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SQUIRREL PARKOUR

Learning to leap and land pp. 620 & 697

BIOMECHANICS

Acrobatic squirrels learn to leap and land on tree branches without falling

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Arboreal animals often leap through complex canopies to travel and avoid predators. Their success at making split-second, potentially life-threatening decisions of biomechanical capability depends on their skillful use of acrobatic maneuvers and learning from past efforts. Here, we found that free-ranging fox squirrels (*Sciurus niger*) leaping across unfamiliar, simulated branches decided where to launch by balancing a trade-off between gap distance and branch-bending compliance. Squirrels quickly learned to modify impulse generation upon repeated leaps from unfamiliar, compliant beams. A repertoire of agile landing maneuvers enabled targeted leaping without falling. Unanticipated adaptive landing and leaping "parkour" behavior revealed an innovative solution for particularly challenging leaps. Squirrels deciding and learning how to launch and land demonstrates the synergistic roles of biomechanics and cognition in robust gap-crossing strategies.

L eaping across gaps in a disconnected canopy presents challenges (*1–4*) to arboreal animals (*5*), shaping interactions between learning and biomechanical capabilities (*6*, *7*). Animals traversing a compliant branch must decide on a launch point. As the distance to a landing target decreases, lessening required momentum, the compliance of the branch underfoot increases, which magnifies the momentum-generating impulse lost to branch bending during takeoff (*4*, *8*). The decision will depend on the inter-

play of an animal's biomechanical capabilities and perception of the physical environment [i.e., branch properties (*9*)]. Although the former may be innate, the latter is only partially observable (*10*) and is likely estimated through trial-and-error learning. We quantified how decision-making and learning capabilities complement biomechanical adaptations for targeted leaping in the canopy. Here, we report three experiments where free-ranging fox squirrels (*Sciurus niger*) leapt across gaps between simulated branches.

In the first experiment, branches were cantilevered, varying in compliance across their lengths (Fig. 1A). The landing perch was a narrow rod oriented perpendicular to the sagittal plane, which constrained successful leap trajectories to a small region.

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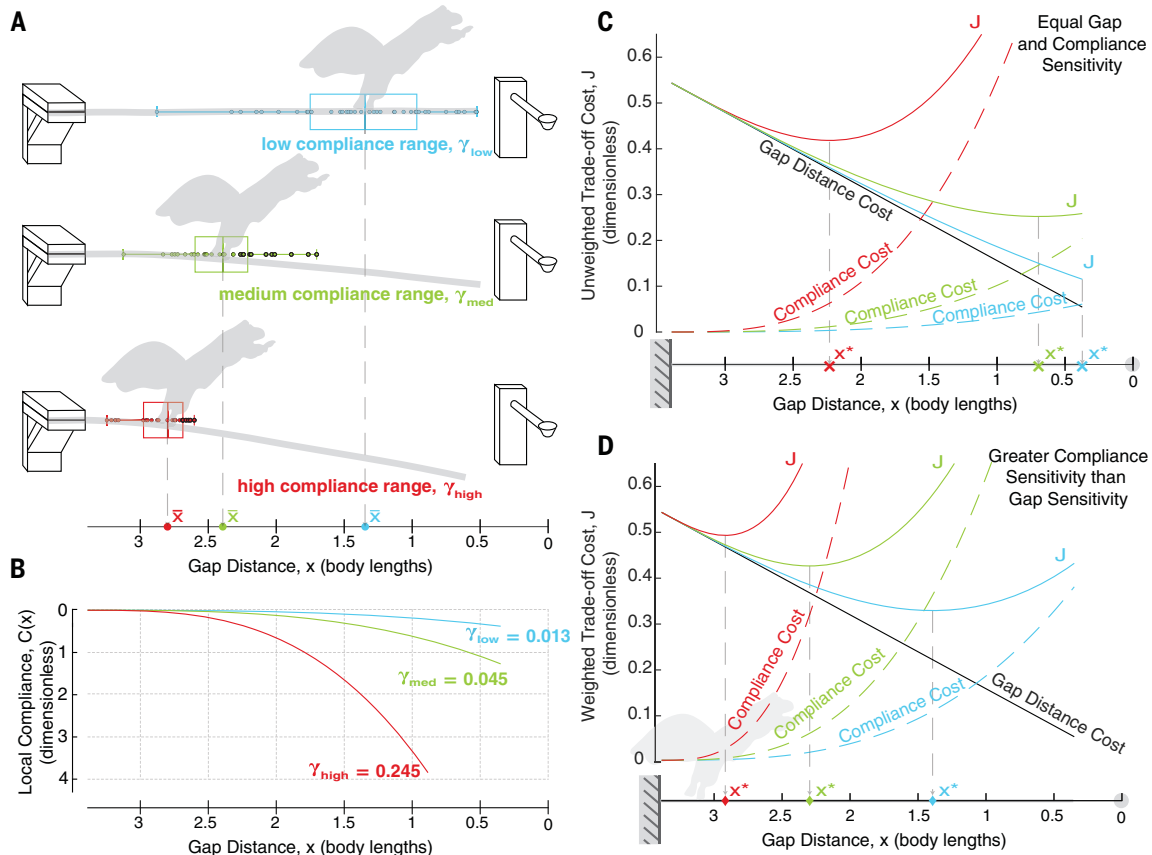
Fig. 1. Launch-point decisions from simulated branches with varying compliance. (**A**) Gap distance (x) launch-point decisions differed on simulated branches designed to represent three ranges of compliance: low (blue), medium (green), and high (red). (**B**) Local compliance increased cubically as gap distance decreased when traversing simulated branches from left to right. (**C** and **D**) Dimensionless costs modeled versus gap distance. Gap distance cost (solid black line) is identical for all branches. Compliance costs (colored dashed lines) increase as gap distance decreases. Solid colored lines represent the total trade-off cost, J, by summing gap cost and compliance cost. A trade-off model assuming equal weights for gap cost and compliance cost (C) and a trade-off model assuming independent weights (D) are shown.
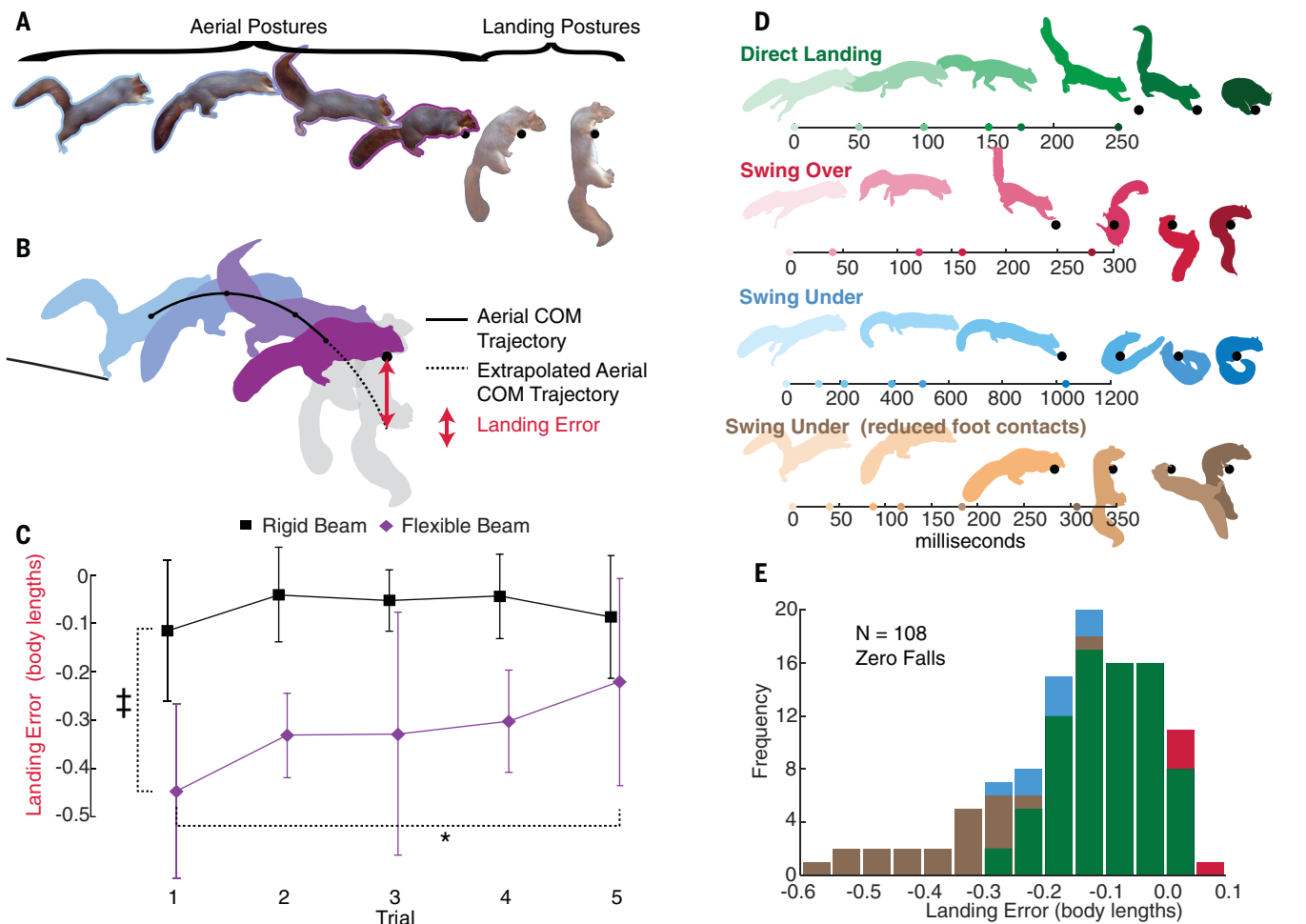
Fig. 2. Learning to leap from an unfamiliar compliant beam and land robustly. (**A**) Aerial and landing postures (fig. S2) (*12*). (**B**) Landing error was quantified as the height discrepancy between the landing perch and the extrapolated trajectory of the COM during the aerial phase (red arrow) (*12*). (**C**) Five individual squirrels performed sequential leaps from both the rigid and compliant beam (movie S2). Landing error (mean ± 95% CI) for the rigid beam (black) and compliant beam (purple) is shown for each trial. Negative landing error values indicate undershooting the perch. The asterisk and double dagger (‡) symbols indicate statistically significant differences. (**D**) Four landing maneuvers observed in the first two experiments. Color-coded markers on the time scale indicate the time of each body position. (**E**) Frequency distribution of landing maneuvers across a range of landing errors.

We hypothesized that squirrels leaping from a branch to a target perch in the canopy perceive and adapt their leaping behavior as a trade-off between branch compliance and leap distance. Launching closer to a branch attachment provides a stiffer (less compliant) substrate but increases leap distance. Launching farther from the attachment increases compliance—magnifying loss of impulse from substrate deformation (*4*)—but reduces leap distance. To test this hypothesis, we created three simulated branches with different ranges of local compliance represented by γ (Fig. 1, A and B) but of equal diameter to obscure visual cues of compliance.

Squirrel launch-point decisions showed a balanced trade-off between preferences for low compliance and short gap distance [likelihood ratio test, $\chi^2(1) = 27.69$, $P < 0.001$; Fig. 1A and movie S1]. On the least-compliant branch, launch points included gap distances less than

a body length with no aerial phase. As squirrels traversed branches with higher compliance, they leapt earlier with gap distances greater than three body lengths (Fig. 1A).

To compare the relative sensitivity of squirrels' launch-point decisions to compliance and gap distance, we used selections made across the simulated branches to infer an optimality model of the launch-point decision (x^*) (*11, 12*). The models represent the trade-off between gap distance and branch compliance with an objective (cost) function with weights, a_g and a_c, that quantified the response to gap distance and branch compliance, respectively. The unweighted model assumed equal sensitivity ($a_g = a_c$) and poorly predicted launch-point decisions [mean absolute error = 1.16 body lengths (BLs); Fig. 1C]. The weighted model, which allowed different sensitivities, accurately described the launch-point decisions across all three simulated branches [mean

absolute error = 0.31 BLs; Fig. 1D). It indicated that launch-point decisions are more sensitive to compliance than to gap distance ($a_c / a_g = 6.2$). Although the trade-off objective function predicts an optimal launch point (fig. S3), squirrels leapt from a range of locations on each branch. The range of launch points increased with decreasing branch compliance range, indicating a wider range of sufficient (*13*) launch points (Fig. 1A). Constrained launch points on high-compliance branches may be a result of insufficient leaping momentum with a fixed-leg extension. Although not observed here, this biomechanical limitation may be mitigated through branch elastic energy storage and return (*4, 14, 15*).

Throughout the experiment, squirrels leapt gaps without falling. To quantify leaping performance, we defined landing error as the height discrepancy between the landing perch and a squirrel's extrapolated center of mass
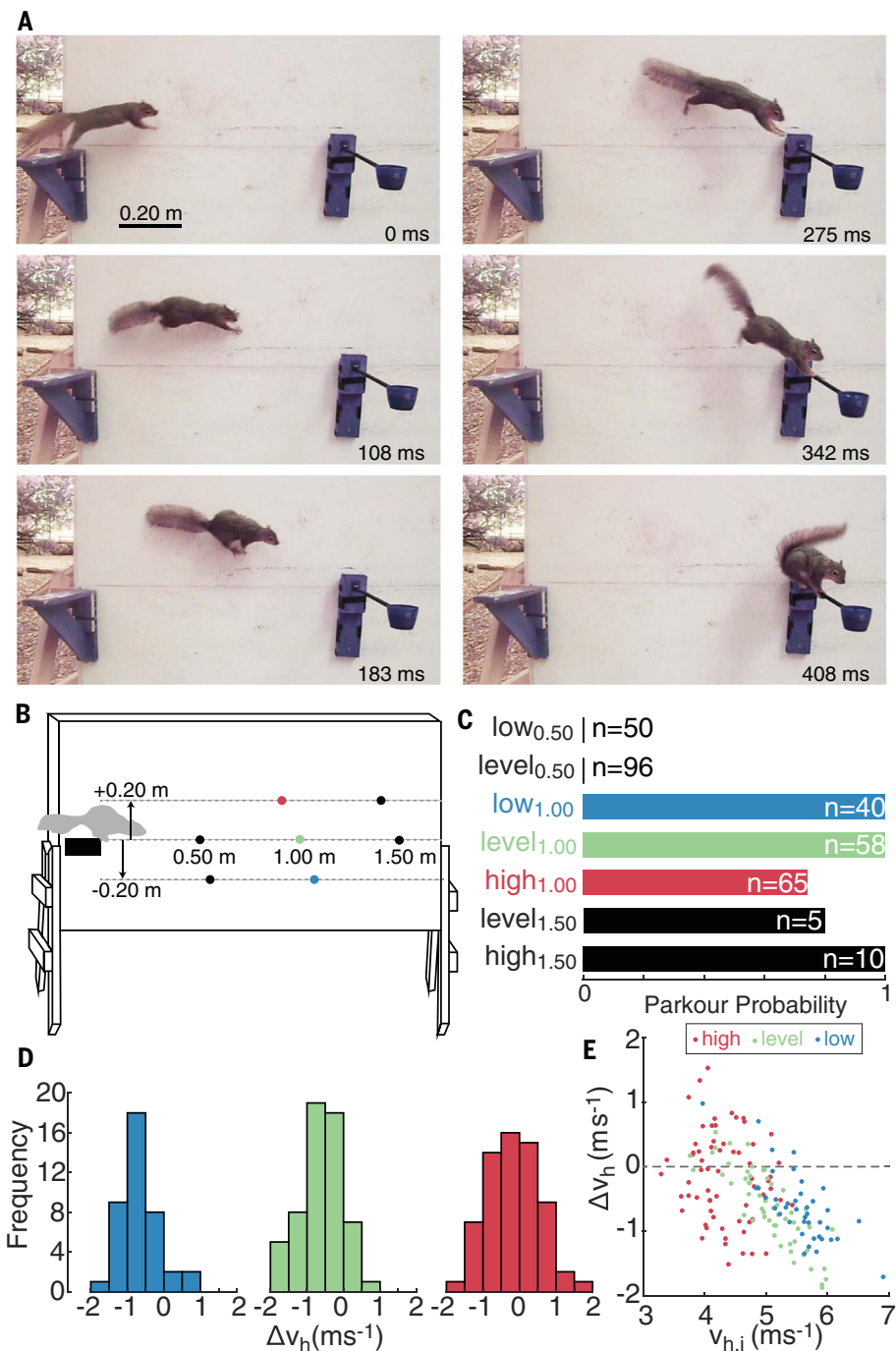
Fig. 3. Parkour leaping. (**A**) Parkour maneuver. (**B**) Diagram of the apparatus with vertical surface, launch platform, and landing perch positions. (**C**) Probabilities of using the parkour maneuver for different placements of the landing perch, where *n* equals the total number of trials. Probability estimates at the 1.50-m distance are uncertain because of the small sample size. (**D**) Change in horizontal velocity (Δv_h) for low, level, and high perch placements at the 1.00-m distance. (**E**) Change in horizontal velocity (Δv_h) versus the initial parkour contact phase landing velocity ($v_{h,i}$).

(COM) (*16*) using the ballistics of the aerial phase standardized by the squirrel's body length (Fig. 2B, fig. S2A, and movie S2). There was no significant correlation between launch-point decision and landing error [likelihood ratio test, $\chi^2(1) = 1.00$, $P = 0.32$]. Landing errors were small for low-compliance (-0.12 ± 0.08 BLs), medium-compliance (-0.12 ± 0.08 BLs), and high-compliance branches (-0.09 ± 0.08 BLs).

We hypothesized that constraining the squirrels to leap from a launch point with even greater compliance would result in greater initial landing errors but that they would demonstrate error-based learning to improve their leaping performance. Error-based motor learning—in contrast to other forms of motor learning like action selection, use-dependent, and skill learning (*17*, *18*)—is a recalibration of an existing motor control policy to compensate for differences between expected and experienced sensory information resulting from changing animal-environment dynamics (*19*), and it reoptimizes plans for future movements (*20*).

To increase the challenge of leaping in our second experiment, we introduced a thin steel beam with a compliance 2.9 times as great as that for any previous leaps (fig. S4) and a minimum gap distance 1.7 times as long as the previous average (2.2 BLs). A rigid beam was used as a control.

Five squirrels performed repeated leaps from both rigid and compliant beams. Leaping from the rigid beam led to relatively small landing errors, similar to those exhibited from the simulated branches (Fig. 2C). The compliant beam caused larger landing errors [two-way repeated measures analysis of variance (ANOVA), $F_{(1,4)} = 16.2$, $P = 0.016$] up to half a body length (Fig. 2C). Squirrels learned to improve their landings over five trials [$F_{(4,16)} = 4.60$, $P = 0.012$; movie S2]. Error reduction was achieved by changes in launch velocity [$F_{(4,16)} = 3.38$, $P = 0.035$] rather than launch angle [$F_{(4,16)} = 2.59$, $P = 0.076$], vertical launch COM position [$F_{(4,16)} = 0.75$, $P = 0.57$], or horizontal launch COM position [$F_{(4,6)} = 1.71$, $P = 0.20$].

Squirrels used swinging landing maneuvers that included caudal-led (swinging under; negative landing errors) and cranial-led (swinging over; positive landing errors) inversion of the COM about the landing perch (Fig. 2D and movie S3). Landing errors varied from -0.57 to 0.10 BLs (*12*), but no squirrels fell. The landing maneuver depended upon the landing error [Fig. 2E, mutual information measurement (*21*)].

In a third experiment, we further challenged the squirrels by manipulating gap distance and landing height. Unexpectedly, squirrels perceived the vertical surface of the apparatus as an additional affordance—an opportunity for action using its biomechanical capabilities (*9*, *22*)—and used an innovative strategy where they selectively established an additional control point midleap using a parkour leaping maneuver, a dynamic form of locomotion that extends mobility using additional forces. In this maneuver, they reoriented some or all of their legs by rolling toward the vertical surface, generating forces that could alter their trajectory (Fig. 3A and movie S4).

To determine how often squirrels use this parkour strategy, we varied the distance (0.50, 1.00, and 1.50 m) and the height of the landing perch relative to the launching platform (± 0.20 m) at each perch distance along an

isocline of constant impulse (Fig. 3B). Squirrels consistently used the parkour maneuver for the medium and long leaps (ranging 3 to 5 BLs) but never for short leaps (1.5 BLs; Fig. 3C). There was a preference for using the parkour maneuver regardless of height. However, at 1.00-m distance, squirrels used the parkour maneuver less for the high perch position (74%) compared with the level and low positions (100%).

We hypothesized that squirrels use contact on a vertical surface as an additional control point to modify horizontal velocity before landing. To test this hypothesis, we quantified initial horizontal velocity before contact ($v_{h,i}$) and final horizontal velocity after contact ($v_{h,f}$) for the medium-distance leaps. Initial and final horizontal velocities ranged widely from ~3 to 7 ms^{-1} (Fig. 3E). Squirrels modified horizontal velocity (v_h) depending on the height of the landing perch [linear mixed-effects model controlling for individual, $t_{(161)} = 2.3$, $P = 0.02$]. When squirrels used the parkour strategy, they generally reduced horizontal velocity during the contact phase to reach lower perch heights ($\Delta v_h = -0.63 \pm 0.54$ ms^{-1}, mean ± SD), level perch heights ($\Delta v_h = -0.61 \pm 0.59$ ms^{-1}, mean ± SD), and high perch heights ($\Delta v_h = -0.17 \pm 0.69$ ms^{-1}, mean ± SD; Fig. 3D). In addition to an opportunity for deceleration before landing, squirrels used the parkour maneuver to make midleap velocity corrections that countered variations in initial horizontal velocity. Initial horizontal velocity predicted parkour horizontal velocity changes [linear mixed-effects model controlling for individual and perch height, $t_{(161)} = -11.0$, $P < 0.001$]

$\{\Delta v_h = [-0.86 \pm 0.15,$ estimate ± confidence interval (CI)] $v_{h,i}\}$.

Gap traversibility depends on the complement of environmental properties with an animal's locomotive capacities. The synergy between biomechanical energy management and learned information for launching and landing likely determines arboreal leaping and ultimately the path through the canopy. The role of fast and accurate leaping in driving the evolution of biomechanical capabilities, learning-based decision-making, and innovation promises to reveal the mechanisms and origins of arboreal agility (7, 23–25).

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SUPPLEMENTARY MATERIALS

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Science

Acrobatic squirrels learn to leap and land on tree branches without falling

Nathaniel H. Hunt, Judy Jinn, Lucia F. Jacobs and Robert J. Full

Squirrel parkour

Every day, there are acrobatic extravaganzas going on above our heads. Squirrels navigate remarkably complex and unpredictable environments as they leap from branch to branch, and mistakes can be fatal. These feats require a complex combination of evolved biomechanical adaptations and learned behaviors. Hunt *et al.* characterized the integration of these features in a series of experiments with free-living fox squirrels (see the Perspective by Adolph and Young). They found that the squirrels' remarkable and consistent success was due to a combination of learned impulse generation when assessing the balance between distance and branch flexibility and the addition of innovative leaps and landings in the face of increasingly difficult challenges.

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