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Take-off and landing forces and the evolution of controlled gliding in northern flying squirrels *Glaucomys sabrinus*

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Summary

Flying squirrels are well known for their ability to glide between trees at the top of a forest canopy. We present experimental performance and behavioural evidence that flight in flying squirrels may have evolved out of a need to control landing forces. Northern flying squirrels were filmed jumping from a horizontal branch to a much larger vertical pole. These were both slightly compliant (less than 1.9 mm N^{-1}), and instrumented using strain gauges so that forces could be measured. Take-off and landing forces were both positively correlated with horizontal range between 0.5 and 2.5 m (*r*=0.355 and *r*=0.811, respectively, *P*<0.05), but not significantly different to each other at each range tested. Take-off forces ranged from 1 to 10 bodyweights, and landing forces were between 3 and 10 bodyweights. Glide angles increased rapidly with horizontal range, approaching 45° at 3 m, above which they gradually decreased, suggesting that northern flying squirrels are optimised for long distance travel. We show that northern flying squirrels initiate full gliding posture at ranges of less than 1 m, without landing any higher than an equivalent ballistic projectile. However, this gliding posture enables them to pitch upwards, potentially stalling the wing, and spreads the landing reaction force over all four extended limbs. At steeper approach angles of close to 45°, flying squirrels were unable to pitch up sufficiently and landed forelimbs first, consequently sustaining higher impact forces. We investigate four hypotheses to explain the origin of flight in these animals and conclude that the need to reduce landing impact forces was most likely to have stimulated the development of aerial control in flying squirrels.

Key words: flying squirrels, *Glaucomys sabrinus*, jumping, gliding, kinetics, substrate reaction forces, biomechanics.

Introduction

There are three principal hypotheses to explain the divergence of flying squirrels from other types of squirrel. The first suggestion (Norberg, 1985) is that gliding may have evolved as a means of reducing the energetic cost of foraging. The squirrel can jump and glide from one tree to the next, enabling it to cover greater distances within the canopy more quickly than would be possible by climbing down and moving across the forest floor. An alternative suggestion was that, rather than reducing cost of transport, gliding may offer a means of foraging over a larger area in a certain time, making flying squirrels better able to exploit a patchy food resource than non-gliders of similar size (Scheibe et al., 2006). The third hypothesis is that gliding evolved primarily as an escape mechanism (Scheibe et al., 1990; Keith et al., 2000). Tree squirrels react to disturbances by moving to the opposite side of their tree, whereas flying squirrels climb upwards and then glide to another tree. However, this behaviour may increase susceptibility to attack from their most likely predator, owls (Scheibe and Robins, 1998). We propose a fourth hypothesis: that the patagia, the flexible membranes that squirrels stretch by fully extending their forelimbs and hindlimbs, evolved to reduce or control landing forces. There is published evidence to support this (Caple et al., 1983), where it was calculated that increasing the amount of lift available to a body from 0 to 5% would not noticeably lengthen the jump nor allow much turning, but would give the animal significantly improved control around the pitch and roll axes. Of course, none of these four hypotheses are mutually exclusive.

This paper will investigate these hypotheses through experimental determination of the performance and behaviour of these animals. By measuring take-off and landing forces, we propose to quantify the advantage flying squirrels can achieve as a result of their unique morphology. The outcome of these measurements will be directly affected by substrate compliance. The majority of previous studies measuring ground reaction forces used rigid force measuring devices, while others investigated the effects of substrate compliance on ground reaction forces (Demes et al., 1999; Bonser, 1999). Demes et al. found that take-off forces were higher than landing forces when testing seven primate species of varying body sizes using compliant apparatus, contradicting previous studies based on rigid platforms (Demes et al., 1999). Some of the take-off force is used in bending the compliant branch before toe-off, whereas the reaction force on landing is damped as the substrate yields in the direction of motion, allowing more time for deceleration. Likewise, Bonser showed that the magnitude of landing forces for starlings was lower than their take-off forces (Bonser, 1999). He proposed both that the birds used their wings to decelerate during landing, and that additional energy is dissipated in deflecting their compliant perch during take-off.

In arboreal locomotion, flying squirrels must generate higher take-off forces when jumping from narrow (and hence compliant) tree branches, and encounter their highest impact forces when landing on rigid tree trunks. Compliant substrates have been instrumented for this study, and so we expect take-off forces to exceed landing forces over short distances. At higher ranges, the squirrels will have accelerated due to gravity and their landing force will likely increase unless the squirrel can use its morphology to slow itself aerodynamically. Therefore our hypothesis that gliding in the squirrel evolved primarily to enable aerodynamic control of its landing speed can be rejected if measured landing forces continually rise at high ranges.

It is possible for animals to utilise stored elastic energy within a branch by timing their take-off with its motion. However, primates do not seem to take advantage of this (Demes et al., 1995), which supports the proposition (Alexander, 1991) that they would not intentionally recover this energy. Therefore, we do not expect flying squirrels to take advantage of the recoil of our instrumented branch either. However, they have been observed using a bounding gait before launching with both fore- and hind-feet together at the end of a platform just before take-off (Keith et al., 2000). It is probable that this bounding is used to maximise take-off velocity and hence increase range.

The northern flying squirrel *Glaucomys sabrinus* is the larger of two species of North American flying squirrel, although still much smaller than some species found in SE Asia (Ando and Shiraishi, 1993). Flight is made possible by the presence of patagia, a morphological feature which has evolved independently several times in vertebrates, the earliest known being from the Mesozoic era (Meng et al., 2006). By manipulating their limbs, flying squirrels are able to actively modify the shape of this lift-generating surface during flight. The body proportions of flying squirrels were compared with those of tree squirrels to determine what morphological changes might be attributed to gliding (Thorington and Heaney, 1981). Increased leg length allows more energy to be expended during take-off, offering superior horizontal range. In comparison with other similar-sized squirrels, the forelimbs of flying squirrels are significantly longer, a trait that has almost certainly evolved to improve aerodynamics during gliding (Essner, 2002). This is further improved by the styliform cartilage, which is a flexible projection from the wrist held upward from the rest of the lift surface during gliding. This combines with the manus (or hand, which points ventrally towards the mid-line of the squirrel) to form a wing tip very similar to a NASA designed winglet (Thorington et al., 1998), who proposed that it reduces induced drag by diffusing and directing vortices away from the patagia. Smaller flying squirrels tend to have greater manoeuvrability and agility, whereas the larger species must glide faster to achieve the same glide ratio.

Materials and methods

Animals

Study animals came from a laboratory colony of northern flying squirrels *Glaucomys sabrinus* (Shaw 1801) housed in the Department of Biology at Southeast Missouri State University. Two young females and a young male were chosen because they had been consistent performers in previous kinematic work. All animals were born in the same week and approximately 27 months old. The mass, wing span and wing area of each animal is given in Table 1. Other members of the colony were required for other projects and were not available. The colony has been maintained for 5 years on a diet of pecans, walnuts, sunflower seeds, mushrooms and birdseed in a large, temperature-controlled room (20°C). The room is on a continuous 12 h:12 h light:dark cycle. There are various branches and sufficient space for jumping and gliding to take place. Initially, measurements were made in the squirrel lab, but longer glides were measured in a 7 m×14 m×7 m barn on the university farm.

Apparatus

As flying squirrels often land on tree trunks, allowing vertical variation in contact point, we used a vertical landing pole based on the design of Demes et al. (Demes et al., 1995; Demes et al., 1996; Demes et al., 1999). The squirrels were acclimated to it for several months prior to experimentation and used it regularly. It was constructed in two pieces: a 1.52 m long PVC tube (114 mm o.d.) covered in carpet and marked at 10 cm intervals (for calibration and image analysis), mounted 80 cm of the way up a 2.41 m long galvanised steel tube (23 mm o.d.). A concrete base secured this steel tube, which had four strain gauges (FLA-2-11-3L, TML, Tokyo, Japan) equally spaced around its circumference and aligned vertically (Fig. 1). A half-bridge circuit was used for each tension/compression pair so that force parallel and perpendicular to the squirrel's direction of motion could be determined. The compliance of the pole was measured to be 1.5 mm N^{-1} at the free end, gradually decreasing down the pole, reducing to 0.2 mm N^{-1} close to the fixed end and the resonant frequency was 2.2 Hz.

For the take-off branch, a horizontal cantilevered beam was designed to mimic a tree branch because northern flying squirrels predominantly launch from a crouched, horizontal

Table 1. *Summary table of all the measured forces generated by northern flying squirrels during leaping and landing*

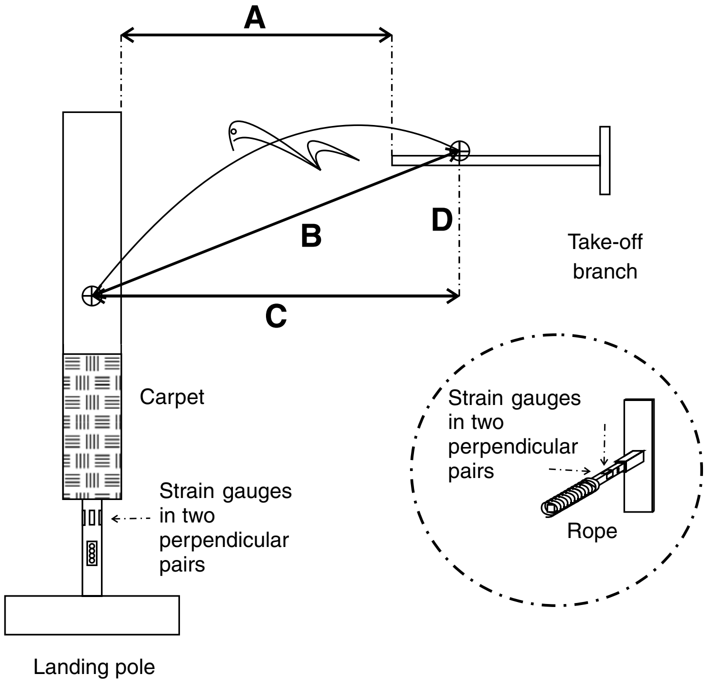
Squirrel ID	Wing span (cm)	Wing area (cm^2)	Leap distance (m)	Mass on day of testing (g)	Take-off force (bw) Count	Take-off force (bw) Mean ± s.d.	Landing force (bw) Count	Landing force (bw) Mean ± s.d.
YF1	28.0	511	0.5	272	9	3.70±1.99	–	–
			1	274	6	4.64±1.17	6	3.47±0.37
			1.5	267	10	4.36±1.64	10	4.88±0.35
			2	256.5*	7	5.57±1.53	7	7.58±0.96
			2.5	256.5*	5	5.91±1.49	5	6.16±0.54
YF2	27.5	500	0.5	200	8	2.56±1.28	–	–
			1	201	10	5.21±2.47	10	3.56±0.30
			1.5	198	11	3.30±1.70	11	4.28±0.21
YM	25.9	554	0.5	259	9	3.38±0.96	–	–
			1	260	4	6.97±1.23	4	3.79±0.44

YF, young female; YM, young male; bw, body weight.

There are 79 take-offs but only 53 corresponding landings because no landing force data was obtained for the shortest range jumps of 0.5 m. Only one individual, YF1, performed in the barn but it would not land on the force pole at distances greater than 2.5 m. Unfortunately, for reasons beyond our control, YF2 only cooperated at 0.5, 1 and 1.5 m and YM at 0.5 and 1 m.

*Squirrels seemed to lose a considerable percentage of their weight before testing at this distance. The reason for this is unknown but it could have been caused by the change of environment as these tests were carried out in a barn, which was very hot and humid compared to the temperature-controlled lab.

position (Vernes, 2001). Four standard linear strain gauges (CEA-13-240UZ-120, Vishay, Basingstoke, UK) were mounted in two pairs, 50 mm from the fixed end of the 10 mm square aluminium bar (Fig. 1) and connected in a half-bridge circuit. Alignment was simplified because the chosen gauge width was almost as large as the 10 mm width of the aluminium bar, but not critical because any cross-talk was eliminated during calibration. The aluminium branch was covered by tightly wound rope to simulate the surface of a tree branch. The strain gauges were protected using polystyrene foam, which was itself covered by plastic. A length of 4 cm×9 cm timber was fixed vertically to the wall, and drilled with mounting holes every 10 cm to allow height adjustment of the launch branch. The design of the branch was such that the compliance was similar to that of the landing pole, measured to be 1.9 mm N^{-1} at the free end and decreasing as would be expected towards 0.0 mm N^{-1} at the fixed end. The resonant frequency of the take-off branch was 17.3 Hz. The signal outputs from the strain gauges on both instruments were amplified using AD524 chips or equivalent and the sampling rate was 250 Hz. There was no need to acclimatise the squirrels to the take-off pole as, unlike the landing pole, they had no choice over whether or not to use it.



Experimental design

The take-off branch was raised as the experimental range increased such that the angle between the tip of the branch and the base of the landing pole remained consistent at approximately 55°. This configuration was chosen because it was not possible with our equipment, and in the locations available, to set up short jumps at high altitudes, and the

Fig. 1. A diagrammatic representation of the experimental set-up, showing the instrumentation used to measure take-off and landing forces including the carpet-covered landing pole, the rope-covered take-off branch and the location of the strain gauge pairs on each. Also shown are the measurements used to analyse the results, relative to an approximate squirrel trajectory. (A) The controlled horizontal distance between the end of the take-off branch and the vertical landing pole, (B) the total distance covered in the glide calculated from the exact horizontal distance (C) and the drop (D).

squirrels were unable to reach the landing pole unless given sufficient starting height. Animals were released individually on the instrumented branch and responded by running along the branch, usually pausing and then leaping to the instrumented landing pole. The horizontal range was increased progressively from a low distance of 0.5 m, to capture the leap-to-glide transition point, below which squirrels merely leap around, and above which the flying squirrels achieve aerodynamic advantage over other types of squirrel. Analysing this range of arboreal locomotion was considered to be more critical for investigating the initial divergence of flying squirrels.

Three digital video cameras (Canon GL2, Sony TRV 108, and Panasonic NV-DS55B) were used to film jumps. The first was positioned to capture take-off angle, the second to capture lateral landing angle and the third to capture a ventral view of landing. In the large squirrel barn it was not possible to mount a camera level horizontally with the take-off branch, so the resultant images represent frames perpendicular from the known camera angle. A minor trigonometric correction was therefore necessary to adjust all vertical distances measured from this take-off footage.

Calibration

With strain gauges, large changes in the external environment are potentially significant, so a record of temperature was kept using two I-buttons (Maxim Integrated Products, Sunnyvale, CA, USA), fixed to the top and bottom of the 4 cm×9 cm timber stud, respectively. These recorded temperature every hour. This daily verification of calibration was particularly important because testing was carried out in two contrasting environments; a temperature-controlled laboratory, and a hot and humid metal barn.

Only the landing forces were measured by converting the output from strain gauges into force, for which a static calibration was performed daily by applying forces to different points along the pole. Resultant steady signals were used to draw calibration graphs that established the force constant, k, where F=kx; F is force (N) and x is the measured strain signal (V). Forces equivalent to between 1 and 10 body weight units (bw) were applied, producing good linearity across the full range of marking points on the pole. (On average, the square of the Pearson product moment correlation coefficient r^2=1.00 in line and 0.99 transverse to the expected direction of motion.) Position of the animal along the instrumented poles was taken into account and a linear equation allowed the correct calibration to be used at any point. The cross-talk magnitudes were 13% and 17%, respectively, for parallel and transverse forces. Cross talk, in this context, is the unwanted output signal measured on one pair of strain gauges for a force applied perpendicularly. The frequency response of our equipment is sufficient to measure impulses generated by the squirrels. The effect of temperature on the calibration was found to be unimportant, as although it varied considerably between the two test areas, calibration graphs remained consistent throughout the study.

Results processing

Although both could measure force in two directions, neither the take-off branch nor the landing pole were capable of measuring forces along their long axes. To overcome this limitation, video footage from laterally positioned cameras was recorded to determine the angle of action of the force, which allowed the force vector to be resolved in 3D from the two measured force components. This was an acceptable procedure for the landing forces because the squirrels were arriving at angles perpendicular to the pole. For the median data point at medium range, 1.5 m, a trigonometric calculation showed that a 5° shift in measured landing angle would cause a 10% change in the resultant force. During take-off the squirrels were consistent in their behaviour, always choosing to move towards the free end of the branch and jump away in the same direction. However, the resulting shallow take-off angles mean that a 5° measurement error leads to an unacceptable 39% change to the median resultant force at 1.5 m. Hence, resultant take-off forces had to be calculated by integrating the output from the strain gauges with respect to time, so that measured take-off velocity could be used to determine the acceleration. This was multiplied by the known mass of each flying squirrel for all jumps to calculate the resultant force. The frame rate of the lateral take-off camera was 30 frames s^{-1} so an estimate of velocity between the first two consecutive frames after toe-off could be obtained by measuring the change in position of the centre of mass. The resultant force calculated by this method is the total force required to accelerate the squirrel to its actual take-off velocity based on its known acceleration profile. This method does not take into account losses caused by deforming the branch, but is completely independent of the accuracy in measurement of take-off angle.

The video records were digitised using edge-detection software, which tracked the outline of the squirrel in each frame of a sequence of images from the laterally positioned camera (LabView – National Instruments, Austin, TX, USA). The tail was deliberately excluded from this outline, because it constitutes only a small percentage of the total weight of the animal and was often dorsally flattened and moving at high velocity outside the plane of the images. The centre of the region enclosed by the lateral outline of the squirrel was used as an approximation for its centre of mass and could be tracked from frame to frame, enabling both the landing point on the pole, and the angle of impact to be determined. Hence the resultant reaction force for each landing squirrel could be calculated.

To measure the take-off angle of the squirrel, principal components analysis was applied in the LabView squirrel tracking program to find the best-fitting ellipse to the outline detected in each frame. The take-off angle was taken to be the angle between the major axis of this ellipse and the axis of the branch in the final frame before toe-off. This program was also used to estimate the change in pitch during the landing sequence shown in Fig. 2C. Another program was written in NI Labview to determine the wing span and wing area of each

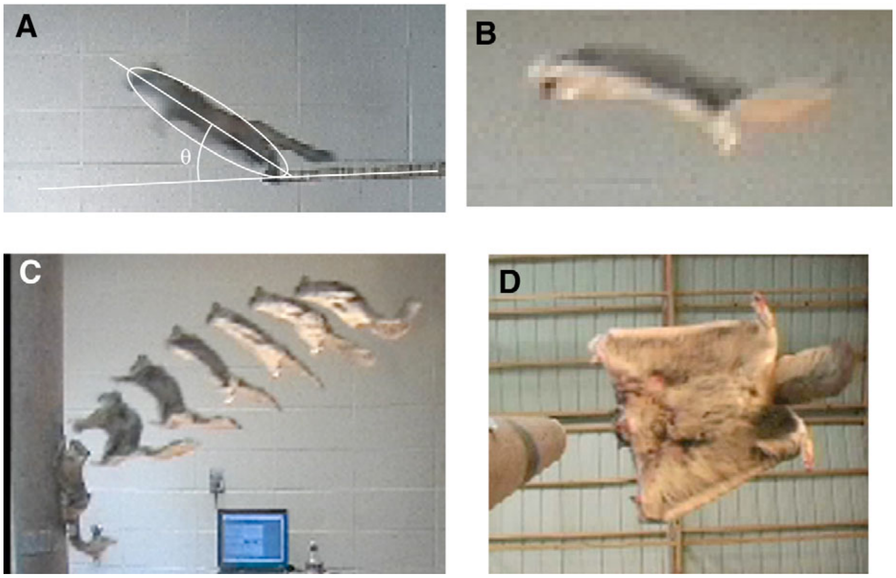


Fig. 2. Video stills of the squirrels in the three postures observed. (A) The forelimbs being abducted prior to the hindlimbs leaving the substrate during take-off, and how the take-off angle, θ, is calculated as the angle between the branch and the major axis of the best-fitting ellipse to the squirrel (excluding its tail). (B) Normal gliding flight, (C) landing from the side and (D) a ventral view landing on the pole on the left. In C, the last few frames of a landing sequence have been superimposed onto one image to demonstrate the landing behaviour, although the penultimate frame had to be omitted for clarity. In this short, 1 m jump, the squirrel initially pitches upwards and flattens its body and tail against the direction of motion. Immediately prior to landing, the head is tilted backwards while the limbs are all pushed forwards with the tail simultaneously rotated back so that it is parallel with the ground.

squirrel from ventral images of a glide. Lateral images were used in conjunction with these to ensure that only frames in which the squirrels were in plane with a calibration bar were used for these measurements.

A calculation was performed to determine the percentage of body weight supported during each measured glide, relative to the equivalent ballistic trajectory (that is the trajectory of an object with the same take-off velocity and angle subject to no drag or lift). For a simple free-falling mass, the gravitational force acting downwards is opposed by any lift generated. The resultant force acting on the body is hence:

$$F = M_\mathrm{b}\mathbf{a} = M_\mathrm{b}\mathbf{g} - L\,, \qquad (1)$$

where M_b=mass (kg), $\mathbf{a}$=resultant acceleration (m s^{-2}), $\mathbf{g}$ is gravitational acceleration (9.814 m s^{-2}) and L is the lift force (N). The percentage weight supported is simply this lift force divided by the animal's weight. Measured take-off angle, θ, velocity, v (m s^{-1}), and jump duration, t (s), are sufficient to calculate the vertical drop, y (m), from the resultant acceleration using the standard kinematic equation below:

$$y = (v\sin\theta)t - \tfrac{1}{2}\mathbf{a}t^2\,. \qquad (2)$$

Therefore, by combining Eqn 1 and Eqn 2 we get an expression for the overall lift force generated during the glide:

$$L = M_\mathrm{b}[\mathbf{g} - (2tv\sin\theta - y)/t^2]\,. \qquad (3)$$

Jumps observed, general mixed model, and other statistics

We measured 79 take-offs and 53 corresponding landings with the number of jumps of each animal at each range specified in Table 1. No landing force data were obtained for the shortest range jumps of 0.5 m, but with this exception, all measured take-off forces have a corresponding landing force. Only one squirrel, young female 1, performed in the barn but it did not leap to the force pole at distances greater than 2.5 m, landing instead on the ground beyond the instrumented pole. This was the only animal to perform at all ranges tested. Unfortunately, young female 2 only cooperated at 0.5, 1 and 1.5 m and the young male at 0.5 and 1 m. Owing to the number of missing data points, the typical multivariate ANOVA could not be applied to our data, and so a general mixed model (Krueger and Tian, 2004) was applied to both take-off and landing forces, with range as a fixed factor and squirrel ID a random factor. Unless otherwise stated, all correlation statistics use Pearson's product moment correlation.

Results

Video stills from the lateral camera illustrate the consistent take-off, gliding and landing postures of the squirrels (Fig. 2). During take-offs, the forelimbs were abducted prior to toe-off enabling the squirrel to immediately adopt gliding posture. During gliding all limbs were abducted creating a cambered wing surface held at a small positive angle of attack. The tail was dorsally flattened, presumably to generate lift. Prior to landing, the squirrel pitched upwards keeping its body and tail in line and flattened against the direction of motion. Immediately prior to landing, the head tilted backwards while the limbs were all pushed forwards with the tail simultaneously rotated back so that it was parallel with the ground. In the example landing sequence (Fig. 2C), the pitch angle of the body changed from approximately 22.5° relative to the horizontal, towards 90° immediately prior to landing.

In the barn, the squirrels tended to have a steeper approach and did not pitch up very much prior to landing. The head still tilted backwards but the tail was rotated forwards towards the vertical. As a consequence of the lower angle of attack, the forelimbs contacted the pole first, causing the body to rotate around rapidly onto the hindlimbs due to the conversion of linear to angular momentum. Occasionally the tail was cambered such that the inside of the curve faced the landing pole. In some jumps, the squirrels were clearly banking or

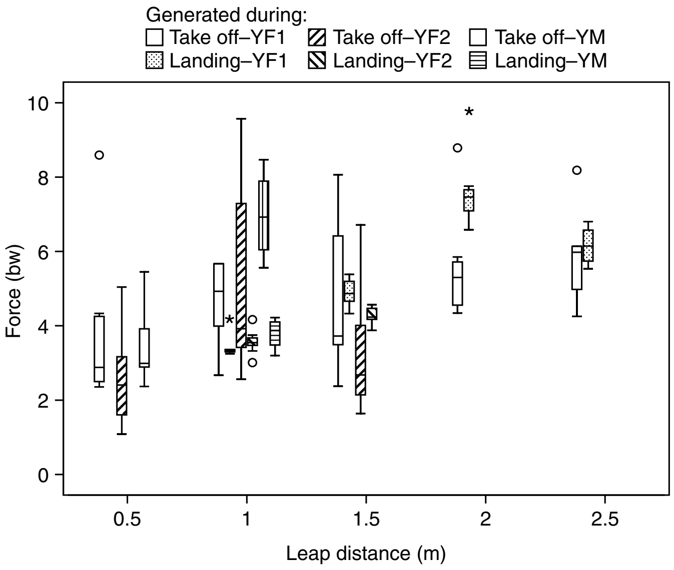


Fig. 3. A box plot directly comparing the landing forces with the corresponding take-off forces for three of the flying squirrels (young females YF1 and YF2, and young male YM) at each horizontal range (from the end of the take-off branch to the landing pole). Asterisks and circles show values that were outside the interquartile range, the former being statistically significantly far away.

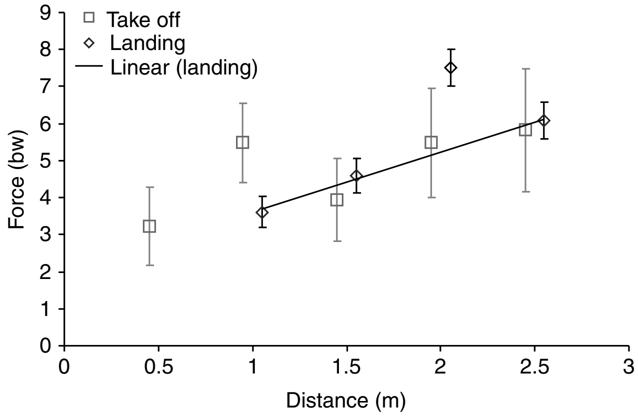


Fig. 4. A graph showing the output from the mixed model statistics of mean take-off and landing forces at each horizontal range. The error bars represent the 95% confidence intervals. By ignoring the few jumps at 2 m, when the squirrel consistently landed at the more rigid base of the pole, the square of the Pearson product moment correlation coefficient (the r^2 value) improves from 0.61 to 0.99.

turning in the penultimate frames to correct misalignment with the pole and in one instance, a subject landed on the side of the pole. As it was simple to calculate the forces for these jumps too, these results were included in our analysis.

A summary of take-off and landing forces recorded as a multiple of body weight is shown in Table 1. There was considerable variation between take-off and landing forces measured for each squirrel at each distance. Take-off forces normalised by body weight increased significantly with leap distance (Fig. 3; r=0.323, P=0.004). The same box plot also shows the positive correlation between landing forces and horizontal range (r=0.816, P<0.001).

The general mixed model introduced above provides statistical verification that normalised take-off forces were significantly dependent on range ($F_{5,11.5}$=45.182, P<0.001) but not squirrel identity (P=0.602). Likewise, landing forces were dependent on range ($F_{4,9.5}$=409.341, P<0.001) but independent of the particular squirrel (P=0.548). The means and 95% confidence intervals produced by the mixed model are plotted in Fig. 4.

All landing and take-off forces are not correlated to one another (r=0.094, P=0.507). A paired sample t-test comparing landing force with its corresponding take-off force for each jump was not statistically significant (t_{51}=0.374, P=0.710). The standard deviations of the mean forces for each animal at each distance are shown in Table 1. Standard deviation in take-off forces at each range is clearly larger than that for landing forces. Excluding the 0.5 m range, for which there is no landing force data, the standard deviation ranges from 1.37 to 6.10 bw for take-off force, compared with only 0.04 to 0.92 bw for landing.

Landing force is positively correlated with angle of descent (r=0.740, P<0.001).

The outputs from all strain gauges were recorded simultaneously, enabling the duration of each glide to be measured. There is, unsurprisingly, a strong positive correlation (r=0.923, P<0.001) between glide distance and glide duration. Mean glide velocity based on the linear distance from take-off to landing position and not the actual trajectory, was strongly positively correlated (r=0.951, P<0.001) with horizontal range. This reached 4.5 m s^{-1} across a horizontal range of 2.5 m.

Average take-off angle for each squirrel at each distance was negatively correlated with range (r=–0.684, P<0.001) (Fig. 5).

Fig. 6 shows the percentage of bodyweight supported by lift during gliding, as a function of horizontal range. The average value for each squirrel at each range is plotted against horizontal range and the error bars represent plus and minus one standard deviation. At ranges of 1.5 m and above, the squirrel was able to support the equivalent of approximately 40% of its weight by gliding, but none when jumping smaller distances. The advantage gained by gliding increases with range (r=0.609, P<0.001).

Landing force was found to be significantly correlated to the position of impact on the pole (r=–0.713, P<0.001).

Glide angles increased steeply with horizontal range until they reached approximately 45° beyond 2.5 m (Fig. 7), the angle at which gliding is distinguished from parachuting, after which they gradually improve as seen by a strong, negative correlation between the 17 longest jumps (r=–0.816, P<0.001). At this point, only one animal was still performing but it did not land on the pole, and instead glided past it and landed on the floor.

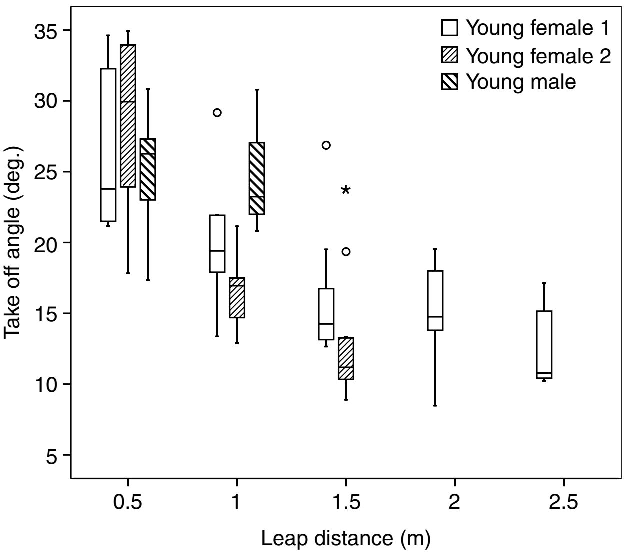


Fig. 5. Average take-off angle for each individual flying squirrel as a function of the horizontal distance travelled in the jump (labelled C in Fig. 3). This implies that the squirrels are planning ahead, which in turn may imply that they are considering their landing. Asterisk and circles, see Fig. 3.

Discussion

In this study, take-off and landing forces were measured for northern flying squirrels traversing various distances between compliant substrates. Extensive analysis of video recordings of their movements was also carried out. To our knowledge no such data has been published before and we believe our results provide more insight into the evolution of gliding in these mammals. We link our observations, where possible, to the following four hypotheses for the divergence from other tree squirrels: (1) to reduce energetic cost of foraging; (2) to maximise the potential foraging area in a given time without thought to transport cost; (3) to improve predation escape capability; and (4) to enable superior control of landing.

Take-off, landing and gliding performance are discussed separately.

Take-off

Flying squirrels generated take-off forces ranging from 1.08 to 9.57 bw. The amount of force was proportional to the distance the animal travelled (Fig. 3). It is logical that squirrels generate a larger take-off force to go further, as ballistic theory dictates they require a higher velocity in order to cover the distance. However, there must be a maximum force the squirrel can generate. Our results suggest this might be approximately 10 bw, which is equivalent to occasional high jump forces at shorter ranges. (These occasional jumps support the idea that flying squirrels jump more forcefully when startled, incidentally.)

The highest take-off angle recorded was 35° and this occurred at the shortest range of 0.5 m, which was short enough that landing position was often higher than take-off position. Take-off angle decreased as range of the jump increased (Fig. 5) but this may have been influenced by a confounding factor, the height of the branch. With sufficient height the animal can afford a shallower take-off angle, allowing it to generate a higher horizontal velocity.

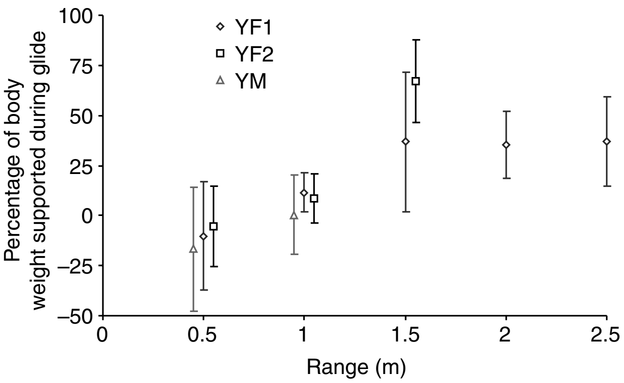


Fig. 6. Percentage of body weight supported by lift during gliding as a function of horizontal range in flying squirrels (young females YF1 and YF2, and young male YM). Values are means for each squirrel at each range ± 1 s.d.

Overall velocities of the squirrels increased with range. The animals usually ran and jumped immediately after release onto the branch, but occasionally it was necessary to startle them. It is unknown if the apparent levelling off of glide angle that we observed for longer jumps is a general trend because we did not obtain results for longer leaps.

Gliding performance

Squirrels used lower glide angles in the lab, but angles near 45° (parachuting) for the longer ranges of 2 m and above in the barn. This may have been a behavioural change due to unfamiliarity, and is based on only one squirrel at these ranges. In a study describing the kinematics of two southern flying squirrels *Glaucomys volans*, glides from both animals were shorter and significantly steeper after moving to a new test arena (Bishop, 2006). However, our measured glide angles improved with increasing range (Fig. 7) and are comparable with similar distance results from two field studies of northern flying squirrels (Vernes, 2001; Scheibe et al., 2006), so it is more likely a consequence of the need for this species (the larger of the two North American species) to reach a higher velocity before it is able to exhibit superior aerodynamic performance. Average glide velocities measured in this study increased with range as would be expected. Observations of the Japanese giant flying squirrel on long glides (Ando and Shiraishi, 1993) sometimes showed an initial steep descent with the glide angle decreasing with increasing velocity, until both became constant. Likewise, northern flying squirrels dropped steeply prior to gliding, and often even managed to gain altitude slightly, just before landing (Vernes, 2001). The squirrels in this study may have initiated a similar behaviour, but the possible ranges were too short for the effect to be noticed. This would help to explain why field observations of northern flying squirrels have reported significantly better glide

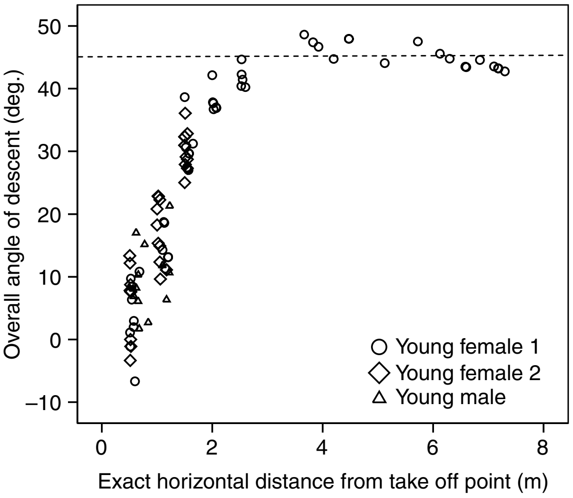


Fig. 7. Scatter plot showing how the glide angle increases with horizontal range until it reaches approximately 45°, represented by a broken line, after which the glide ratio begins to improve slightly. High take-off angles and limited time spent in the air are the factors responsible for the low vales of glide angle across low ranges. Glide angle is strongly negatively correlated with range above 4 m (r=–0.816, P<0.001) where higher glide speeds enable northern flying squirrels to exhibit superior lift to drag ratios.

ratios. In Alaska, USA, Scheibe et al. evaluated 168 glides from 82 different squirrels with mean glide distances of 12.46 m and 14.39 m in successive years, and corresponding mean glide angles were 41.31° and 36.31° (Scheibe et al., 2006). Vernes reports a mean angle of descent of just 26.8° for glides which were longer, averaging 16.4 m (Vernes, 2001). Gliding behaviour is therefore likely to be optimised for significantly longer ranges than were possible in this study.

Flying squirrels use their patagium as a low-aspect-ratio wing, which has good aerodynamic stability at the relatively low speeds involved, generating lift at high angles of attack of up around 40° without stalling (Torres and Mueller, 2004). This shape allows the squirrel to overcome any detrimental rotational momentum that it might have generated during take-off. In the present study, full gliding posture was always initiated before the hindlimbs left the substrate, allowing the angular momentum produced by forelimb abduction to be transmitted directly to the branch, even over the shortest leaps of just 0.5 m. It has been argued (Essner, 2000) that this behaviour enabled the squirrel to begin gliding earlier, resulting in a flatter trajectory with more immediate manoeuvrability and control. We quantified the gliding performance of each squirrel by calculating the percentage of its bodyweight supported during each glide and showed that flying squirrels exploited their unique morphology to generate lift at ranges greater than 1.5 m (Fig. 6). However, these values were negative over 0.5 m, implying that the squirrels generated down-force. It could be that the combination of steep take-off angles with immediate initiation of gliding results in their large patagial surface area working against the squirrels on these steeper take-off angles. Alternatively our estimate for the percentage body weight supported could be slightly conservative. In any case, we have established that the transition from leaping to gliding occurs at a horizontal range of 1.5 m for northern flying squirrels. They are not able to benefit from gliding over distances of less than 1 m, so although the resultant glide angles may appear to be superior at these ranges, this is only a consequence of the higher take-off angles and limited time in the air.

Landing

Landing forces varied between 3.01 and 9.52 times body weight. The impact force on the landing pole was proportional to the range of the leap. This is expected because the measured gliding velocity increased with horizontal distance, reflecting the effects of gravitational acceleration.

The correlation of measured landing force with the contact position of the animal on the pole is due to the compliance decreasing towards the fixed end. Higher forces were experienced by squirrels landing lower down on the pole, where it was relatively stiffer and did not deflect so far. This is inevitable because the kinetic energy of the squirrel becomes the product of reaction force and deceleration distance – proportional to the deflection of the pole given that leg length remains constant. This has an important implication for the use of compliant substrates when quantifying forces for comparison. Ideally, only forces measured at points of equal compliance should be compared directly, or there should be a random scattering of landing positions. This was the case for our results, with the exception of the 2 m range, at which the squirrel consistently landed at the base of the pole. The reason for this is unknown, because the angle between the base of the landing pole and the tip of the take-off branch was consistent at 55° for all ranges. However, by removing the data from the 2 m range (7 data points out of 53), a strong linear relationship can be observed between the means of the other 46 jumps where more compliance was available (Fig. 4). The square of the Pearson product moment correlation coefficient (the r^2 value) improves from 0.61 to 0.99 when the 2 m data is ignored. Such a good linear fit means that the flying squirrels adopt a consistent landing technique. On stiffer substrates, we would expect a similar, but steeper, linear increase in landing force with range.

Over short leaping distances, take-off forces are not significantly different from landing forces (Fig. 3; t-test). This fits with the expectation (see Introduction) that landing forces would not be higher than take-off forces on compliant substrates, as they are on rigid platforms (Demes et al., 1995).

Landing force was correlated with angle of descent, suggesting the squirrels are better able to absorb landing impacts with a flatter approach. Some of the impact force is likely absorbed as a result of the consistent landing posture observed, which it seems the squirrels were unable to accomplish with steeper approaches. During shallower glides the squirrels are able to increase their drag force by transforming the patagia and distichous tail from a cambered surface with low angle of attack, high lift and low drag, to a more parachute-like surface orientated against the direction of motion. Additionally, this posture enabled the squirrel to absorb the remaining impact forces more evenly over its four extended limbs on contact. Aerodynamically, the flying squirrel has a low aspect ratio (close to 1) and glides at low speed so an angle of attack in excess of 40° would be required for it to stall in flight (Torres and Mueller, 2004). The squirrel has additional aerodynamic implications associated with its morphology, such as its fur, so it is not possible to measure whether or not they are actually stalling from our video footage. However, it is clear from the example landing sequence shown in Fig. 2C that the pitch angle of the body has increased to effectively 90° immediately prior to landing, supporting the theory that they deliberately stall themselves (Alexander, 1995).

Caple et al. stated that the vector sum of angular momentum must be conserved during any mid-air movement of a body with no lift or drag (Caple et al., 1983). Although flying squirrels will also be able to generate some external force from their patagium, this could help explain the origin of some of the consistent landing movements observed. For example, the rotations of the head and tail backwards would directly counteract the thrusting of the limbs ventrally, although it is equally likely that the head tilt may be for defence against accidental impact. A falling cat also uses counter-rotations in order to right itself when falling from an upside-down position (McDonald, 1960). Caple's calculations (Caple et al., 1983) also show that some of the morphological features of flying squirrels, such as long forelimbs with dense, distally located mass (hands and feet) and a lightweight tail that can produce lift, are optimisations for controlling pitch and roll. We show that the squirrels were able to reduce landing forces by pitching upwards as they approach, and it is this behaviour which may have applied selective pressure to these morphological features rather than glide range, which increases negligibly in comparison. Increasing forelimb length allows the landing energy to be absorbed over a larger distance. Likewise, the flexed back on impact should further reduce the peak landing force. A falling cat also tries to land with its back arched and all four limbs outstretched towards the ground (McDonald, 1960).

Unfortunately the squirrels could not be persuaded to land on the pole above the relatively small horizontal range of 2.5 m, compared to their normal arboreal glide distances (Vernes, 2001; Scheibe et al., 2006), choosing instead to deliberately manoeuvre past the landing pole and land on the floor. It is possible that the squirrels may have a sense for a maximum speed at which they can safely or comfortably land on a stiff or unknown substrate for a given approach angle. Glide angles achieved at ranges between 3 and 6 m exceeded 45° (Fig. 7), which would normally be defined as parachuting rather than gliding (Oliver, 1951), and we speculate that this is likely to be the most difficult distance for northern flying squirrels to land. The steeper approach angles inhibit their ability to pitch up and absorb the landing across all four limbs simultaneously, and there is more energy to dissipate due to the inevitable increase in velocity with range. Velocity continues to increase above the proposed awkward range but this also improves the flying squirrel's aerodynamic ability, allowing a progressive improvement in approach angle and consequent landing posture. It is likely that these animals would try to avoid making hard landings on tree trunks at this unfavourable range. Vernes reported that in 21% of his 100 glides observed (Vernes, 2001), northern flying squirrels landed on the ground or in dense undergrowth. The other landings were on trees and it should be noted that the mean glide distance was much higher in the Vernes study than ours. Likewise, Scheibe et al. noted that sometimes squirrels released onto a tree trunk at breast height did not climb and glide, choosing instead to jump to the ground and run to a nearby tree (Scheibe et al., 2006). Future experimental designs should consider that northern flying squirrels might be more likely to land on an instrumented pole positioned at a high rather than medium horizontal distance from the take-off position, but this would necessitate an arena allowing sufficient take-off height.

The equation for the linear relationship between landing force and range on the compliant part of the pole is shown on Fig. 4 and can be used to predict the landing force at longer ranges than we were able to measure. However, the squirrels would not keep accelerating indefinitely during long glides; rather their speed would stabilise as they approach terminal velocity. Maximum glide velocities of close to 12 $\mathrm{m\,s^{-1}}$ have been reported (Scheibe et al., 2006), although the weighted means were 6.26 $\mathrm{m\,s^{-1}}$ and 8.11 $\mathrm{m\,s^{-1}}$ in two consecutive years. These values are much higher than our highest observed speed of 4.5 $\mathrm{m\,s^{-1}}$, although this was measured across a relatively much shorter horizontal glide distance. With more time in the air, squirrels must be able to control their trajectories, otherwise they would be subject to extremely high impact forces. Depending on substrate compliance, we can use the equation from Fig. 4 to calculate that squirrels trying to land from an ordinary 16 m glide would be subject to impact forces of upwards of 28 bw if they did not slow themselves, as we have shown, by pitching up and employing air braking.

Evolution of gliding

Hypothesis 1

Hypothesis 1 that gliding developed to reduce the energetic cost of foraging supposes that the squirrels' primary objective should be to maximise range in every jump while minimising the loss in altitude. Therefore, from ballistic theory we would expect the squirrels to jump at close to the optimum take-off angle of 45°, but they did not. As expected, the advantage gained by gliding increases with range. This vertical advantage achieved relative to the ballistic trajectory enables flying squirrels to reach trees beyond normal jumping range, or reduces the amount of climbing required after a glide is completed, thus saving energy. However, during this study flying squirrels did not try to take off at 45°, which would be expected for maximising range, and take-off angle decreased with range. However, the non-optimum take-off angles and frequently observed range-reducing aerial manoeuvres are evidence to suggest that energetic transport cost is not of primary importance to flying squirrels.

Hypothesis 2

If gliding evolved to maximise the foraging area that could be reached in a given time, as proposed by Hypothesis 2, then we would expect the squirrels to glide at high velocities. We have shown that velocity increases with range, and that flying squirrels can generate higher lift forces when travelling further, so we cannot reject the hypothesis that gliding is an optimisation to maximise speed and potential foraging area.

Hypothesis 3

Hypothesis 3 is that gliding evolved primarily to facilitate escape from predation. One might expect that an escaping squirrel would jump horizontally, or downwards given sufficient altitude, in order to ensure that it did not decelerate due to gravity. Bonser and Rayner proposed that starlings may deliberately vary take-off trajectory for predator avoidance (Bonser and Rayner, 1996), but we have shown a negative correlation of the take-off angle with range, suggesting that during this experimentation at least, flying squirrels choose a take-off trajectory to suit their intended destination. Caple et al. stated that all gliders pre-select a landing site, which must be large enough to allow some vertical variation in the contact point (Caple et al., 1983). Vernes also observed that flying squirrels appeared to think about their intended flight path before launching and we saw no evidence to suggest otherwise (Vernes, 2001). Given that the squirrels seem to exhibit this behaviour even during the jumps that were initiated by startling, it seems unlikely that gliding evolved primarily for escape, at least not from high-speed chases.

The ability to make sudden aerial direction changes could potentially help to lose a predator. However, their most likely aerial predator is the owl (Scheibe et al., 1990), and it is unlikely that such sophisticated fliers would be troubled by the relatively clumsy swerving squirrel.

Hypothesis 4

Hypothesis 4 relates the development of flight to the control of landing. Even at the relatively short ranges in this study, we observed direction changes being introduced by rapid beating of the tail from side to side. Additionally, last-second manoeuvres were observed, such as banking and using the tail as a rudder, implying that flying squirrels are able to make precise adjustments to improve their landing. As range increases, any error in take-off trajectory would become more significant without aerial control; in this case squirrels could face serious consequences for misjudging long leaps at the top of the forest canopy.

Flying squirrels choose to initiate a full gliding posture even though they do not produce significant lift during glides of less than 1 m, suggesting that this behaviour is innate. It might be that the squirrel is simply throwing its arms out conveniently widely for rapid rotation of the joint in order to gain forward momentum during take off. They do exhibit a consistent landing behaviour at these distances, with the gliding posture enabling them to pitch upwards as they approach and spread the landing reaction force over all limbs. It is likely that the squirrels deliberately stall themselves by this quick increase of their angle of attack immediately prior to landing.

Landing control of pitch and roll improves much more rapidly than range for the same incremental improvements in forelimb length and tail surface area. Increasing forelimb length simultaneously reduces the landing force further by increasing the deceleration distance. Landing force was correlated with angle of descent, suggesting flying squirrels were unable to pitch up sufficiently to execute the evenly distributed four-limbed landings when approaching steeply, demonstrating the utility of aerial control in longer jumps. Given the reported values of terminal velocity for flying squirrels, and the measured landing forces on compliant substrates that increase with range, we know that if the squirrels could not slow themselves or improve landing posture aerodynamically prior to landing, they would have to sustain impact forces of upwards of 28 bw.

Evolution of gliding in flying squirrels has undoubtedly reduced their energetic cost of transport, while improving potential foraging area and response to predation, but we conclude that the selective pressure for their divergence from ground squirrels was the improvement of landing control.

Conclusions

Take-off and landing forces generated by northern flying squirrels are both positively correlated with horizontal range, at least up to 2.5 m. The maximum take-off force measured was 9.57 bodyweights, although the squirrels would occasionally produce close to this force when jumping only short distances, most likely a natural behavioural response to alarm. Take-off forces were not significantly different to the corresponding landing forces on these similarly compliant substrates. They are able gliders, abducting all limbs to create a wing-like surface, which is held at a low angle of attack for maximum lift/drag ratio. Glide angle increased rapidly with horizontal range up to approximately 4 m, before progressively improving, suggesting that gliding in northern flying squirrels is optimised for significantly longer ranges than were possible in this study.

Any compliant force-measuring device will likely have some variation in its compliance along its length. In the case of a cantilever beam, this begins to behave more like a rigid instrument towards its fixed end. Valuable comparisons can only be made between forces measured at known points of equal compliance. If this is not possible, then sample sizes should be chosen to ensure a random scattering of landing positions.

It seems unlikely that gliding evolved in flying squirrels to reduce the energetic cost of transport even though the measured lift generated would lessen the amount of climbing required. Take-off angle decreased with range without getting close to 45°, the value for maximum ballistic range, and further height would be lost to the aerial manoeuvres occasionally observed. The flying squirrels in this study did not attempt to make either unplanned or deliberately unpredictable take offs, casting doubt on the theory that gliding might improve predatory escape response.

Gliding might have evolved to maximise the foraging area that could be reached in a given time. High glide speeds were measured and this velocity increases with range, but the development of improved landing control is a necessary consequence of faster flight. We provide evidence that if northern flying squirrels could not slow themselves aerodynamically from terminal velocity, prior to landing, they would have to try and sustain impact forces of upwards of 28 bw. Flying squirrels seem to innately adopt a gliding posture on take off, even during leaps of less than 1 m when no vertical advantage is gained, but this leaves them better prepared for aerial control. At these low distances, a consistent landing strategy was exhibited by flying squirrels, allowing the impact force to be spread over all four limbs and their arched back, thanks to a dramatic pitch upwards immediately prior to contact with the pole. This rapid increase of their angle of attack immediately prior to landing is likely a behaviour evolved to enable rapid deceleration by stalling, although this would have greater effect at high speeds. We conclude that at divergence, small glide producing surfaces were developing in flying squirrels allowing mid-air adjustments in pitch and roll, and improving their resilience during high-speed arboreal transport.

List of symbols and abbreviations

$\boldsymbol{a}$	resultant acceleration (of centre of gravity)
bw	body weight
F	force
$\boldsymbol{g}$	gravitational acceleration
k	force calibration constant
L	lift force
M_b	body mass
r^2	the square of the Pearson product moment correlation coefficient
t	jump duration (time between take off and landing)
v	velocity
x	strain gauge signal voltage
y	vertical drop
θ	take-off angle

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