical adaptations. For example, canopy ants have the ability for directed aerial descent using a controlled, abdomen-first glide. Using this maneuver they can take a path back to a tree's trunk after falling from its branches (Yanoviak, Dudley, & Kaspari, 2005). Regions of a path through the canopy may be statically stable, such as walking along a branch. Other regions may require highly dynamic movements, like the aerial phase of leaping to a target. This chapter describes a novel, highly dynamic behavior in which an arboreal specialist, the Fox squirrel, generates ground reaction forces mid-leap on a vertically oriented surface.

Choosing among alternative paths depends on the affordances presented by the environment, but may also depend on cognitive factors. For example, if the animal has prioritized speed of movement for escape, this may affect decision making. There are physiological and psychophysical mechanisms for a speed-accuracy tradeoff in decision making (Chittka, Skorupski, & Raine, 2009), which likely factor into performance during rapid navigation of a canopy. Furthermore, the task priorities of the animal and even the perceived affordances may depend on action selection learning. Learning which action to take in a given context doesn't affect the quality of the controller that executes the movement (Lior Shmuelof et al., 2012), but may greatly improve performance. One interesting example of this is the discovery of the Fosbury flop in the sport of high-jumping.

This alternative strategy allowed performance increases that led to a string of new world records in this sport.

An arboreal environment provides many affordances for creating intermittent reaction forces affecting the center of mass trajectory. These impulses could be used for different purposes such as altering velocity to cross long gaps, decreasing speed to reduce the required landing impulses, redirection of the center of mass around an obstacle, re-orientation of the body for landing, and as additional control points to make adjustments after high-speed error-prone initial movements (C. Harris & Wolpert, 1998) or after additional information becomes available. Here, three hypotheses are made regarding the Fox squirrels wall-jumping behavior: 1) gap distance affects the choice to wall jump or not, 2) gap height affects the choice to wall jump or not and 3) gap height affects the impulse generated during the wall-contact phase of the wall jump.

4.2 Methods

Study Subjects and Location

For description of the squirrel population and location See Chapter 3.2, Methods. Six squirrels were recruited and trained from this population. Three females and three males were drawn from the population with a mass that ranged from 750-985 grams.

Apparatus

See Chapter 3.2, Methods for description of the wall apparatus. In this experiment, the leaping platform was changed from a metal beam to a rigid wooden platform. The gap geometry between the leaping platform and the landing perch was manipulated as described subsequently.

Gap geometry was systematically varied by placing the landing perch at eight different prescribed distances and heights relative to the leaping platform. Heights for the landing perch were either level with the leaping platform, 20 cm higher, or 20 cm lower. For the level landing perch, the shortest distance was at 50 cm, the medium distance was 100 cm, and the longest distance was 150 cm. These distances ranged from approximately 1.5 – 5 times body length. The horizontal distance to the high and low perches for each distance was chosen to place them along a line of constant impulse. This means that if the squirrels were to leap to the medium level jump using the minimum impulse, then leaping to high medium or low medium landing perches would require the identical minimum impulse (Figure 4.1).

Figure 4.1

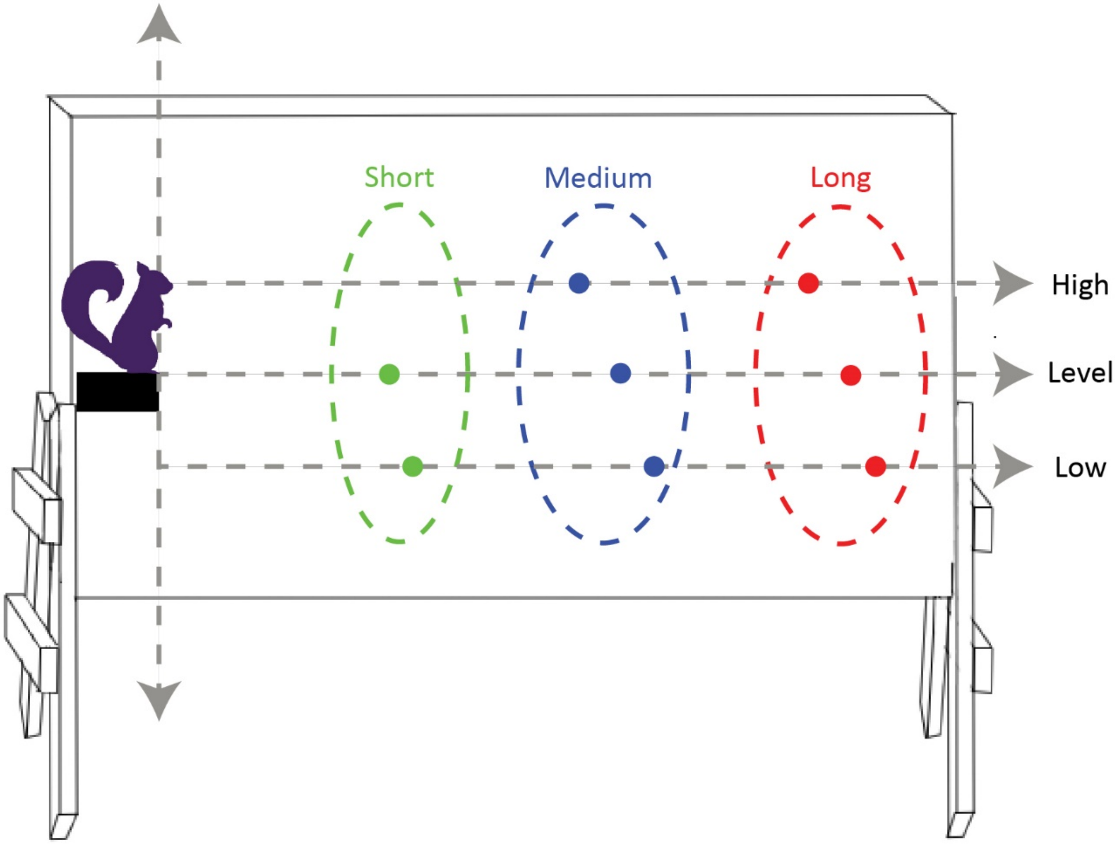

Figure 4.1: Diagram shows the eight different gap geometries that were used. For each trial, the landing perch was placed at either the short, medium or long, and at low, level or high position. For each of the short, medium or long levels, the low, level and high were placed along a constant momentum isocline. Thus, if the squirrels leapt at the optimal angle, it would require the same impulse to jump to the low, level or high perch. Squirrels leapt from a rigid platform. They were freely able to choose a direct leap to the landing perch or to use an intermittent wall-jump maneuver.

Training

Squirrels were habituated to the wall and trained to climb onto the leaping platform as described in Chapter 3.2, Methods.

Once squirrels were habituated to the apparatus, they were trained to leap onto a perch. The perch was initially placed next to the leaping platform, allowing them to step directly onto the landing perch and retrieve a peanut reward from the cup. The landing perch was gradually extended on subsequent leaps until the gap distance reached approximately 50 cm. After squirrels were leaping without hesitation, training was considered complete. This process took approximately 30 minutes for each squirrel.

Testing

Squirrels were presented with a single landing perch placed either at short level, short low, medium high, medium level, medium low, long high, long level, long low in a randomized order. Short high was not used because squirrels were able to reach it directly without leaping. Squirrels then leapt from the jumping platform to the landing perch to receive a peanut. Occasional coaxing from an experimenter by waving a peanut over the landing perch was used to encourage the squirrel to leap. Squirrels were then coaxed to leap back to the start platform for another trial. All trials were continuously recorded by two cameras (GoPro). One camera captured the sagittal plane movement, while another captured the horizontal plane from above. Cameras recorded at 120 Hz and were synchronized using a discrete visual event in each camera view.

Kinematic Analysis

Tracking the center of mass was done using custom software (MATLAB). For Methods on Tracking Center of Mass See Chapter 3.2, Methods.

Horizontal impulse generated off the wall per body mass was calculated from the center-of-mass trajectory, using difference between the horizontal speed after wall contact phase and the horizontal speed before wall contact phase. The probability of wall contact was calculated using the proportion of trials at that gap geometry which used a wall jumping strategy.

Horizontal Impulse

Horizontal impulse was calculated using the center of mass trajectory before and after wall contact phase (Figure 4.2). Horizontal impulse was quantified for each trial at the medium distance and compared across the three perch heights at that distance.

Figure 4.2

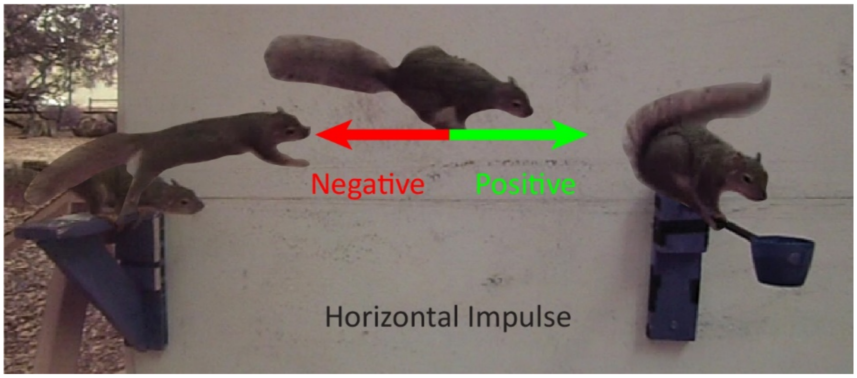

Figure 4.2: Horizontal impulse per body mass was calculated by subtracting the horizontal velocity of the center of mass during the aerial phase before making contact with the wall from the horizontal velocity after all limbs have left the wall, and before contact was made with the perch. Positive horizontal impulse corresponds to an increase in horizontal velocity.

4.3 Results and Discussion

To determine the effects of gap geometry on the proportion of targeted leaps directly to the target versus leaps that used a wall jump, we trained free ranging Fox squirrels to leap to a landing perch placed at eight distinct positions. We obtained 144 leaping trials from six squirrels. A squirrel's choice to use a wall jump maneuver across this range of gap geometry depended solely on the length of the gap and was not affected by height. Squirrels used the wall jump maneuver for medium and long jumps, but rarely for short jumps. Low, level and high perch placement had no effect on the probability of using the wall jump maneuver. The decreased wall jump probability at the medium-high configuration was due solely to one animal. We were unsuccessful at training the squirrels to leap across the long-low gap geometry.

The wall-jumping maneuver used to cross the gap used an intermediate point of contact in the middle of the aerial phase. The squirrels leapt from a takeoff platform, rotating their body along the anteroposterior axis reorienting their legs towards the vertical surface, and generate wall-reaction forces to reorient their center-of-mass trajectory before landing (Figure 4.3 and 4.4). Wall jumping behavior is exhibited by Fox squirrels navigating in the trees, and not just a behavior induced by the apparatus. During the experiments in the grove, we observed many examples of Fox squirrels using wall jumps. For example, squirrels would often use wall jumps off a trunk to change direction during chasing behaviors, and to ascend from one branch to another, using the vertical surface of a large branch as an intermediate contact point. In one extremely dynamic episode, a squirrel used a rapid pattern of wall-jump maneuvers to ascend approximately two meters from the ground into the lower branches of a tree with three trunks.

The ability of small animals to leap as far as larger animals is likely due more to morphological and behavioral adaptations rather than differences in muscle physiology. Muscles used for jumping are faster than other muscles. Maximum jumping height is thought to be independent of size. This invariance is thought to be due to increased relative power in smaller animals, but the fastest muscle fiber types appear to be relatively constant over body sizes. Leaping compensation in smaller animals may be due to elastic storage and return mechanisms, relatively longer hind limbs and alteration of origin and insertion of muscles to improve jump performance (Harris & Steudel, 2002; James, Navas, & Herrel, 2007).

Animals use various maneuvers to cross a discontinuous canopy. Leaping performance is a result of physiological, morphological, behavioral and environmental factors (Bennett, 1990). Arboreal species exhibit better leaping performance than semi-terrestrial species of the same family (Delciellos & Vieira, 2009) and likely have physiological, morphological, and/or behavioral adaptations for leaping. Small gaps in the canopy may be simply crossed by bridging the gap with the animal's body without leaping (Hildebrand, Bramble, Liem, & Wake, 1985). This behavior was observed with Fox squirrels for the short/high gap geometry. Also, different animals have different preparatory approaches to the leap. Primate jumping can be separated into running jumps and standing jumps (Schweizerbart, 2012). Prosimian species swing their tail in dorsiflexion to counter the rotation of the body (Schweizerbart, 2012). Homo sapiens use arm swing maneuver (Schweizerbart, 2012). Many mammalian animals use their tendons, which may be stretched during preparatory crouching to amplify the ground reaction forces during the leg extension (Aerts, 1998). Squirrels also demonstrate a preparatory hop into a crouch. First, they place their front feet, then making a hind-limb hop, bring their hind feet near their front feet while their hind limbs flex into a crouched position immediately prior to leaping. But, to the author's knowledge, this is the only gap crossing behavior to have been characterized in which intermediate substrate reaction forces are generated off a vertical surface that is approximately planar relative to the animal's body size.

Figure 4.3

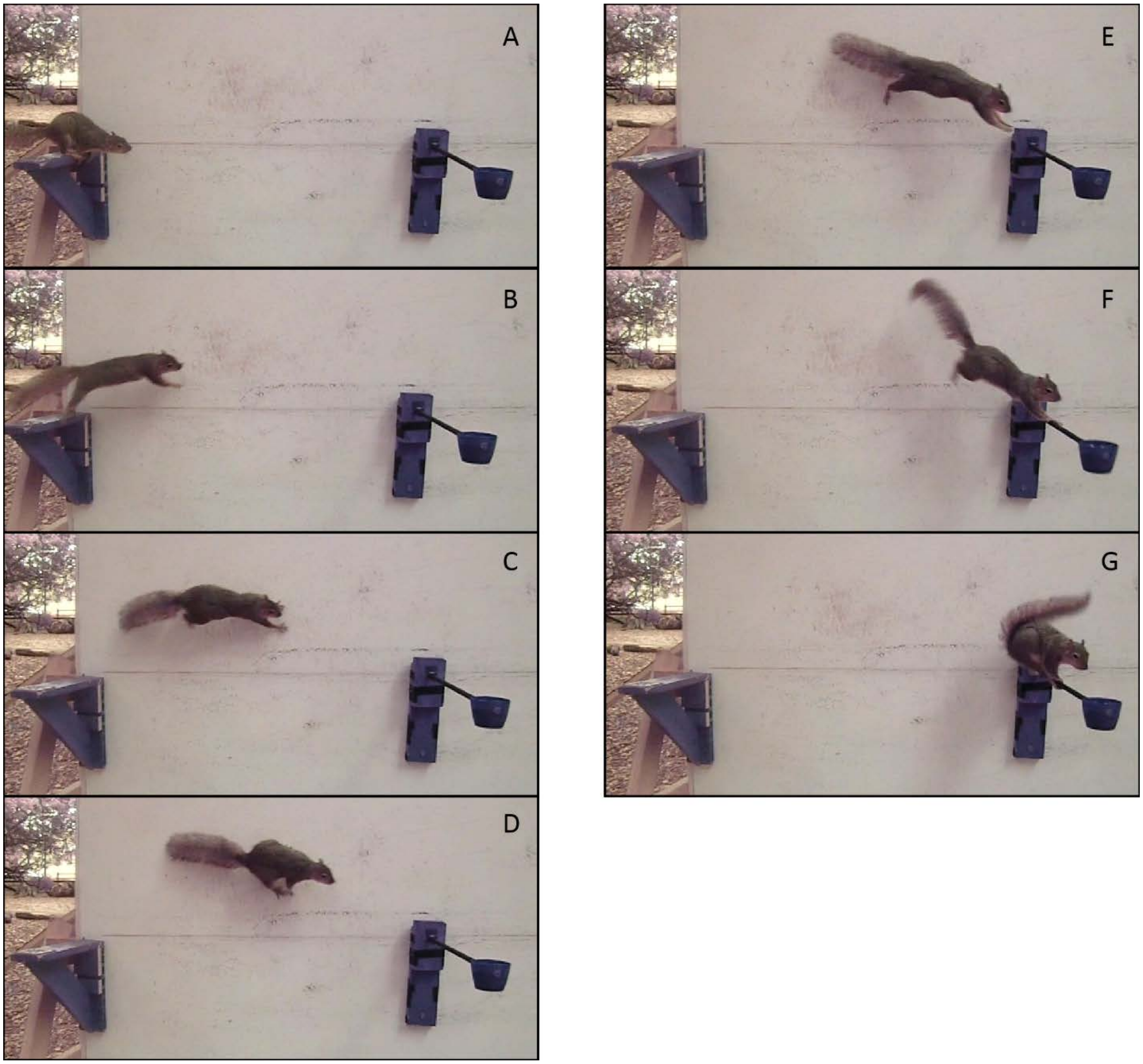

Figure 4.3: Photograph sequence of a squirrel doing a wall-jump in the vertical plane. Synchronous photographs are shown in Figure 4.4.

Figure 4.4

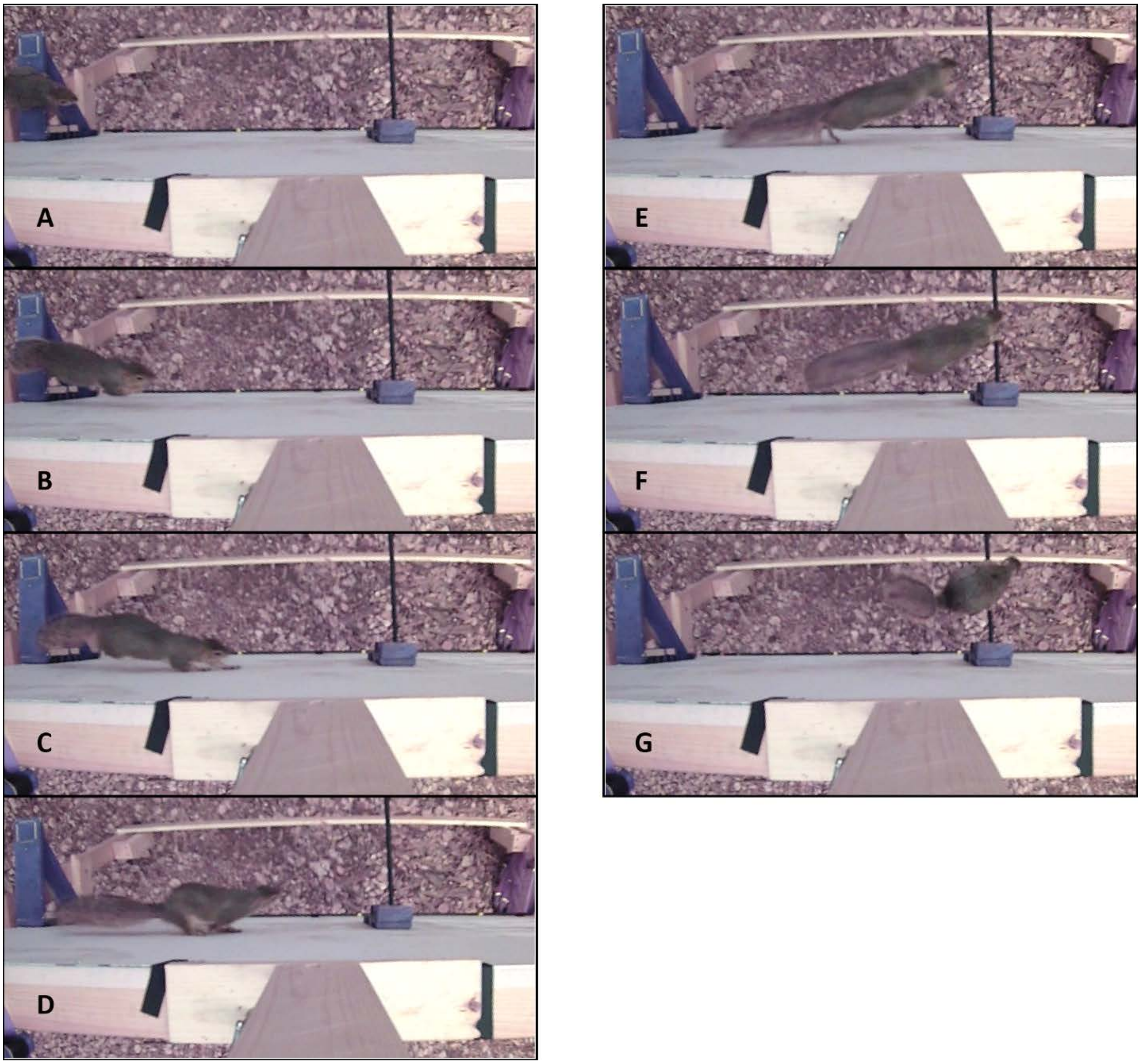

Figure 4.4: Photograph sequence of a squirrel doing a wall jump in the horizontal plane. Synchronous photographs are shown in Figure 4.3.

To test whether squirrels used the wall jump maneuver to gain speed, reduce speed, or if it was neutral with respect to speed, the impulse relative to the animals' mass was calculated. Examining the wall jump maneuvers at the medium distance, it was found that squirrels leaping to the low height perch generally used the wall jump maneuver to decrease horizontal speed (Figure 4.5). When leaping to the level perch, they used the wall jump to decrease speed, or the maneuver was neutral with respect to speed (Figure 4.6). When leaping to the high height perch, they used the wall jump to decrease speed, remain neutral, or increase speed (Figure 4.7).

Fox squirrels predominately used the wall jump maneuver to cross longer gaps of 100 and 150 cm, despite being capable of leaping directly to the perch at these distances. Redundant leaping solutions for this gap crossing task may provide robustness to changes or obstructions. Different gap heights led to different net horizontal impulse during the wall jump. Speed is reduced when wall-jumping to lower perches, and either increased, decreased or neutral for wall-jumping which is consistent with the hypothesis that the wall-jump maneuver is used to control landing speed.

The wall jump maneuver adds an additional contact phase to the targeted leaping behavior. The wall contact phase is distinct from takeoff and landing phase with respect to postural stability. Prior to takeoff, and after landing, squirrels can remain in a statically stable posture. However, during the wall jump phase, squirrels can only generate transient forces to support their bodyweight against gravity. This is similar to the lack of static stability seen in Siberian chipmunks walking along thin branches. These chipmunks use torques to manage angular momentum across multiple strides while never maintaining static stability (Lammers & Gauntner, 2008; Lammers & Zurcher, 2011).

Figure 4.5

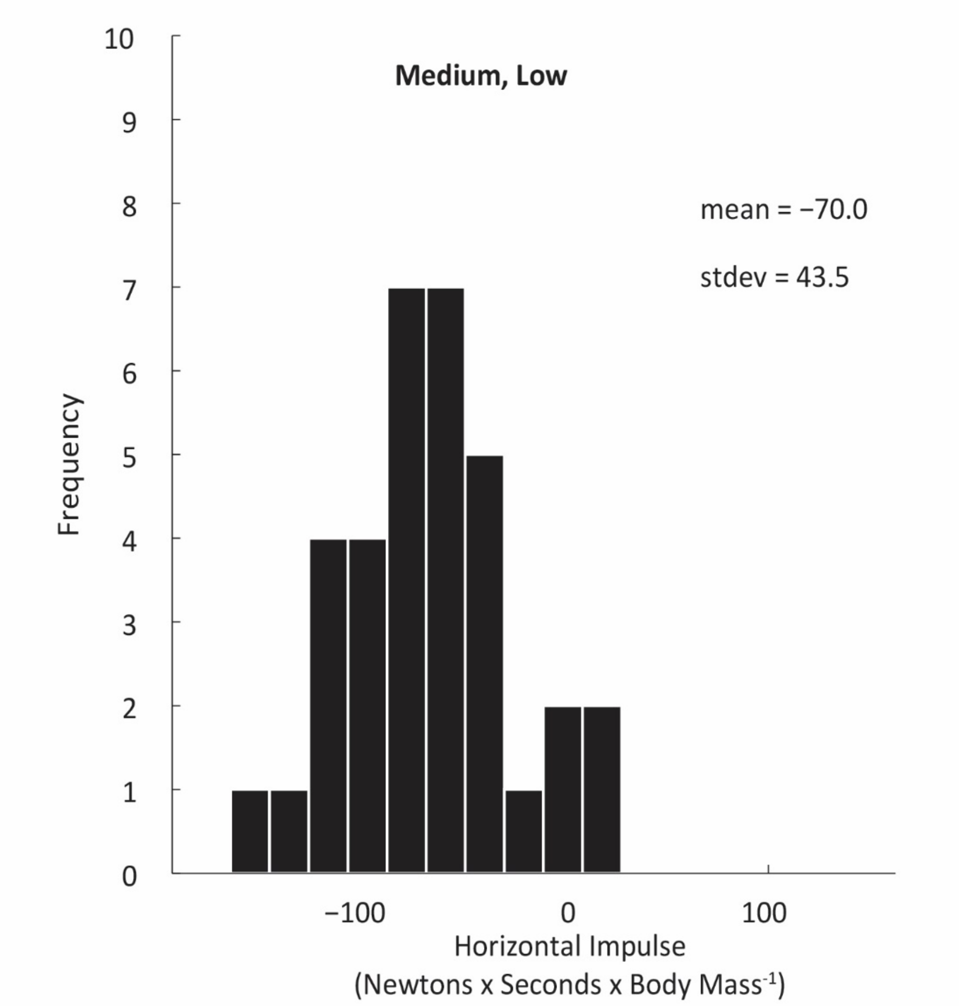

Figure 4.5: Histogram of the horizontal impulse generated off the wall during wall jump maneuvers at the medium length, low height gap geometry. Horizontal impulse was predominately negative indicating using the wall jump to brake when jumping to a lower perch height.

Figure 4.6

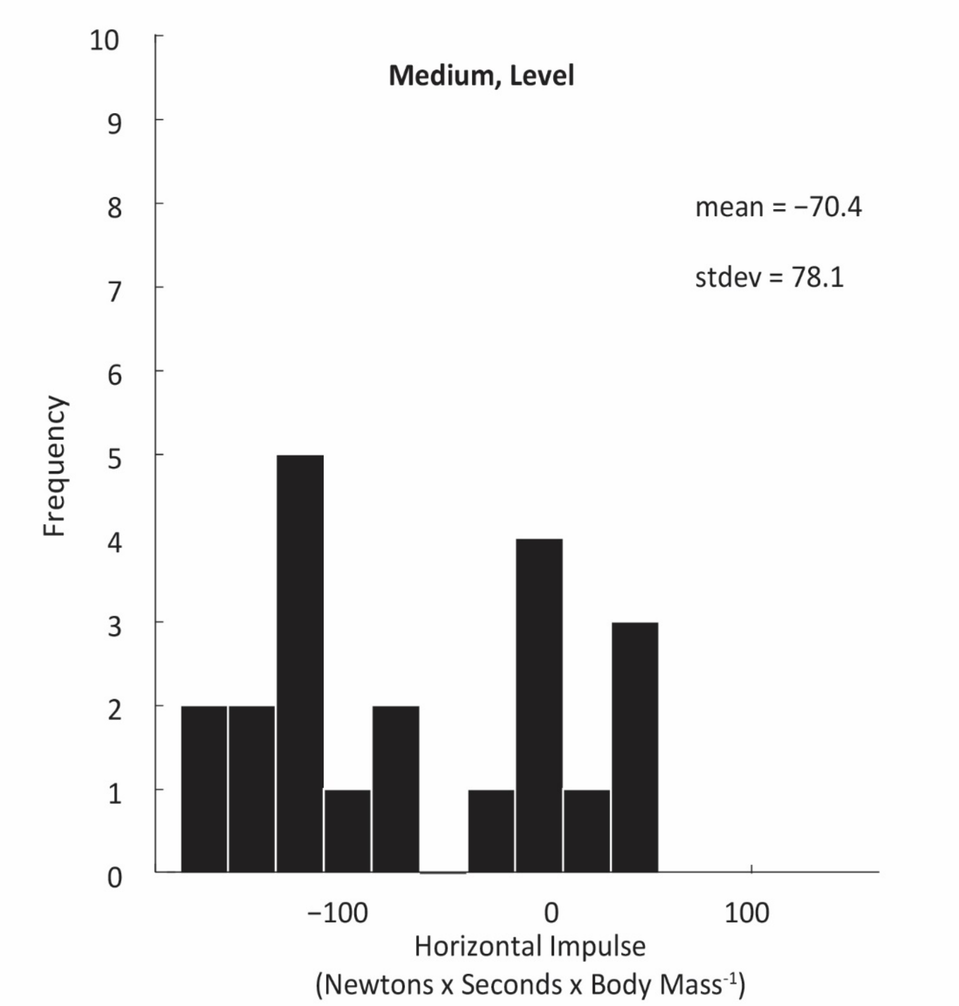

Figure 4.6: Histogram of the horizontal impulse generated off the wall during a wall jump maneuver at medium length, level height. Wall jump impulses were both negative, indicating braking, and neutral.

Figure 4.7

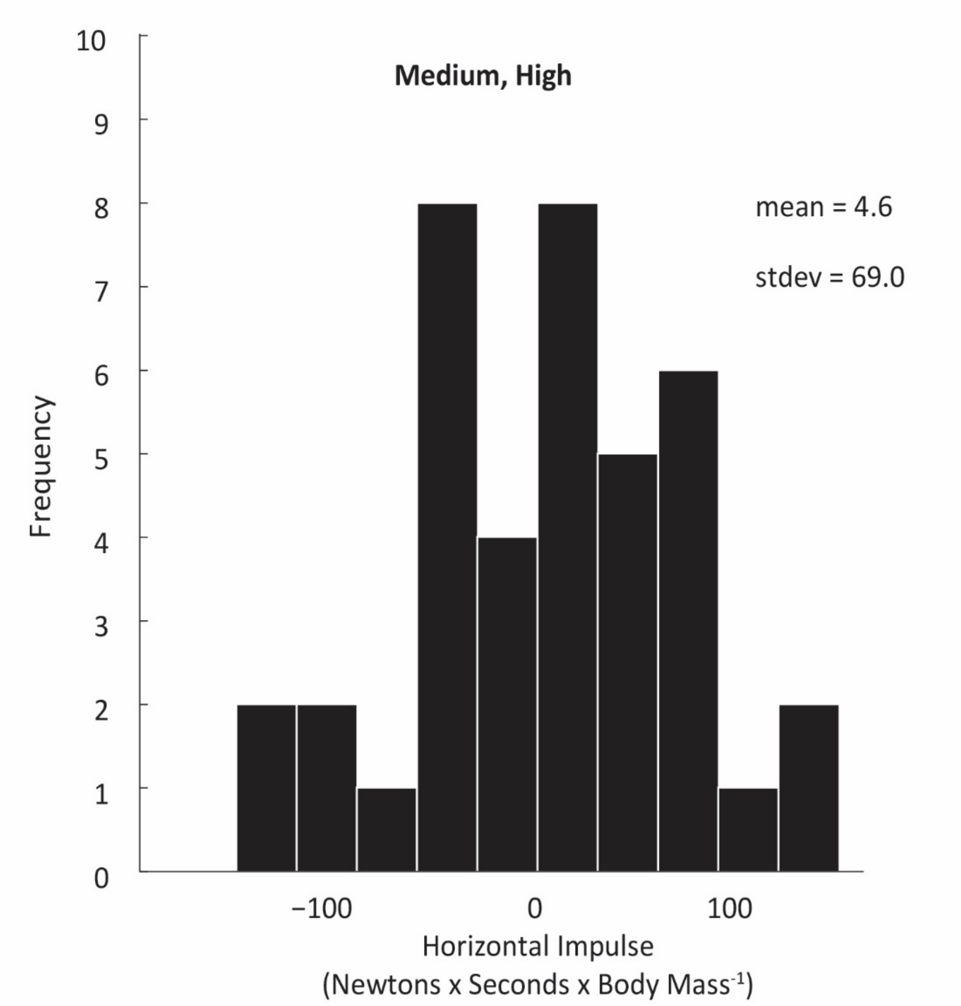

Figure 4.7: Histogram of the horizontal impulse generated off the wall during wall jump maneuvers at the medium length, high height gap geometry. Horizontal impulses were negative, indicating braking, neutral, or positive, indicating accelerating.

4.4 Conclusions

A novel wall jumping maneuver for arboreal gap crossing in fox squirrels is described. The squirrels leapt and rotated their legs towards the wall, then made contact with their feet, creating an additional control point before landing on the target perch.

Height of the gap geometry did not affect the squirrels’ decisions whether or not to employ a wall jump in crossing the gap. But changes in height did affect the horizontal impulse generated during the wall contact phase. Thus, the wall jump is employed at longer distances, but serves different purposes depending on the height of the landing perch.

There are many possible uses for a wall-jump maneuver. Fox squirrels may use the wall-jump phase to manage momentum. Squirrels may use this behavior to increase velocity and cross longer gaps than what is possible for them by leaping directly. Similarly, squirrels may generate positive impulses off the wall to split the work between the leaping phase and the wall jumping phase, reducing the peak forces required to cross a large gap. Alternatively, squirrels may use the wall to brake, to split the work between the wall jumping phase and landing phase, decreasing speed to reduce the peak landing forces. Peak leaping forces from a compliant perch are often greater than peak landing forces (Demes, Fleagle, & Jungers, 1999) which has been interpreted as the animal being risk-averse towards the unknown mechanical properties landing perch (Bonser, 1999). The wall jumping phase may also be used to redirect center of mass velocity based on the orientation of the landing substrate, e.g. to align the squirrel’s anteroposterior axis with the branch

Another hypothesis is that squirrels may be using the reaction forces during the wall jumping phase to correct trajectory errors. Trajectory errors could come from sensory or motor noise (C. Harris & Wolpert, 1998), gap geometry misestimation, errors anticipating the substrate mechanical properties, or dynamic changes in canopy due to wind, etc. These hypotheses are not all mutually exclusive.

Future work involving in-air perturbations of gap geometry (by moving the landing perch) can determine whether wall-jumping is used to control landing speed or to make mid-leap adjustments control for initial leaping errors. Future manipulations may allow us to predict possible creative biomechanical solutions to maneuvering in complex environments. Specifically, how squirrels use impulses during wall jumping and how those may depend on the behavioral and environmental context will be tested.

A bioinspired robot with similar capabilities, Salto, has been constructed inspired by the jumping dynamics of the galago (Haldane, Plecnik, Yim, & Fearing, 2016; Plecnik, Haldane, Yim, & Fearing, 2016). This robot can leap off the ground at high speed, storing energy quickly during the aerial phase, and leaping again off a higher substrate. The analogous squirrel wall jumping ability described here, and future studies of squirrel's decision making can provide inspiration for deciding when, where and how to use wall jumping ability.

Cognitive processes of control and decision making are likely to be closely and bi-directionally coupled with biomechanical capabilities. For example, perception of the environment can be affected by our ability to act within it (Gibson, 1979; W H Warren, 1984; Witt, 2011). For example, parkour athletes trained to leap over walls estimate the absolute height of a wall as shorter than their untrained counterparts (Taylor, Witt, & Sugovic, 2011). The abilities of squirrels to perform a wall jump may cause them to perceive the geometry of the canopy and possible affordances differently than animals that cannot. Differences in perception of the canopy is likely to affect decision making – choosing which sequence of actions to take to reach a goal location. The decisions to wall jump more often is likely to increase their performance level at this maneuver through learning. Future cognitive biomechanics studies may lead to discoveries of interactions between decision making, control, learning that affect biomechanical performance.

Chapter 5

Deciding When to Make a Targeted Leap from a Compliant Branch

5.1 Introduction

Navigation through an arboreal environment presents many decisions that must be made (Green & Cheng, 1998; Hanson, 2016; Schweizerbart, 2012; van Casteren et al., 2013). On the endogenous level, there are the decisions about muscle activation like which combination of muscles to use and which pattern of muscle activation and timing (Diedrichsen, Shadmehr, & Ivry, 2010; Haruno & Wolpert, 2005; W. Li, Todorov, & Pan, 2004; Lena H Ting, 2007). Animals are over-built such that there are many muscles that span a joint or multiple joints and sets of antagonistic muscles that act in opposition. Because of this redundancy, there is an infinite combination of muscle activation patterns that can produce the identical joint moments (Bernstein, 1967). And, animals make use of these different options to adjust muscle activation to fatigue or injury (Enoka & Stuart, 1992; Turpin, Guével, Durand, & Hug, 2011). At a more macro level, there is the choice of what combination of joint angle trajectories to use to produce a desired end effector trajectory. Again, for many end effector trajectories, there is an infinite number of joint angle trajectories for which it can be produced (Bernstein, 1967). Going up another level in the organization of movement, an animal may identify a desired foothold, and thus has a desired position for an end effector as well as a desired time it chooses that end effector to reach that position. There are an infinite number of spatiotemporal trajectories for the end effector that satisfy the desired foot placement constraint. An analogous situation occurs at the level of producing substrate reaction forces. For example, if an animal is running, then during its stride period it must produce vertical ground reaction forces to create an impulse that satisfies the following constraint to counter the impulse generated by its mass under gravity. There are infinite number of different vertical reaction force combinations the animal may choose to create the required net impulse. This redundancy exists at the level of whole body trajectories. To get from point A to point B, there are an infinite number of paths. Selecting a single movement among the infinite possibilities is called the degrees of freedom problem (Bernstein, 1967).

The degrees of freedom problem is exacerbated in the complex three-dimensional terrain that includes the stems of bushes and branches of trees, and the gaits and maneuvers that animals possess which create affordances to navigate that terrain. While running on flat ground also provides infinite paths to take, the path selection degrees of freedom problem may be solved simply. For example, an animal may choose to follow a heuristic such as place the foot a set angle in front of the body every time and produce muscle activation patterns on each step such that the body moves like a spring-mass system (Blickhan, 1989). Of course, the real world isn't completely flat, and the ground properties are not completely homogenous, and parameters of gait must be adjusted, and morphology exploited to successfully locomote – giving rise to the more recently focused research area of terradynamics (Aguilar et al., 2016). But, following a course through the arboreal environment requires rapid switching between gaits and maneuvers. Animals must make many choices to create a sequence of movements that take advantage of the network of three-dimensional affordances. How animals exploit their cognitive and biomechanical machinery to choose a single path out of the infinite possibilities in the arboreal environment is unknown.

Researchers have approached the problem of how animals choose a unique movement in two principal ways: 1) animals may reduce the space of movement possibilities by constraining their degrees of freedom, following a heuristic that tends to produce success at the task (Chapman, 1968); 2) animals may choose an optimal movement that is better than all other movements with respect to some objective function that reflects the priorities of the task (Diedrichsen et al., 2010).

There are many models of specific movements that successfully employ the first method, reduction of the movement possibility space *via* constraints, to explain movement choice. One of the early models of movement choice *via* constraints comes from baseball (Chapman, 1968). The task of an outfielder is to catch a fly-ball. The task can be solved by constraining a visual parameter directly to locomotion. Specifically, if the outfielder moves forward or backward at the only velocity that leads to cancellation of the apparent vertical velocity of the ball on an image plane, then the player and the ball are constrained to a path of interception. This heuristic called optical acceleration cancellation, and extensions to 3D space (McBeath, Shaffer, & Kaiser, 1995; McLeod, Reed, & Dienes, 2006) have been tested under virtual reality environments (Fink, Foo, & Warren, 2009). While a constraint type model, and an optimization type model give the same beginning and end-point predictions, only the heuristic constraint correctly predicts the path to the catch. A similar model of interception is used in predicting predator prey interactions. By moving at an acute angle to prey, a predator can hold the visual angular acceleration of the prey constant and guarantee interception (Mischiati et al., 2015). Models of these tasks may have important implications in possible robot control algorithms for reaching (Mistry, Theodorou, Schaal, & Kawato, 2013), and walking (Griffin & Grizzle, 2016)s. Another example of constraining degrees of freedom can be seen in coupled oscillator models. In coordination between contralateral hands, a group of tasks often called bimanual coordination, there is an especially interesting example that imposes a coupled oscillator constraint based a potential energy landscape of the relative phase possibilities (Haken, Kelso, & Bunz, 1985). The task is to wag two index fingers. It was found that there were only two stable phase relationships, in-phase and anti-phase. Also, the stability of the anti-phase coordination pattern exhibited a bifurcation, transitioning from stable to unstable at high frequencies. This example has been extended to other dynamical systems based models of coordination like behavioral dynamics (William H Warren & Fajen, 2004) and dynamic primitives (Hogan & Sternad, 2012). These examples of body/environment coordination and kinematic coordination are a counterpoint to the optimal control literature, but there are also emerging examples of models of muscle coordination constraints.

One of the primary tasks of optimal motor control is to determine the objective function animals may use to determine their movement. Objective functions may consist of a combination of positive and negative effects of movement that are relevant to how the animal completes the task. One of the earlier hypotheses of optimal control of animal movement comes from human arm reaching. The objective function is hypothesized to penalize deviations from movement smoothness. To do this, researchers proposed that humans use arm reaching movements that minimize jerk, (the derivative of acceleration) (Flash & Hogan, 1985). This model predicts the time series for position and velocity of the hand during the task of reaching to a target. Further optimal control models of arm reaching have proposed an objective function that maximizes accuracy by choosing hand trajectories that minimize end-point variance (Wolpert & Ghahramani, 2000). These models have been successful in predicting many arm reaching datasets (Todorov, 2004; Wolpert, Diedrichsen, & Flanagan, 2011). Another clever study examined how optimal control may predict the step frequency chosen by human walking subjects. Humans choose a step frequency that appears to minimize their cost of transport. To test this hypothesis, experimenters altered the relationship between the metabolic cost and step frequency by using a prosthetic device to introduce a frequency dependent penalty and measure the cost using indirect calorimetry. They found that the subjects adjusted their step frequency to walk at the new metabolic minimum (Selinger, O'Connor, Wong, & Donelan, 2015). Although most attempts at modeling movement choice use either a dimension constraint approach or optimal control approach, these two approaches are not necessarily mutually exclusive.

Optimal control and dimension constraint may be combined to model animal motor control. A templates and anchors framework (Full & Koditschek, 1999) suggests that animal movement may be constrained to lie on lower dimensional dynamics. But those lower dimensional dynamics may then be used to plan movements from an optimal control framework.

Here, contributions to an arboreal animal's objective function for the task of targeted leaping are considered. It was previously shown that compliance of the substrate a Fox squirrel is leaping from can lead to increased landing errors. Also, larger gap sizes lead to the adoption of the wall jump maneuver, utilizing an additional control point before reaching the landing perch. Based on this previous work, we hypothesize that, when deciding where to leap off a branch, squirrels will consider a tradeoff between gap size and compliance. Branches can be considered as cantilevered structures, supported on one end by a trunk, or larger branch. Thus, as a squirrel travels from proximal to distal positions on the branch the compliance of the branch will increase. Also, depending on the position of the leaping target, the gap that must be leapt across will decrease. So, it was hypothesized that as the squirrel is using a branch and a leaping maneuver to cross a gap, they will choose a leaping point that balances a gap-size/compliance tradeoff. This tradeoff is illustrated in Figure 5.1.

Figure 5.1

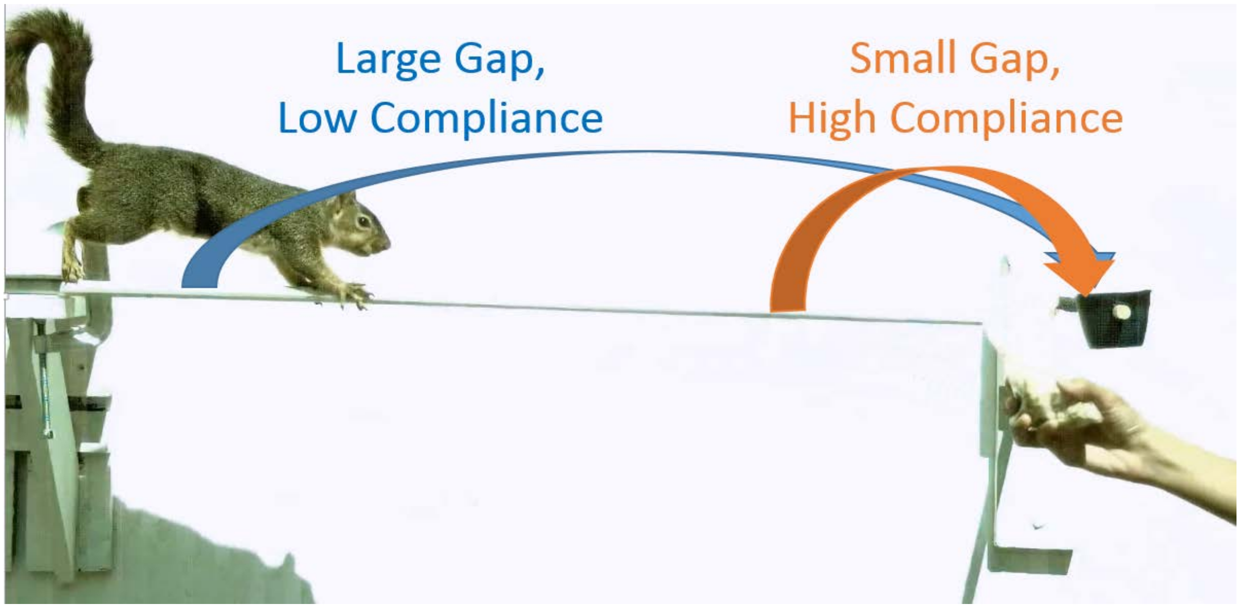

Figure 5.1: Photograph with cartoon overlay illustrates the tradeoff between gap distance and beam compliance when choosing where to leap from on a cantilevered branch. As the animal moves further out on the branch the compliance increases proportionally to distance to third degree, but simultaneously gap distance decreases. Jumping near the base of the branch allows leaping from a point of low compliance, but necessitates leaping across a large gap. Leaping from the end of a branch requires the squirrel to leap from a place of high compliance, but only across a small gap distance.

5.2 Methods

Study Subjects and Location

For description of the field site and the animal population, see Chapter 3.2, Methods.

Ten squirrels were drawn from the population with a mass of 750-985 g. Squirrels were trained with peanuts to perform leaps from a compliant beam onto a landing perch. Nintey-seven trials were obtained.

Apparatus

For description of the wall apparatus, see Chapter 3.2, Methods.

A gap of 100 cm was created between a rigid support structure and a landing perch. Three rods with different compliance properties were manufactured. One of the three compliant rods was mounted to a rigid support and cantilevered 90 cm into the gap (Figure 5.2).

Figure 5.2

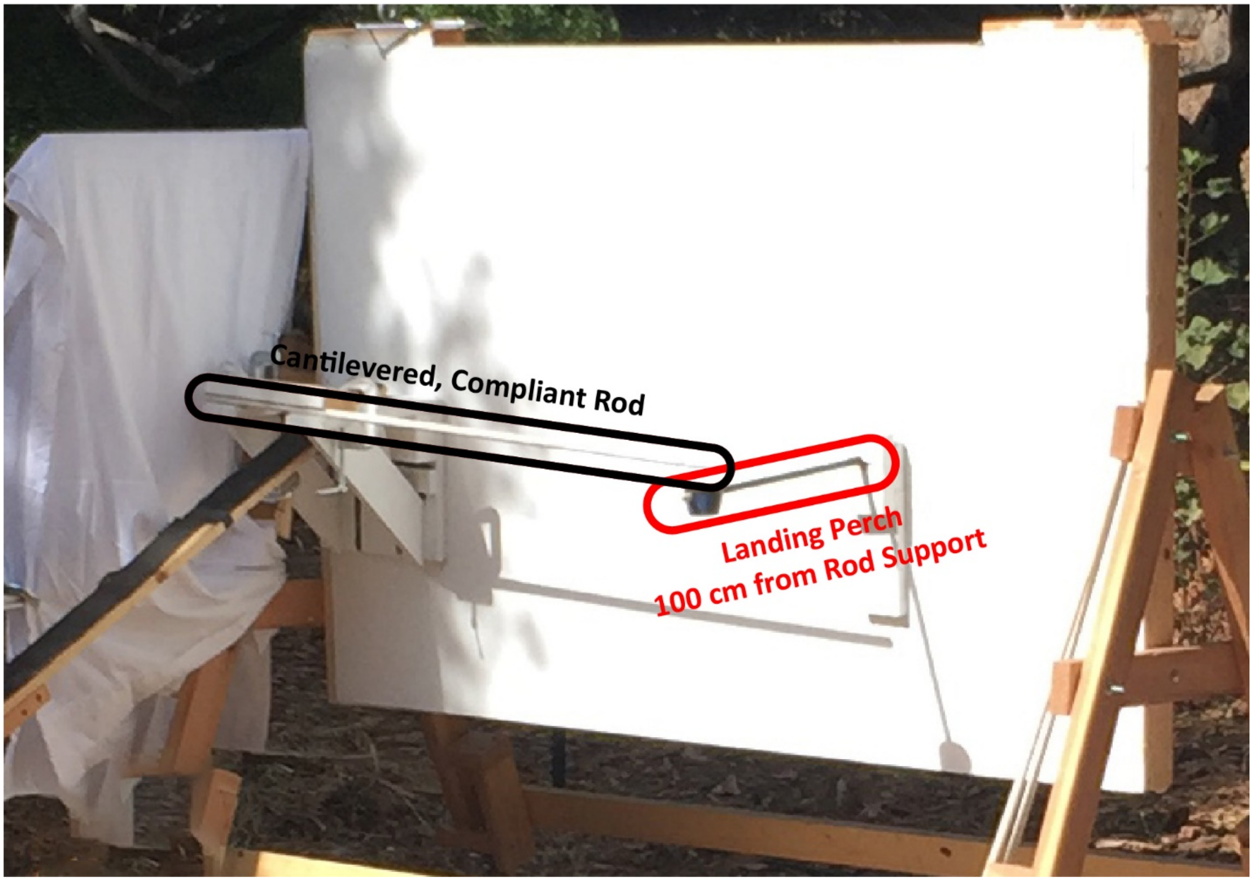

Figure 5.2: Photograph of the wall, branch and perch set up in the field. The rod is cantilevered 90 cm beyond its support. The landing perch is positioned 100 cm from the rod support.

Video recordings of each gap crossing trials were recorded with two synchronized, high speed cameras (Vision Research Inc., Wayne, NJ). One camera was placed to record kinematics in the sagittal plane, and another to record kinematics in the frontal plane (Figure 5.3). Cameras were frame synchronized in a master/slave setup using Phantom's IRIG device.

Figure 5.3

Figure 5.3: Photograph illustrating placement of two high speed cameras. Two synchronized phantom V10.0 cameras were placed to collect movement of the animal in the frontal plane and the sagittal plane.

Manufacturing and Testing Compliant Rods

We manufactured rods with three different levels of compliance: low compliance, medium compliance and high compliance. Rods consisted of 110 cm acetyl tubes wrapped in athletic tape. Their outward appearance was identical with respect to diameter, and surface material. Internal materials were either nothing (low compliance), an additional acetyl rod (medium compliance), or a brass rod (high compliance). These different internal materials gave the rods different compliance properties (Figure 5.4).

To test the compliance properties of each rod, the rod was mounted into the rod support and weights were hung to measure force/displacement properties at five different points along the length of the rod. Specifically, weights of 0, 200, 400, 600, 800, and 1000 grams were hung at points 0, 10, 30, 50 and 70 cm along the length of the rod. Pictures of each equilibrium position were taken, and vertical rod displacement was calculated using ImageJ software. A standard cantilevered-beam deflection model (Beer et al., 1972) was fit to the data for each beam (Figure 5.5).

Figure 5.4

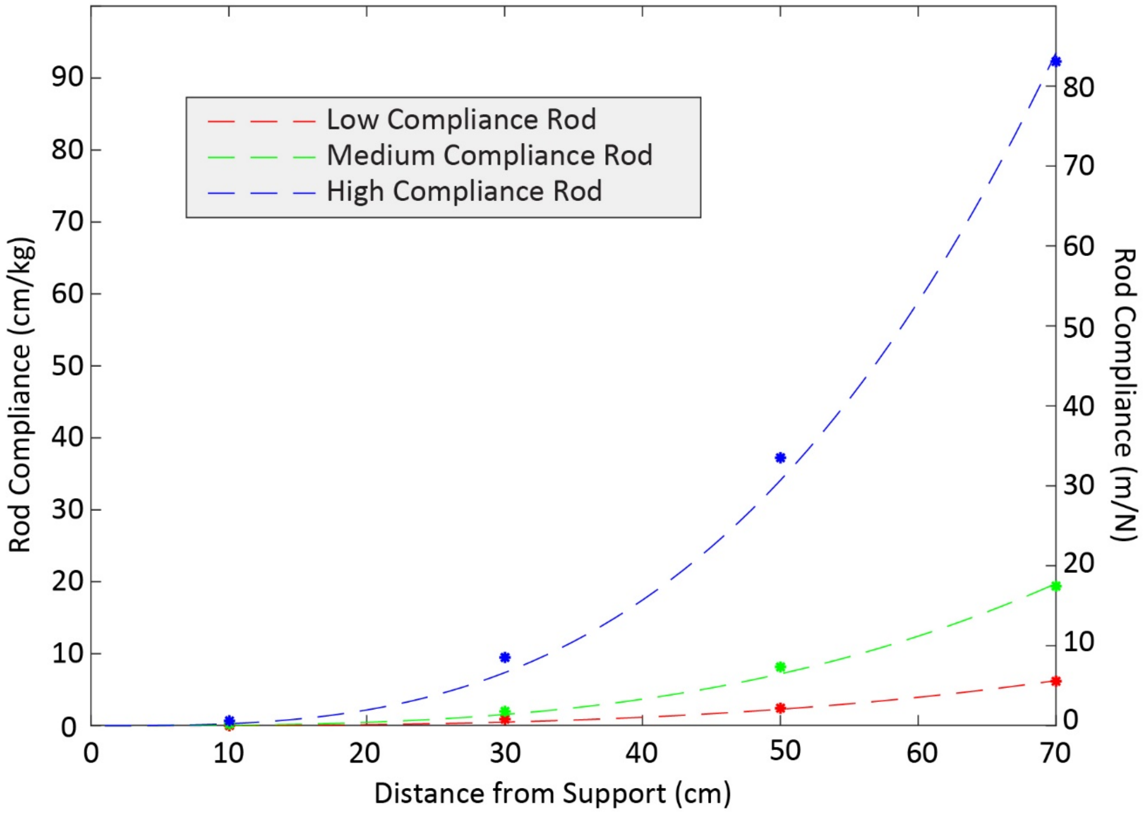

Figure 5.4: Rod compliance as a function of distance for three different rods. Low compliance is shown in red, medium compliance in green and high compliance in blue. For each rod, a standard beam compliance model was fitted, (Beer et al., 1972), and displayed with the dashed lines.

Training

Squirrels were habituated to the wall and trained to climb onto the leaping platform as described in Chapter 3.2, Methods.

Once squirrels were habituated to the apparatus, they were trained to leap onto a perch. The perch was initially placed next to the leaping platform, allowing them to step directly onto the landing perch and retrieve a peanut reward from the cup. The landing perch was gradually extended on subsequent trials. As the gap was extended during training, the compliant rod rested on the landing perch, thus was supported at both ends. Once the squirrel would cross the length of the rod to the landing perch it was considered trained. This process took approximately 15 minutes for each squirrel.

Testing

After training was completed, squirrels were coaxed to navigate the compliant beam and leap across the gap by placing a peanut into the cup at the end of the landing perch. Then they were coaxed back to the starting platform with another peanut, and were given small peanut pieces *ad libitum* until the videos from each of the cameras were transferred to the computer. Squirrels were presented with different compliant beams in a randomized order.

Center-of-mass and Landing Error Analysis

We used a standardized method to estimate the center of mass (COM) position in each video frame of a squirrel's jump (Figure 3.5). First, the rostrum of the squirrel and the base of the tail were hand-tracked in a custom MATLAB program. The program fit a line between these two points (anterior-posterior line), which was then bisected by a line which represents the transverse plane of the squirrel's body. On the transverse line, the points intersecting the dorsal and ventral sides of the animal were then tracked. A line segment (dorsal-ventral line) connected the two points, and the midpoint was found. This dorsal-ventral midpoint was then translated to the origin, with all other features also translated respective to it. All features were then rotated around the origin such that the anterior-posterior line was parallel to the x-axis of the coordinate plane. A quadratic function was fit using the anterior point, dorsal-ventral midpoint, and posterior point. The curve of the squirrel's body was recorded as the coefficient of the quadratic fit. More negative coefficients represented a greater arching of the squirrel's back. The center of mass was designated as the point where 60% of the total length of the fitted quadratic line lay from the anterior point. This value of 60% was determined by balancing a squirrel specimen on a knife edge that had been frozen in a leaping posture. Finally, all estimated features were then translated and rotated to the original positions in the frame, along with the newly calculated features. The center of mass point was then recorded according to its true position in the image frame. (Figure 3.5)

Using the tracked COM trajectory over the entire aerial phase, a quadratic formula was fit to estimate the parabolic trajectory. Landing error is characterized by the vertical offset from the landing perch predicted by the extrapolated quadratic fit intersecting the vertical line through the perch location. The theoretical justification for choosing this definition of landing error is that, under this definition, a landing error of zero will be one where the extrapolated COM trajectory intersects the landing perch and does not require any torque to be produced to stabilize landing.

Leap Takeoff Position

Leap takeoff position on the rod was calculated using the sagittal plane video data and ImageJ software (National Institute of Health). Each hindfoot takeoff position was determined by the linear distance from the point of compliant beam intersection with its support to each respective rear foot contact immediately prior to aerial phase. Leap takeoff position was calculated as the average of the two hindlimb takeoff positions.

5.3 Results and Discussion

96 trials from 12 individuals were collected. To test the effect of individual on takeoff point, a likelihood ratio test was used to compare a model with fixed effects of compliance and individual, to a model with only a fixed effect of compliance. The model including squirrel was a better fit, $F(1,11) = 8.35$, $p=1.44*10^{-9}$. This indicates an individual effect. Therefore, when testing the effect of compliance on takeoff position, a mixed model was used that included squirrel as a random factor.

There was a significant effect of rod compliance level on leap takeoff position, $\chi^2(1)=27.69$, $p = 1.42*10^{-7}$. Follow up independent t-tests showed that the takeoff position at each compliance level was significantly different from the takeoff position at every other compliance level (Figure 5.5).

The movement choices an animal makes hypothetically depends on what it values during and as a result of the movement, and what it considers costs of the movement. Choosing movements that maximize an objective function, a function that considers values and costs, is the motivation of optimal control theory. As the dominant framework in motor control for robotic systems, optimal control theory has provided useful hypotheses about animal motor control. An important question is what's the structure of the objective function – e.g. how may different factors tradeoff against one another?

Based on previous work, it was asked, as a Fox squirrel is using a branch to cross a gap, does the decision of when to leap depend on both compliance and gap distance? Compliance and gap distance may both factor into a squirrel's decision of when to leap. Furthermore, due to the cantilevered structure of the arboreal environment, these two factors naturally tradeoff.

We found that squirrels' choice of takeoff point depends on a tradeoff between the gap distance from, and the branch compliance at that point (Figure 5.5). For a high compliance beam, in which the compliance increases faster as you move distally, squirrels choose to leap across a longer gap. For low compliance beams, squirrels will travel further out on the beam and leap across a shorter gap. This result supports the hypotheses of a gap-distance/compliance tradeoff.

This result adds to the many examples of tradeoffs at many levels described in the locomotion biomechanics literature. There is a natural tradeoff between stability and maneuverability that comes from increases or decreases in rotational inertia (Dickinson et al., 2010; Webb, 2005). For example, bees carrying loads near the body have better maneuverability and worse stability. But, if the loads are carried further from the body then it favors stability over maneuverability (Mountcastle, Ravi, & Combes, 2015). But this tradeoff between stability and maneuverability can be bypassed. By producing opposing forces, an animal can enhance both stability and maneuverability simultaneously. But, creating opposing forces takes energy and thus creates a new tradeoff between 1) bypassing the stability/maneuverability tradeoff and 2) energy efficiency (Sefati et al., 2013). There is a tradeoff between speed of locomotion and stabilization via sensory feedback (More et al., 2010). But this tradeoff may be bypassed by passive stabilization, like inverted running (see Chapter 1). There are tradeoffs in muscle physiology, for example power output and fatigue resistance trade-off in the muscle tissue of many animals (Vanhooydonck, Van Damme, & Aerts, 2001; Wilson & James, 2004; Wilson, James, & Van Damme, 2002). Tradeoffs are also possible between cognitive and biomechanical factors. For example, walking while performing a simultaneous cognitive task increased gait variability, suggesting that there is a tradeoff between paying attention to an external cognitive task and control of gait (Decker et al., 2016).

Despite the result supporting the hypothesis that squirrels factor both compliance and gap size into their decision of when to leap, this result doesn't necessarily support an optimal control theory hypothesis of motor control. Optimal control theory is limited in predicting two aspects of this behavior: 1) high variability in the choice of when to leap, and 2) highly effective landing recovery strategies. There is substantial variability in the choice of takeoff position. This contradicts the optimal control theory prediction, that the squirrel should choose a unique optimal takeoff position from which to leap. The variations in leaping trajectories led to landing errors from negative nine to one centimeters. But squirrels never fell on any trials. We observed squirrels to have a repertoire of landing recovery maneuvers that may reduce any costs of leaping errors. This suggests that instead of choosing the optimal gap crossing strategy, the Fox squirrel may choose one of the many good-enough solutions (Loeb, 2012a). Error recovery allows a broader space of leaping trajectories that are successful with respect to the task of crossing a gap. Wall jumping maneuvers further expand this space of successful gap crossing leaps. These redundant solutions to targeted leaping across gaps may permit creativity to respond to a new situation with a novel behavior that is useful.

Figure 5.5

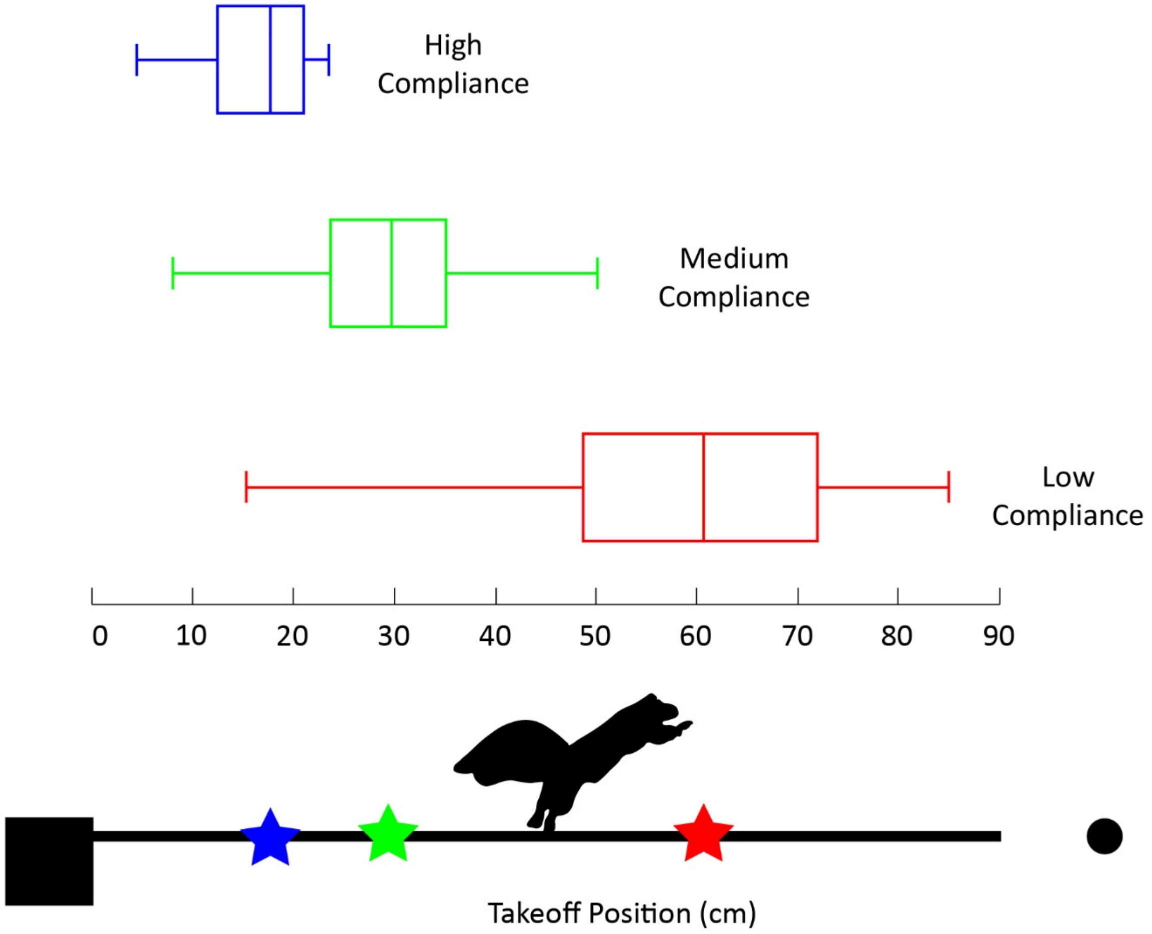

Figure 5.5: Box and whisker plot shows leap takeoff position chosen by the Fox squirrels versus the compliance level of the rod. Leap position is in reference to the rod support. So, a leap takeoff position of 0 means the squirrel leapt from the beginning the rod, whereas leaping from the end of the rod would be a leap takeoff position of 90.

There was no effect of rod compliance level on landing error $\chi^2(1)=1.00$, $p = 0.32$ (Figure 5.6).

The invariance of landing error to rod compliance suggests that on each compliance level, squirrels may choose a takeoff position that balances compliance and gap size to minimize the landing error. This interpretation is consistent with many reaching studies (Franklin & Wolpert, 2011; C. Harris & Wolpert, 1998; Haruno & Wolpert, 2005; W. Li et al., 2004).

Figure 5.6

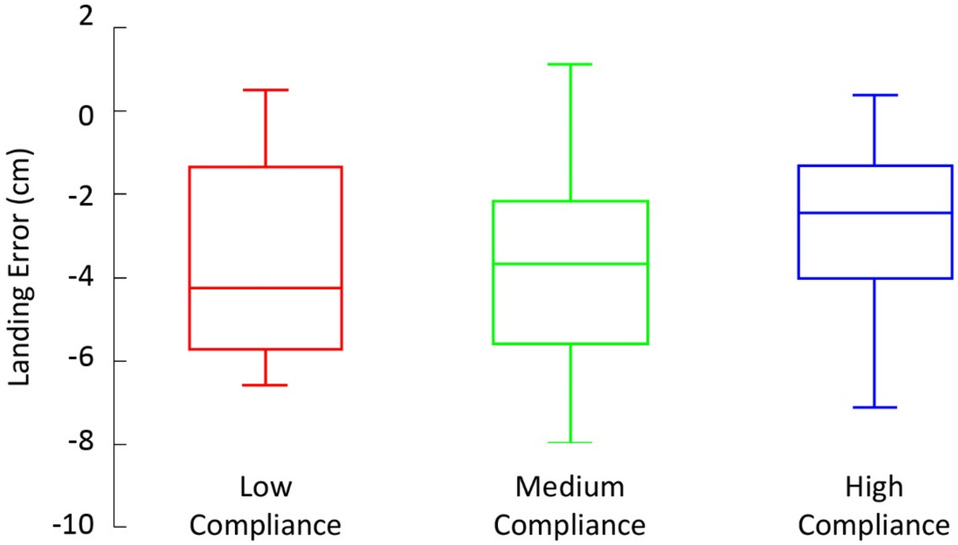

Figure 5.6: Landing error was not significantly different across the three rod compliance levels.

5.4 Conclusions

Squirrels were trained to use a compliant beam to leap across a gap. By presenting the squirrel with rods of three different compliance properties, the hypothesis that they choose a takeoff point that balances a tradeoff between gap distance and rod compliance was tested. Squirrels leapt from a position closer to the support on the high compliance rod and further from the support on the low compliance rod, supporting the tradeoff hypothesis (Figure 5.1).

The degrees of freedom problem was reduced by the tradeoff between gap size and compliance. The choice of takeoff position is limited to one that balances a tradeoff between gap distance and substrate compliance at the takeoff point. Although, there was still variability in the takeoff position for a given rod compliance level. The presence of variability under an optimal control hypothesis suggests differences in objective function between the varying takeoff positions are small. If the squirrel is choosing takeoff conditions to optimize an objective function, then the objective function may be relatively flat with respect to slight changes in the takeoff point. This interpretation supports the hypothesis that squirrels don’t choose a single optimal takeoff condition, but instead they choose one within a range that is good enough (G.E. Loeb, Levine, & He, 1990; Gerald E. Loeb, 2012).

Future studies will perform substrate manipulations in the canopy to distinguish whether squirrels rely on habit to guide action (de Rugy, Loeb, & Carroll, 2012; Dezfouli & Balleine, 2012), e.g. making decisions using a stable map of what actions to take in what location, or if they decide their action, and moreover, their route based upon a task dependent objective function and immediate sensory stimulus.

Bibiliography

Adolph, K. E., Cole, W. G., Komati, M., Garciaguirre, J. S., Badaly, D., Lingeman, J. M., … Sotsky, R. B. (2012). How do you learn to walk? Thousands of steps and dozens of falls per day. *Psychological Science*, *23*(11), 1387–94. https://doi.org/10.1177/0956797612446346

Aerts, P. (1998). Vertical jumping in Galago senegalensis: the quest for an obligate mechanical power amplifier. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *353*(1375), 1607–1620. https://doi.org/10.1098/rstb.1998.0313

Aguilar, J., Zhang, T., Qian, F., Kingsbury, M., McInroe, B., Mazouchova, N., … Goldman, D. I. (2016). A review on locomotion robophysics: the study of movement at the intersection of robotics, soft matter and dynamical systems. *Reports on Progress in Physics*, 1–61. https://doi.org/10.1088/0034-4885/79/11/110001

Ankarali, M. M., Tutkun Sen, H., De, A., Okamura, A. M., & Cowan, N. J. (2014). Haptic feedback enhances rhythmic motor control by reducing variability, not improving convergence rate. *Journal of Neurophysiology*, *111*(6), 1286–99. https://doi.org/10.1152/jn.00140.2013

Ashe, J., Lungu, O. V, Basford, A. T., & Lu, X. (2006). Cortical control of motor sequences. *Current Opinion in Neurobiology*, *16*(2), 213–21. https://doi.org/10.1016/j.conb.2006.03.008

Astley, H. C., & Jayne, B. C. (2007). Effects of perch diameter and incline on the kinematics, performance and modes of arboreal locomotion of corn snakes (Elaphe guttata). *The Journal of Experimental Biology*, *210*(Pt 21), 3862–72. https://doi.org/10.1242/jeb.009050

Autumn, K., Hsieh, S. T., Dudek, D. M., Chen, J., Chitaphan, C., & Full, R. J. (2006). Dynamics of geckos running vertically. *The Journal of Experimental Biology*, *209*(Pt 2), 260–72. https://doi.org/10.1242/jeb.01980

Bartling, C., & Schmitz, J. (2000). Reaction to disturbances of a walking leg during stance. *The Journal of Experimental Biology*, *203*(Pt 7), 1211–1223.

Beer, F. P., Johnston Jr, E. R., Mazurek, D. F., Cornwell, P. J., Eisenberg, E. R., & Sanghi, S. (1972). *Vector mechanics for engineers* (Vol. 1). Tata McGraw-Hill Education.

Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, *77*(4), 771–783. https://doi.org/10.1016/j.anbehav.2008.12.022

Benhamou, S. (2007). HOW MANY ANIMALS REALLY DO THE LEVY WALK? *Ecology*, *88*(8), 1962–1969. https://doi.org/doi:10.1890/06-1769.1

Bennett, a F. (1990). Integrated studies of locomotor performance. *Complex Organismal Functions: Integration and Evolution in Vertebrates*, 191–205.

Bernstein. (1967). The Co-ordination and regulation of movements.

Bertram, J. E. A., Ruina, A., Cannon, C. E., Chang, Y. H. U. I., & Coleman, M. J. (1999). A POINT-MASS MODEL OF GIBBON LOCOMOTION, *2617*, 2609–2617.

Blackwell, P. G. (1997). Random diffusion models for animal movement. *Ecological Modelling*, *100*(1–3), 87–102. https://doi.org/10.1016/S0304-3800(97)00153-1

Blickhan, R. (1989, January). The spring-mass model for running and hopping. *Journal of Biomechanics*. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/20824280

Bolnick, D. I., Svanbäck, R., Fordyce, J. a, Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: incidence and implications of individual specialization. *American Naturalist*, *161*(1), 1–28. https://doi.org/10.1086/343878

Bonser, R. H. C. (1999). Branching out in locomotion: The mechanics of perch use in birds and primates. *Journal of Experimental Biology*, *202*(11), 1459–1463.

Burde, J. H., & Feldhamer, G. A. (2005). *Mammals of the national parks*. JHU Press.

Büschges, A. (2005). Sensory control and organization of neural networks mediating coordination of multisegmental organs for locomotion. *J*

Neurophysiol, *93*(3), 1127–1135. https://doi.org/93/3/1127 [pii] 10.1152/jn.00615.2004

Byl, K., & Tedrake, R. (2009). Metastable Walking Machines. *The International Journal of Robotics Research*, *28*(8), 1040–1064. https://doi.org/10.1177/0278364909340446

Byrnes, G., Lim, N. T.-L., & Spence, A. J. (2008). Take-off and landing kinetics of a free-ranging gliding mammal, the Malayan colugo (Galeopterus variegatus). *Proceedings. Biological Sciences / The Royal Society*, *275*(1638), 1007–1013. https://doi.org/10.1098/rspb.2007.1684

Camhi, J. M., & Tom, W. (1978). The escape behavior of the cockroach Periplaneta americana - I. Turning response to wind puffs. *Journal of Comparative Physiology □ A*, *128*(3), 193–201. https://doi.org/10.1007/BF00656852

Carlton, L. G., & Newell, K. M. (1993). Force variability and characteristics of force production. *Variability and Motor Control*, 15–36.

Cartmill, M. (1974). Pads and claws in arboreal locomotion. *Primate Locomotion*, 45–83.

Channon, A. J., Günther, M. M., Crompton, R. H., D'Aoǔt, K., Preuschoft, H., & Vereecke, E. E. (2011). The effect of substrate compliance on the biomechanics of gibbon leaps. *The Journal of Experimental Biology*, *214*(Pt 4), 687–96. https://doi.org/10.1242/jeb.046797

Chapman, S. (1968). Catching a baseball. *American Journal of Physics*, *36*(10), 868. https://doi.org/10.1119/1.1974297

Chittka, L., Skorupski, P., & Raine, N. E. (2009). Speed-accuracy tradeoffs in animal decision making. *Trends in Ecology and Evolution*, *24*(7), 400–407. https://doi.org/10.1016/j.tree.2009.02.010

Christou, E. a, Grossman, M., & Carlton, L. G. (2002). Modeling variability of force during isometric contractions of the quadriceps femoris. *Journal of Motor Behavior*, *34*(January 2015), 67–81. https://doi.org/10.1080/00222890209601932

Clemente, C. J., & Federle, W. (2008). Pushing versus pulling: division of labour between tarsal attachment pads in cockroaches. *Proceedings. Biological Sciences / The Royal Society*, *275*(1640), 1329–1336. https://doi.org/10.1098/rspb.2007.1660

Cowan, N. J., Ankarali, M. M., Dyhr, J. P., Madhav, M. S., Roth, E., Sefati, S., … Daniel, T. L. (2014). Feedback control as a framework for understanding tradeoffs in biology. *Integrative and Comparative Biology*, *54*(2), 223–37. https://doi.org/10.1093/icb/icu050

Crompton, R. H., Sellers, W. I., & Gunther, M. M. (1993). Energetic Efficiency and Ecology as Selective Factors in the Saltatory Adaptation of Prosimian Primates. *Proceedings of the Royal Society B: Biological Sciences*, *254*(1339), 41–45. https://doi.org/10.1098/rspb.1993.0124

Cruse, H., Dürr, V., & Schmitz, J. (2007). Insect walking is based on a decentralized architecture revealing a simple and robust controller. *Philosophical Transactions. Series A, Mathematical, Physical, and Engineering Sciences*, *365*(1850), 221–250. https://doi.org/10.1098/rsta.2006.1913

de Jager, M., Weissing, F. J., Herman, P. M. J., Nolet, B. a, & van de Koppel, J. (2011). Levy Walks Evolve Through Interaction Between Movement and Environmental Complexity. *Science*, *332*(6037), 1551–1553. https://doi.org/10.1126/science.1201187

de Rugy, A., Loeb, G. E., & Carroll, T. J. (2012). Muscle coordination is habitual rather than optimal. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *32*(21), 7384–91. https://doi.org/10.1523/JNEUROSCI.5792-11.2012

Decker, L. M., Cignetti, F., Hunt, N., Potter, J. F., Stergiou, N., & Studenski, S. A. (2016). Effects of aging on the relationship between cognitive demand and step variability during dual-task walking. *Age*, *38*(4), 363–375. https://doi.org/10.1007/s11357-016-9941-y

Delbrück, M. (1940). Statistical Fluctuations in Autocatalytic Reactions. *The Journal of Chemical Physics*, *8*(1), 120. https://doi.org/10.1063/1.1750549

Delciellos, A. C., & Vieira, M. V. (2009). Jumping Ability in the Arboreal Locomotion of Didelphid Marsupials, *16*(2), 299–307. Retrieved from http://www.sarem.org.ar

Delgado, M. M., Nicholas, M., Petrie, D. J., & Jacobs, L. F. (2014). Fox squirrels match food assessment and cache effort to value and scarcity. *PLoS ONE*, *9*(3), 1–8. https://doi.org/10.1371/journal.pone.0092892

Demes, B., Fleagle, J. G., & Jungers, W. L. (1999). Takeoff and landing forces of leaping strepsirhine primates. *Journal of Human Evolution*, *37*(2), 279–292. https://doi.org/10.1006/jhev.1999.0311

Demes, B., Franz, T. M., & Carlson, K. J. (2005). External forces on the limbs of jumping lemurs at takeoff and landing. *American Journal of Physical Anthropology*, *128*(2), 348–358. https://doi.org/10.1002/ajpa.20043

Demes, B., Jungers, W. L., Gross, T. S., & Fleagle, J. G. (1995). Kinetics of leaping primates: Influence of substrate orientation and compliance. *American Journal of Physical Anthropology*, *96*(4), 419–429. https://doi.org/10.1002/ajpa.1330960407

Dezfouli, A., & Balleine, B. W. (2012). Habits, action sequences and reinforcement learning. *The European Journal of Neuroscience*, *35*(7), 1036–51. https://doi.org/10.1111/j.1460-9568.2012.08050.x

Dickinson, M. H., Farley, C. T., Full, R. J., Koehl, M. A. R., Kram, R., & Lehman, S. (2010). How Animals Move : An Integrative View, *100*(2000). https://doi.org/10.1126/science.288.5463.100

Diedrichsen, J., Shadmehr, R., & Ivry, R. B. (2010). The coordination of movement: optimal feedback control and beyond. *Trends in Cognitive Sciences*, *14*(1), 31–9. https://doi.org/10.1016/j.tics.2009.11.004

Donelan, J. M., & Pearson, K. G. (2004). Contribution of sensory feedback to ongoing ankle extensor activity during the stance phase of walking. *Canadian Journal of Physiology and Pharmacology*, *82*(8–9), 589–598. https://doi.org/10.1139/y04-043

Dudek, D. M., & Full, R. J. (2007). An isolated insect leg's passive recovery from dorso-ventral perturbations. *The Journal of Experimental Biology*, *210*(Pt 18), 3209–17. https://doi.org/10.1242/jeb.008367

Enoka, R. M., & Stuart, D. G. (1992). Neurobiology of muscle fatigue. *Journal of Applied Physiology (Bethesda, Md. : 1985)*, *72*(5), 1631–1648. https://doi.org/0161-7567/92

Fairweather, H., & Hutt, S. J. (1978). On the rate of gain of information in children. *Journal of Experimental Child Psychology*, *26*(2), 216–229. https://doi.org/10.1016/0022-0965(78)90002-4

Fink, P. W., Foo, P. S., & Warren, W. H. (2009). Catching fly balls in virtual reality : A critical test of the outfielder problem, *9*, 1–8. https://doi.org/10.1167/9.13.14.Introduction

Fitts, P. M., & Peterson, J. R. (1964). Information Capacity of Discrete Motor Responses. *Journal of Experimental Psychology*, *67*(2), 103–112.

Flash, T., & Hogan, N. (1985). The coordination of arm movements: an experimentally confirmed mathematical model. *The Journal of Neuroscience*, *5*(7), 1688–1703. https://doi.org/4020415

Franklin, D. W., & Wolpert, D. M. (2011). Computational mechanisms of sensorimotor control. *Neuron*, *72*(3), 425–42. https://doi.org/10.1016/j.neuron.2011.10.006

Full, R. J., & Koditschek, D. E. (1999). Templates and anchors: neuromechanical hypotheses of legged locomotion on land. *The Journal of Experimental Biology*, *202*(Pt 23), 3325–32. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10562515

Full, R. J., Kubow, T. ., Schmitt, J., Holmes, P., & Koditschek, D. E. (2002). Quantifying Dynamic Stability and Maneuverability in Legged Locomotion. *Integrative and Comparative Biology*, *42*(1), 149–157. https://doi.org/10.1093/icb/42.1.149

Full, R. J., & Tu, M. S. (1991, March). Mechanics of a rapid running insect: two-, four- and six-legged locomotion. *The Journal of Experimental Biology*. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/2051129

Full, R. J., & Tullis, A. (1990). Energetics of ascent: insects on inclines. *J Exp Biol*, *149*, 307–317. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/2324672

Garcia, M., Chatterjee, a, Ruina, a, & Coleman, M. (1998). The simplest walking model: stability, complexity, and scaling. *Journal of Biomechanical Engineering*, *120*(2), 281–288. https://doi.org/10.1115/1.2798313

Gibson, J. J. (1979). *The ecological approach to visual perception: classic edition*. Psychology Press.

Gilman, C. a, Bartlett, M. D., Gillis, G. B., & Irschick, D. J. (2012). Total recoil: perch compliance alters jumping performance and kinematics in green anole lizards (Anolis carolinensis). *The Journal of Experimental Biology*, *215*(Pt 2), 220–6. https://doi.org/10.1242/jeb.061838

Gladun, D., & Gorb, S. N. (2007). Insect walking techniques on thin stems. *Arthropod-Plant Interactions*, *1*(2), 77–91. https://doi.org/10.1007/s11829-007-9007-2

Goldman, D. I., Chen, T. S., Dudek, D. M., & Full, R. J. (2006). Dynamics of rapid vertical climbing in cockroaches reveals a template. *The Journal of Experimental Biology*, *209*(Pt 15), 2990–3000. https://doi.org/10.1242/jeb.02322

Graham H. Pyke. (1984). Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology and Systematics*, *15*(March), 523–575. https://doi.org/doi:10.1146/annurev.es.15.110184.002515

Green, P. R., & Cheng, P. (1998). Variation in kinematics and dynamics of the landing flights of pigeons on a novel perch. *The Journal of Experimental Biology*, *201 (Pt 24*(24), 3309–16. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9817828

Griffin, B., & Grizzle, J. (2016). Nonholonomic virtual constraints for dynamic walking. *Proceedings of the IEEE Conference on Decision and Control*, *2016–Febru*, 4053–4060. https://doi.org/10.1109/CDC.2015.7402850

Haken, H., Kelso, J. a. S., & Bunz, H. (1985). A theoretical model of phase transitions in human hand movements. *Biological Cybernetics*. https://doi.org/10.1007/BF01068748

Haldane, D. W., Plecnik, M. M., Yim, J. K., & Fearing, R. S. (2016). Robotic vertical jumping agility via series-elastic power modulation. *Science Robotics*, *2048*(1), eaag2048. https://doi.org/10.1126/scirobotics.aag2048

Hanson, N. K. I. (2016). *Cognitive and locomotor strategies of arboreal locomotion in non-human apes and humans*. University of Birmingham.

Harris, C., & Wolpert, D. (1998). Signal-dependent noise determines motor planning. *Nature*, *394*(August), 780–784. Retrieved from http://www.nature.com/nature/journal/v394/n6695/abs/394780a0.html

Harris, M. a, & Steudel, K. (2002). The relationship between maximum jumping performance and hind limb morphology/physiology in domestic cats (Felis silvestris catus). *The Journal of Experimental Biology*, *205*(Pt 24), 3877–89. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12432010

Haruno, M., & Wolpert, D. M. (2005). Optimal control of redundant muscles in step-tracking wrist movements. *Journal of Neurophysiology*, *94*(6), 4244–4255. https://doi.org/10.1152/jn.00404.2005

Hauser, H., Ijspeert, A. J., Füchslin, R. M., Pfeifer, R., & Maass, W. (2012). The role of feedback in morphological computation with compliant bodies. *Biological Cybernetics*, *106*(10), 595–613. https://doi.org/10.1007/s00422-012-0516-4

Hauser, H., Sumioka, H., Füchslin, R. M., & Pfeifer, R. (2013). Introduction to the Special Issue on Morphological Computation. *Artificial Life*, *19*(1), 1–8. https://doi.org/10.1162/ARTL_e_00083

Hildebrand, M., Bramble, D. M., Liem, K. F., & Wake, D. B. (1985). Functional vertebrate morphology.

Hoffmeister, B., Jänig, W., & Lisney, S. J. W. (1991). A proposed relationship between circumference and conduction velocity of unmyelinated axons from normal and regenerated cat hindlimb cutaneous nerves. *Neuroscience*, *42*(2), 603–611. https://doi.org/10.1016/0306-4522(91)90402-A

Hogan, N., & Sternad, D. (2012). Dynamic primitives of motor behavior. *Biological Cybernetics*, *106*(11–12), 727–39. https://doi.org/10.1007/s00422-012-0527-1

Holmes, P., Full, R., Koditschek, D., & Guckenheimer, J. (2006). The dynamics of legged locomotion: Models, analyses, and challenges. *Siam Review*, *48*(2), 207–304. Retrieved from http://epubs.siam.org/doi/pdf/10.1137/S0036144504445133

Hunt, K. D., Cant, J. G. H., Gebo, D. L., Rose, M. D., Walker, S. E., & Youlatos, D. (1996). Standardized descriptions of primate locomotor and postural modes. *Primates*, *37*(4), 363–387. https://doi.org/10.1007/BF02381373

Hyams, S. E., Jayne, B. C., & Cameron, G. N. (2012). Arboreal habitat structure affects locomotor speed and perch choice of white-footed mice (Peromyscus leucopus). *Journal of Experimental Zoology. Part A, Ecological Genetics and Physiology*, *317*(9), 540–51. https://doi.org/10.1002/jez.1746

Izawa, J., Rane, T., Donchin, O., & Shadmehr, R. (2008). Motor Adaptation as a Process of Reoptimization. *Journal of Neuroscience*, *28*(11), 2883–2891. https://doi.org/10.1523/JNEUROSCI.5359-07.2008

Jacobs, L. F., & Menzel, R. (2014). Navigation outside of the box: what the lab can learn from the field and what the field can learn from the lab. *Movement Ecology*, *2*(1), 3. https://doi.org/10.1186/2051-3933-2-3

James, R. S., Navas, C. A., & Herrel, A. (2007). How important are skeletal muscle mechanics in setting limits on jumping performance? *J. Exp. Biol.*, *210*, 923–933. https://doi.org/10.1242/jeb.02731

Jenkins, F. A. (1974). Tree shrew locomotion and the origins of primate arborealism. *Primate Locomotion*, 85–115.

Jenkins, F. A., & McClearn, D. (1984). Mechanisms of hind foot reversal in climbing mammals. *Journal of Morphology*, *182*(2), 197–219. https://doi.org/10.1002/jmor.1051820207

Jindrich, D. L., & Full, R. J. (2002). Dynamic stabilization of rapid hexapedal locomotion. *The Journal of Experimental Biology*, *205*(Pt 18), 2803–23. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12177146

Jusufi, A., Goldman, D. I., Revzen, S., & Full, R. J. (2008). Active tails enhance arboreal acrobatics in geckos. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(11), 4215–4219. https://doi.org/10.1073/pnas.0711944105

Kawato, M. (1999). Internal models for motor control and trajectory planning. *Current Opinion in Neurobiology*, *9*(6), 718–727. https://doi.org/10.1016/S0959-4388(99)00028-8

Kelso, J. a S. (2012). Multistability and metastability: understanding dynamic coordination in the brain. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*(1591), 906–18. https://doi.org/10.1098/rstb.2011.0351

Komsuoglu, H., Sohn, K., Full, R., & Koditschek, D. (2008). A Physical Model for Dynamical Arthropod Running on Level Ground. *Departmental Papers (ESE)*.

Krakauer, J. W., & Shadmehr, R. (2006). Consolidation of motor memory. *Trends in Neurosciences*, *29*(1), 58–64. https://doi.org/10.1016/j.tins.2005.10.003

Kubow, T. M., & Full, R. J. (1999). The role of the mechanical system in control: a hypothesis of self-stabilization in hexapedal runners. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *354*(1385), 849–861. https://doi.org/10.1098/rstb.1999.0437

LaDage, L. D., Roth Ii, T. C., Fox, R. A., & Pravosudov, V. V. (2009). Effects of Captivity and Memory-Based Experiences on the Hippocampus in Mountain Chickadees. *Behavioral Neuroscience*, *123*(2), 284–291. https://doi.org/10.1037/a0014817

Laine Martin, T., & Huey, R. B. (2008). Is Optimal: Jensen's Inequality and Ectotherm Thermal Preferences. *Source: The American Naturalist*, *171*(3), 102–118. https://doi.org/10.1086/527502

Lammers, A. R., & Biknevicius, A. R. (2004). The biodynamics of arboreal locomotion: the effects of substrate diameter on locomotor kinetics in the gray short-tailed opossum (Monodelphis domestica). *The Journal of Experimental Biology*, *207*(Pt 24), 4325–36. https://doi.org/10.1242/jeb.01231

Lammers, A. R., & Gauntner, T. (2008). Mechanics of torque generation during quadrupedal arboreal locomotion. *Journal of Biomechanics*, *41*(11), 2388–95. https://doi.org/10.1016/j.jbiomech.2008.05.038

Lammers, A. R., & Zurcher, U. (2011). Torque around the center of mass: Dynamic stability during quadrupedal arboreal locomotion in the Siberian chipmunk (Tamias sibiricus). *Zoology*, *114*(2), 95–103. https://doi.org/10.1016/j.zool.2010.11.004

Larson, S. G., & Stern, J. T. (2006). Maintenance of above-branch balance during primate arboreal quadrupedalism: coordinated use of forearm rotators and tail motion. *American Journal of Physical Anthropology*, *129*(1), 71–81. https://doi.org/10.1002/ajpa.20236

Li, C., Pullin, A. O., Haldane, D. W., Lam, H. K., Fearing, R. S., & Full, R. J. (2015). Terradynamically streamlined shapes in animals and robots enhance traversability through densely cluttered terrain. *Bioinspiration & Biomimetics*, *10*(4), 46003. https://doi.org/10.1088/1748-3190/10/4/046003

Li, W., Todorov, E., & Pan, X. (2004). Hierarchical optimal control of redundant biomechanical systems. *Conference Proceedings : ... Annual International Conference of the IEEE Engineering in Medicine and Biology Society. IEEE Engineering in Medicine and Biology Society. Annual Conference*, *6*, 4618–21. https://doi.org/10.1109/IEMBS.2004.1404280

Libby, T., Moore, T. Y., Chang-Siu, E., Li, D., Cohen, D. J., Jusufi, A., & Full, R. J. (2012). Tail-assisted pitch control in lizards, robots and dinosaurs. *Nature*, *481*(7380), 181–184. https://doi.org/10.1038/nature10710

Loeb, G., Brown, I., & Cheng, E. (1999). A hierarchical foundation for models of sensorimotor control. *Experimental Brain Research*, (126), 1–18. Retrieved from http://link.springer.com/article/10.1007/s002210050712

Loeb, G. E. (2012). Optimal isn't good enough. *Biological Cybernetics*, *106*(11–12), 757–765. https://doi.org/10.1007/s00422-012-0514-6

Loeb, G. E. (2012). Optimal isn't good enough. *Biological Cybernetics*, *106*(11–12), 757–65. https://doi.org/10.1007/s00422-012-0514-6

Loeb, G. E., Levine, W. S., & He, J. (1990). Understanding Sensorimotor Feedback through Optimal Control. *Cold Spring Harbor Symposia on Quantitative Biology*, *55*, 791–803. https://doi.org/10.1101/SQB.1990.055.01.074

Losos, J., & Sinervo, B. (1989). The effects of morphology and perch diameter on sprint performance of Anolis lizards. *Journal of Experimental Biology*, *30*, 23–

30. Retrieved from http://jeb.biologists.org/content/145/1/23.short

Losos, J., Walton, B., & Bennett, A. (1993). Trade-offs between sprinting and clinging ability in Kenyan chameleons. *Functional Ecology*, *7*(3), 281–286. Retrieved from http://www.jstor.org/stable/10.2307/2390206

Manton, S. M. (1952). THE EVOLUTION OF ARTHROPODAN LOCOMOTORY MECHANISMS. GENERAL INTRODUCTION TO THE LOCOMOTORY MECHANISMS OF THE ARTHROPODA. *Zoological Journal of the Linnean Society*, *42*(284), 93–117.

McBeath, M. K., Shaffer, D. M., & Kaiser, M. K. (1995). How baseball outfielders determine where to run to catch fly balls. *Science (New York, N.Y.)*, *268*(5210), 569–73. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/7725104

Mcclintock, B. T., King, R., Matthiopoulos, J., Mcconnell, B. J., & Morales, J. M. (2012). A General Modeling Framework for Animal Movement in Discrete Time Using Multi-State Random Walks. *Ecological Monographs*, *82*(3), 98115. https://doi.org/10.1890/11-0326.1

McLeod, P., Reed, N., & Dienes, Z. (2006). The generalized optic acceleration cancellation theory of catching. *Journal of Experimental Psychology. Human Perception and Performance*, *32*(1), 139–48. https://doi.org/10.1037/0096-1523.32.1.139

Mischiati, M., Lin, H.-T., Herold, P., Imler, E., Olberg, R., & Leonardo, A. (2015). Internal models direct dragonfly interception steering. *Nature*, *517*(7534), 333–8. https://doi.org/10.1038/nature14045

Mistry, M., Theodorou, E., Schaal, S., & Kawato, M. (2013). Optimal control of reaching includes kinematic constraints. *Journal of Neurophysiology*, *110*(April 2013), 1–11. https://doi.org/10.1152/jn.00794.2011

Moffett, M. W. (2000). What's "Up"? A Critical Look at the Basic Terms of Canopy Biology. *Biotropica*, *32*(4a), 569–596. https://doi.org/10.1646/0006-3606(2000)032[0569:WSUACL]2.0.CO;2

More, H. L., Hutchinson, J. R., Collins, D. F., Weber, D. J., Aung, S. K. H., & Donelan, J. M. (2010). Scaling of sensorimotor control in terrestrial mammals.

Proceedings. Biological Sciences / The Royal Society, *277*(1700), 3563–8. https://doi.org/10.1098/rspb.2010.0898

Mountcastle, A. M., Ravi, S., & Combes, S. a. (2015). Nectar vs. pollen loading affects the tradeoff between flight stability and maneuverability in bumblebees. *Proceedings of the National Academy of Sciences*, *112*(33), 10527–10532. https://doi.org/10.1073/pnas.1506126112

Norman, R. W., & Komi, P. V. (1979). Electromechanical delay in skeletal muscle under normal movement conditions.pdf, 241–248.

Pearson, K. G. (2004). Generating the walking gait: Role of sensory feedback. *Progress in Brain Research*, *143*(3), 123–129. https://doi.org/10.1016/S0079-6123(03)43012-4

Plecnik, M. M., Haldane, D. W., Yim, J. K., & Fearing, R. S. (2016). Design exploration and kinematic tuning of a power modulating jumping monopod. *Accepted to Journal of Mechanisms and Robotics*, *9*(February), 1–13. https://doi.org/10.1115/1.4035117

Revzen, S., Burden, S., & Moore, T. (2013). Instantaneous kinematic phase reflects neuromechanical response to lateral perturbations of running cockroaches. *Biological Cybernetics*, *107*, 179–200. https://doi.org/10.1007/s00422-012-0545-z

Rosenbaum, D. A., Barnes, H. J., & Slotta, J. D. (1988). In defense of the advance specification hypothesis for motor control. *Psychological Research*, *50*(1), 58–62. https://doi.org/10.1007/BF00309412

Saglam, C. O., & Byl, K. (2014). Metastable Markov chains. *53rd IEEE Conference on Decision and Control*, 2979–2985. https://doi.org/10.1109/CDC.2014.7039847

Schlag, J., & Schlag-rey, M. (2002). Through the Eye, Slowly : Delays and Localization Errors in the Visual System. *Neuroscience*, *3*(March), 1–10. https://doi.org/10.1038/nrn750

Schmidt, A., & Fischer, M. S. (2010). Arboreal locomotion in rats - the challenge of maintaining stability. *The Journal of Experimental Biology*, *213*(Pt 21), 3615–24. https://doi.org/10.1242/jeb.045278

Schmidt, R. A., Zelaznik, H. N., Frank, J. S., & Stelmach, G. E. (1978). Sources of inaccuracy in rapid movement. *Information Processing in Motor Control and Learning*, 183–203.

Schmitt, J., Garcia, M., Razo, R. C., Holmes, P., & Full, R. J. (2002). Dynamics and stability of legged locomotion in the horizontal plane: A test case using insects. *Biological Cybernetics*, *86*(5), 343–353. https://doi.org/10.1007/s00422-001-0300-3

Schmitt, J., & Holmes, P. (2000). Mechanical models for insect locomotion: dynamics and stability in the horizontal plane I. Theory. *Biological Cybernetics*, *83*(6), 501–15. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11130583

Schweizerbart, E. (2012). The jump as a fast mode of locomotion in arboreal and terrestrial biotopes Author (s): M . M . Günther , H . Ishida , H . Kumakura , Y . Nakano Reviewed work (s): Source : Zeitschrift für Morphologie und Anthropologie , Bd . 78 , H . 3 (April 1991), *3*(April 1991), 341–372.

Sefati, S., Neveln, I. D., Roth, E., Mitchell, T. R. T., Snyder, J. B., Maciver, M. a, … Cowan, N. J. (2013). Mutually opposing forces during locomotion can eliminate the tradeoff between maneuverability and stability. *Proceedings of the National Academy of Sciences of the United States of America*, 1–6. https://doi.org/10.1073/pnas.1309300110/-/DCSupplemental.www.pnas.org/cgi/doi/10.1073/pnas.1309300110

Seipel, J. E., Holmes, P. J., & Full, R. J. (2004). Dynamics and stability of insect locomotion: a hexapedal model for horizontal plane motions. *Biological Cybernetics*, *91*(2), 76–90. https://doi.org/10.1007/s00422-004-0498-y

Seipel, J., & Holmes, P. (2006). Three-dimensional Translational Dynamics and Stability of Multi-legged Runners. *The International Journal of Robotics Research*, *25*(9), 889–902. https://doi.org/10.1177/0278364906069045

Selinger, J. C., O’Connor, S. M., Wong, J. D., & Donelan, J. M. (2015). Humans Can Continuously Optimize Energetic Cost during Walking. *Current Biology*, *25*(18), 2452–2456. https://doi.org/10.1016/j.cub.2015.08.016

Seyfarth, A., Geyer, H., & Herr, H. (2003). Swing-leg retraction: a simple control model for stable running. *The Journal of Experimental Biology*, *206*(Pt 15), 2547–2555. https://doi.org/10.1242/jeb.00463

Shadmehr, R., & Holcomb, H. H. (1997). Neural correlates of motor memory consolidation. *Science (New York, N.Y.)*, *277*(5327), 821–5. https://doi.org/10.1126/science.277.5327.821

Shadmehr, R., Smith, M. A., & Krakauer, J. W. (2010). Error correction, sensory prediction, and adaptation in motor control. *Annual Review of Neuroscience*, *33*, 89–108.

Sherwood, D. E., & Schmidt, R. A. (1980). The relationship between force and force variability in minimal and near-maximal static and dynamic contractions. *Journal of Motor Behavior*, *12*(1), 75–89. https://doi.org/10.1080/00222895.1980.10735208

Shmuelof, L., & Krakauer, J. W. (2011). Are we ready for a natural history of motor learning? *Neuron*, *72*(3), 469–76. https://doi.org/10.1016/j.neuron.2011.10.017

Shmuelof, L., Krakauer, J. W., & Mazzoni, P. (2012). How is a motor skill learned? Change and invariance at the levels of task success and trajectory control. *Journal of Neurophysiology*, *108*(2), 578–594. https://doi.org/10.1152/jn.00856.2011

Shmuelof, L., Krakauer, J. W., & Mazzoni, P. (2012). How is a motor skill learned? Change and invariance at the levels of task success and trajectory control. *Journal of Neurophysiology*, *108*(2), 578–94. https://doi.org/10.1152/jn.00856.2011

Sinervo, B., & Losos, J. (1991). Walking the tight rope: arboreal sprint performance among Sceloporus occidentalis lizard populations. *Ecology*, *72*(4), 1225–1233. Retrieved from http://www.jstor.org/stable/10.2307/1941096

Smouse, P. E., Focardi, S., Moorcroft, P. R., Kie, J. G., Forester, J. D., & Morales, J. M. (2010). Stochastic modelling of animal movement. *Philosophical Transactions: Biological Sciences*, *365*(1550), 2201–2211. https://doi.org/10.2307/25699241

Spagna, J. C., Goldman, D. I., Lin, P.-C., Koditschek, D. E., & Full, R. J. (2007). Distributed mechanical feedback in arthropods and robots simplifies control of rapid running on challenging terrain. *Bioinspiration & Biomimetics*, *2*(1), 9–18. https://doi.org/10.1088/1748-3182/2/1/002

Sponberg, S., & Full, R. J. (2008). Neuromechanical response of musculo-skeletal structures in cockroaches during rapid running on rough terrain. *The Journal of Experimental Biology*, *211*(Pt 3), 433–46. https://doi.org/10.1242/jeb.012385

Sponberg, S., Spence, A. J., Mullens, C. H., & Full, R. J. (2011). A single muscle's multifunctional control potential of body dynamics for postural control and running. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *366*(1570), 1592–605. https://doi.org/10.1098/rstb.2010.0367

Stamps, J., & Groothuis, T. G. G. (2010). The development of animal personality: Relevance, concepts and perspectives. *Biological Reviews*, *85*(2), 301–325. https://doi.org/10.1111/j.1469-185X.2009.00103.x

Stanley, J., & Krakauer, J. W. (2013). Motor skill depends on knowledge of facts. *Frontiers in Human Neuroscience*, *7*(August), 503. https://doi.org/10.3389/fnhum.2013.00503

Stergiou, N., Harbourne, R., & Cavanaugh, J. (2006). Optimal movement variability: a new theoretical perspective for neurologic physical therapy. *Journal of Neurologic Physical Therapy : JNPT*, *30*(3), 120–9. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/17029655

Taylor, J. E. T., Witt, J. K., & Sugovic, M. (2011). When walls are no longer barriers: Perception of wall height in parkour. *Perception*, *40*(6), 757–760. https://doi.org/10.1068/p6855

Thornton, a., & Lukas, D. (2012). Individual variation in cognitive performance: developmental and evolutionary perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1603), 2773–2783. https://doi.org/10.1098/rstb.2012.0214

Ting, L., Blickhan, R., & Full, R. (1994). Dynamic and static stability in hexapedal runners. *Journal of Experimental Biology*, *269*, 251–269. Retrieved from http://jeb.biologists.org/content/197/1/251.short

Ting, L. H. (2007). Dimensional reduction in sensorimotor systems: a framework for understanding muscle coordination of posture. *Progress in Brain Research*, *165*, 299–321. https://doi.org/10.1016/S0079-6123(06)65019-X

Ting, L. H., Blickhan, R., & Full, R. J. (1994). Dynamic and static stability in hexapedal runners. *The Journal of Experimental Biology*, *197*, 251–69. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/7852905

Todorov, E. (2004). Optimality principles in sensorimotor control. *Nature Neuroscience*, *7*(9), 907–15. https://doi.org/10.1038/nn1309

Turpin, N. a, Guével, A., Durand, S., & Hug, F. (2011). Fatigue-related adaptations in muscle coordination during a cyclic exercise in humans. *The Journal of Experimental Biology*, *214*(Pt 19), 3305–3314. https://doi.org/10.1242/jeb.057133

van Casteren, A., Sellers, W. I., Thorpe, S. K. S., Coward, S., Crompton, R. H., & Ennos, A. R. (2013). Factors Affecting the Compliance and Sway Properties of Tree Branches Used by the Sumatran Orangutan (Pongo abelii). *PLoS ONE*, *8*(7), 1–9. https://doi.org/10.1371/journal.pone.0067877

Van Emmerik, R., & van Wegen, E. (2002). On the functional aspects of variability in postural control. *Exercise and Sport Sciences Reviews*, *30*(4), 177–183.

Vanhooydonck, B., Van Damme, R., & Aerts, P. (2001). Speed and Stamina Trade-Off in Lacertid Lizards. *Evolution*, *55*(5), 1040–1048. https://doi.org/10.1554/0014-3820(2001)055[1040:SASTOI]2.0.CO;2

Waisman, A. S., & Jacobs, L. F. (2008). Flexibility of cue use in the fox squirrel (Sciurus niger). *Animal Cognition*, *11*(4), 625–636. https://doi.org/10.1007/s10071-008-0152-5

Warren, W. H. (1984). Perceiving affordances: visual guidance of stair climbing. *Journal of Experimental Psychology. Human Perception and Performance*, *10*(5), 683–703. https://doi.org/10.1037/0096-1523.10.5.683

Warren, W. H., & Fajen, B. R. (2004). Behavioral dynamics of human locomotion, *16*(1), 61–66. Retrieved from http://www.tandfonline.com/doi/abs/10.1207/s15326969eco1601_8%5Cnpapers3://publication/doi/10.1207/s15326969eco1601_8

Watson, H. W., & Galton, F. (1875). On the Probability of the Extinction of Families. *The Journal of the Anthropological Institute of Great Britain and Ireland*, *4*, 138–144.

Webb, P. W. (2005). Stability and Maneuverability. *Fish Physiology*, *23*(C), 281–332. https://doi.org/10.1016/S1546-5098(05)23008-X

Wilson, R. S., & James, R. S. (2004). Constraints on muscular performance: trade-offs between power output and fatigue resistance. *Proceedings. Biological Sciences / The Royal Society*, *271 Suppl*, S222–S225. https://doi.org/10.1098/rsbl.2003.0143

Wilson, R. S., James, R. S., & Van Damme, R. (2002). Trade-offs between speed and endurance in the frog Xenopus laevis: a multi-level approach. *The Journal of Experimental Biology*, *205*(Pt 8), 1145–1152.

Withers, G. S., Day, N. F., Talbot, E. F., Dobson, H. E. M., & Wallace, C. S. (2008). Experience-dependent plasticity in the mushroom bodies of the solitary bee Osmia lignaria (Megachilidae). *Developmental Neurobiology*, *68*(1), 73–82. https://doi.org/10.1002/dneu.20574

Witt, J. K. (2011). Action's Effect on Perception. *Current Directions in Psychological Science*, *20*(3), 201–206. https://doi.org/10.1177/0963721411408770

Witte, H., Preuschoft, H., & Fischer, M. S. (2002). The importance of the evolutionary heritage of locomotion on flat ground in small mammals for the development of arboreality. *Zeitschrift Für Morphologie Und Anthropologie*, *83*(2–3), 221–233.

Wolf, M., & Weissing, F. J. (2010). An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *365*(1560), 3959–68. https://doi.org/10.1098/rstb.2010.0215

Wolpert, D. M., Diedrichsen, J., & Flanagan, J. R. (2011). Principles of sensorimotor learning. *Nature Reviews. Neuroscience*, *12*(12), 739–51.

https://doi.org/10.1038/nrn3112

Wolpert, D. M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience*, *3 Suppl*(november), 1212–1217. https://doi.org/10.1038/81497

Yanoviak, S. P., Dudley, R., & Kaspari, M. (2005). Directed aerial descent in canopy ants. *Nature*, *433*(February), 624–626. https://doi.org/10.1038/nature03268.