# Three-dimensional launch kinematics in leaping, parachuting and gliding squirrels

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## Summary

Leaping, parachuting and gliding are the primary means by which arboreal squirrels negotiate gaps in the canopy. There are notable differences among the three locomotor modes with respect to mid-air postures and aerodynamics, yet it is unclear whether variation should also be expected during the launch phase of locomotion. To address this question, launch kinematic profiles were compared in leaping (*Tamias striatus*), parachuting (*Tamiasciurus hudsonicus*) and gliding (*Glaucomys volans*) squirrels. Animals were filmed launching to the ground from a platform using high-speed video. Statistical comparisons among taxa indicated that only six out of 23 variables were significantly different among the three species. Two were associated with tail kinematics and were a consequence of tail morphology. Two were forelimb-related and discriminated gliding from non-gliding taxa. The remaining two variables were performance attributes, indicating significant variation among the species in take-off velocity and horizontal range. The absence of significant differences in hindlimb kinematics indicates that propulsion is essentially identical in leaping, parachuting and gliding squirrels.

Key words: gliding, parachuting, leaping, take-off, kinematics, squirrel, *Tamias striatus*, *Tamiasciurus hudsonicus*, *Glaucomys volans*.

## Introduction

Squirrels (Family Sciuridae) probably originated from an arboreal ancestry and first appear in the fossil record during the Eocene (Emry and Thorington, 1982; Thorington et al., 1997). Since then, they have undergone a remarkable radiation into a multitude of arboreal and terrestrial environments, ranging from deserts to alpine meadows and forests. With respect to arboreality, the radiation has resulted in the use of an array of locomotor modes by squirrels for negotiating gaps in the canopy, principally through leaping, parachuting or gliding. These locomotor modes are of critical interest since, together, they comprise a considerable proportion of the behavioral repertoire of arboreal squirrels (R. L. Essner, in preparation). In addition, they may have important effects on fitness through reduced costs of transport (compared with descending to the ground and climbing up), predator avoidance or foraging optimization (Rayner, 1981; Scheibe et al., 1990; Keith et al., 2000). While arboreal leaping has been well studied in primates, it remains unexamined in squirrels and other mammalian taxa. Similarly, detailed studies of mammalian parachuting and gliding locomotion are lacking.

The absence of comparative studies involving leaping, parachuting and gliding may be attributable in part to the treatment of these locomotor modes as continuous rather than discrete behaviors (Pennycuick, 1986). For example, parachuting and gliding have traditionally been defined on the basis of the angle of descent from the horizontal

($>45°$=parachuting, $<45°$=gliding), rather than upon specific morphological or behavioral characteristics (e.g. Oliver, 1951; Rayner, 1981). While this definition presents a useful way of classifying locomotion in terms of basic aerodynamics, it is of limited utility for classifying behavior since many animals can actively choose their angles of descent and because these angles are dependent upon unpredictable air currents (Moffett, 2000). Moreover, if a ballistic component is included, it could result in 'gliding' angles over short to moderate distances, making it difficult to apply the criterion universally. A more biologically relevant criterion would incorporate the features that enable an organism to control its descent, rather than strictly defining locomotion on the basis of aerodynamic performance (Moffett, 2000).

Defining leaping, parachuting and gliding on the basis of mid-air postural behavior is a useful criterion for examining functional attributes. Sciurid arboreal leaping is considered here to be a relatively unspecialized locomotor mode, accompanied by minor aerodynamic effects, in which the limbs remain adducted during the airborne phase (Fig. 1A). In contrast, sciurid parachuting is defined as mid-air limb abduction with flexion of the distal elements in order to assume a flattened posture, resulting in significant amounts of drag (Fig. 1B). Finally, sciurid gliding is defined as mid-air limb abduction with full extension of the distal limb elements, generating relatively large amounts of lift (Fig. 1C).
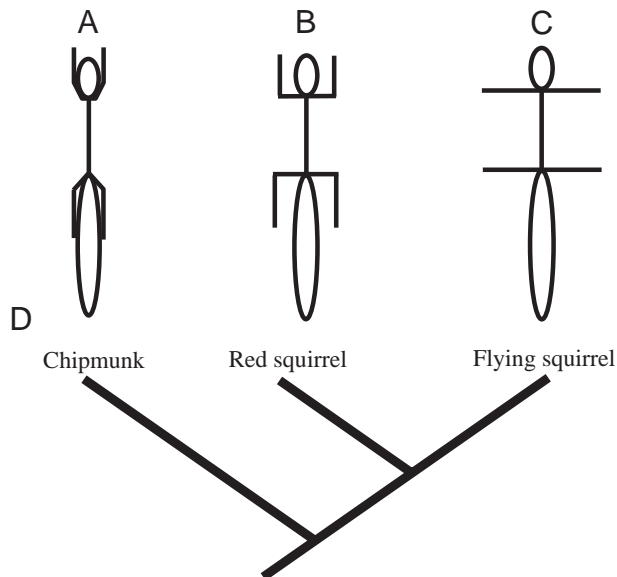
Fig. 1. Defining sciurid arboreal locomotion. Discrete airborne postures are used to define locomotor mode. (A) Chipmunks are relatively unspecialized semiarboreal leapers that exhibit an adducted limb posture in mid-air. (B) Red squirrels are arboreal parachuters that exhibit a flattened posture in mid-air characterized by abduction of the proximal limb elements and flexion of the distal limb elements. (C) Flying squirrels are arboreal gliders that exhibit an abducted posture in mid-air with extension of the distal limb elements. (D) Phylogenetic relationships of the sciurid taxa included in this study (taken from data in Hight et al., 1974; Oshida et al., 1996; Roth, 1996).

Despite key differences among leaping, parachuting and gliding locomotor modes with respect to mid-air posture and associated aerodynamics, it is currently unclear whether such differences are apparent during the initial phase of locomotion, prior to the squirrel becoming airborne. Indeed, there are reasons for suspecting that the locomotor modes may initially be indistinguishable. For example, there seems to be a general reliance on hindlimb propulsion within sciurids. Keith et al. (2000) demonstrated that active launching is relatively inexpensive for a gliding squirrel and suggested that a hindlimb-driven 'leaping' launch may reduce the distance at which gliding becomes cost-effective by improving glide velocity or glide angle. It is not surprising then that parachuting and gliding squirrels actively rely on their hindlimbs for generating propulsion, rather than passively dropping into a parachute or glide (e.g. Keith et al., 2000). Moreover, since the functional demands of take-off are exceptionally high (e.g. Demes et al., 1995, 1999), they may act to limit the degree of variation in hindlimb kinematics among the three locomotor modes. In addition, it is not known whether morphological elements such as the forelimbs and tail, which contribute less significantly to propulsion than the hindlimbs, are free to exhibit kinematic variation. If they are, such variation could help to define these locomotor modes further.

To test for functional differences in the launch phase during leaping, parachuting and gliding locomotion, three-dimensional kinematic data were collected in the eastern chipmunk *Tamias striatus*, a semiarboreal leaper, the red squirrel *Tamiasciurus hudsonicus*, an arboreal parachuter, and the southern flying squirrel *Glaucomys volans*, an arboreal glider. These three North American species represent major lines of divergence within squirrels and provide a good sample of sciurid diversity (Fig. 1D). Phylogenetic evidence provided by morphological, molecular and immunological data points to a sister-group relationship between tree squirrels and flying squirrels, with chipmunks branching off relatively early in the history of the group (Fig. 1D; Hight et al., 1974; Oshida et al., 1996; Roth, 1996). The three taxa included in this study are of relatively similar body mass (chipmunk 99±1.1 g, *N*=5; red squirrel 181±5.7 g, *N*=5; flying squirrel 107±1.9 g, *N*=5; means ± S.E.M.) compared with other sciurids, which range in mass from 10 g to 7.5 kg (Nowak, 1991). In addition, there is some degree of proportional variation among the three species, presumably related to locomotor variation. In general, the fore- and hindlimbs are elongated relative to vertebral column length as the degree of arboreality increases. Thus, semiarboreal chipmunks possess relatively short limbs; at the other extreme, highly arboreal flying squirrels possess relatively elongated limbs (Bryant, 1945). Hence, these three species provide a suitable test for functional differences associated with the launch phase of leaping, parachuting and gliding.

In this study, I define and compare the launch phases in three species that exhibit leaping, parachuting and gliding locomotion, and relate launch movements to differences apparent during the airborne phase. Kinematic variation is then compared with morphological variation to examine the morphological, behavioral and performance bases for differences in arboreal take-offs in squirrels.

## Materials and methods
### Kinematic analysis

Adult animals (eastern chipmunk *Tamias striatus* (Illiger, 1811), red squirrel *Tamiasciurus hudsonicus* (Trouessart, 1880) and southern flying squirrel *Glaucomys volans* (Thomas, 1908)) were collected from the wild and maintained in a colony at Ohio University. Launching trials were filmed in the laboratory with two orthogonally placed JVC GR-DVL9800U high-speed digital camcorders at 120 Hz with the aid of two Nova-Strobe DA Plus stroboscopes (Monarch Instrument). A preliminary study of the three species under natural conditions indicated that horizontal take-offs were the most frequently used method of launching. Animals were therefore filmed in dorsal and lateral views as they launched from a horizontal platform 1.5 m above the ground. The launch platform was constructed from a 5 cm×20 cm×30 cm pine board supported by metal shelf brackets attached to a vertical stand. The surface of the platform was covered with green indoor/outdoor carpet to prevent slipping during the launch. Launches were part of an escape response elicited by tapping the platform immediately behind the tail.

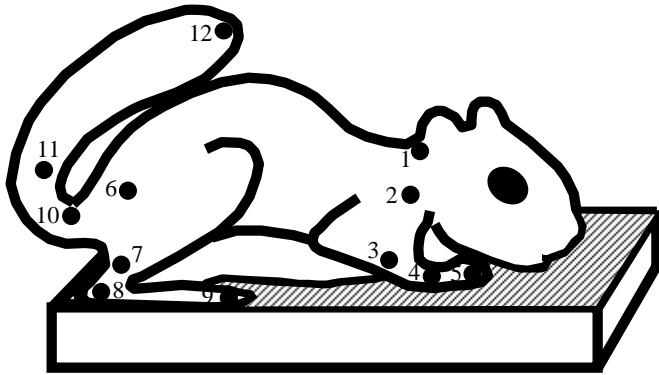Animals were shaved on the right side of the body, and

Fig. 2. Landmarks used to describe limb, body and tail movements in squirrels during the launch phase: 1, occiput; 2, shoulder over the glenoid fossa; 3, point slightly above wrist; 4, wrist; 5, base of the fifth phalanx of the manus; 6, hip over the greater trochanter; 7, point slightly above ankle; 8, ankle at the lateral malleolus; 9, base of the fifth phalanx of the pes; 10, base of the tail; 11, point slightly above tail base; 12, tip of the tail.

markers (5.0 mm cotton pom-poms) were glued over the joint centers to determine joint kinematics for the body, limbs and tail (Fig. 2). Because of problems with skin movement, estimating the location of the knee and elbow using landmarks proved to be unreliable. Instead, these angles were estimated trigonometrically, using limb lengths measured from X-rays to construct two sides of a triangle and video measurement to construct the third side. In addition, markers (landmarks 3 and 7; Fig. 2) were placed slightly above the wrist and ankle, in line with the elbow and knee, to estimate the wrist and ankle angles.

Five individuals (of each species) were filmed, and data from five trials per individual were used in the kinematic analysis. In total, 75 take-offs were included in the analysis (25 per species). Horizontal distances were recorded for all the trials, and only the longest jumps for each individual for which all landmarks were visible were included. Images were captured from both camera views using Ulead VideoStudio v.4.0 and imported into APAS motion-analysis software (Ariel Dynamics) for three-dimensional kinematic analysis. The APAS trim module was used to synchronize the dorsal and lateral images on the basis of a shared kinematic event. The frame at which the toe was last in contact with the platform was used as the synchronization point. Launch sequences were digitized using the autodigitizing function in the digitizing module. Once digitized, sequences were imported into the transformation module to convert the separate sets of two-dimensional coordinates into a unified set of three-dimensional coordinates. Data were unfiltered prior to their input into the display module, where three-dimensional angles were calculated and kinematic plots were recorded.

### Kinematic variables

#### Hindlimb and tail variables

A series of angular and timing variables was taken from each launch sequence to describe and compare statistically the three-dimensional movements of the limbs (see Table 1). Knee and ankle angles were measured to describe movement of the hindlimb during the launch. Knee angles were calculated by measuring the lengths of the femur and tibia from X-rays and using video measurements to obtain the distance between the hip and ankle markers. Ankle angles were calculated using the angle formed by the tibia marker (placed slightly above the ankle, in line with the knee), the ankle and the toe. Minimum, maximum and excursion values for the hindlimb joints were determined and included in statistical comparisons. Tail movement (dorsiflexion/ventroflexion) was described by the angle formed by the point slightly above tail base, the base of the tail and a point projected directly beneath the base of the tail. Minimum and maximum values for the tail angle were also included in statistical comparisons.

#### Forelimb variables

Movement of the entire forelimb was described by measuring angles of forelimb protraction and forelimb abduction. Forelimb protraction was measured by the angle formed by the wrist, the occiput and the base of the tail and describes the movement of the entire limb with respect to the long axis of the body. Forelimb abduction was measured by the angle formed by the wrist, the occiput and a point that was projected directly beneath the occiput. It describes the movement of the limb with respect to an axis running dorsoventrally through the midline of the body. Adduction brings the forelimb closer to the midline of the body, whereas abduction moves it farther away.

During the initial part of the take-off sequence, the forelimbs remain in contact with the platform. At approximately the onset of the propulsive phase, the forelimbs begin to lift from the platform and are brought forward towards the head. The forelimbs were not digitized until they began to lift off since the landmarks were not clearly discernible prior to that point. The timing of this event relative to the onset of a countermovement phase was measured as time to hand-off. Elbow and wrist angles were also measured to describe the position of the forelimb joints. The starting and ending values for these angles were included in the statistical analysis.

#### Performance variables

Performance variables are those characteristics that can be related to take-off performance. They include phase durations, take-off velocity and take-off angle, all of which have effects on horizontal distance (Emerson, 1985). The durations of the preparatory and countermovement plus propulsive phases as well as the entire take-off event were measured from video recordings. Take-off velocities were measured by using the landmark located at the base of the tail (a relatively stable point during the launch sequence) to generate a displacement/time curve and obtaining the slope from the last five frames prior to loss of contact with the platform. Take-off angles were measured using the angle formed by the occiput, the toe and the horizontal and averaging the three frames prior to loss of

contact with the platform. Horizontal range was measured as the horizontal distance from the edge of the launch platform to the center of the landing site on the ground.

### Multispecies comparisons

To illustrate graphically movement patterns for the forelimbs, hindlimbs and tail, mean kinematic profiles were constructed. Data from individuals from each species were pooled, and the means (± S.E.M.) of five trials were calculated from trials exhibiting the same total duration. To compare differences among species statistically, a one-way repeated-measures analysis of variance (ANOVA) was performed on a total of 23 kinematic variables, including timing, angle and performance variables (see Table 1). For each variable, the analysis was run on five trials each from each of the five individuals per species. A repeated-measures design has the advantage of testing differences in the main effects after variation within individuals has been extracted. The *a priori* choice to use the same individuals repeatedly was made to control for the problem of interindividual variation and because the within-subjects design provides more conservative tests for significance than standard analysis of variance tests since the *F*-ratios for the main effects and their interaction are calculated by dividing the mean square rather than the error mean square

(Zolman, 1993). A sequential Bonferroni correction (Rice, 1989) was used to reduce the risk of making a Type I error due to multiple comparisons. Alpha was set at 0.05; however, Bonferroni correction removed marginal values from significance. *Post hoc* tests were performed on significantly different variables to identify differences among species. All statistical analyses were performed using Systat v.6.1.

## Results

Representative video frames portraying a single launch in a flying squirrel are presented in Fig. 3. Mean kinematic profiles for the hindlimbs, tail and forelimbs (all three species) are presented in Figs 4 and 5. Species kinematic data and analysis of variance results are presented in Table 1. Because hindlimb kinematics were similar for all three species, mean kinematic values reported in the text are pooled for the knee and ankle. All other data represent values for particular species.

### Phases of the launch

Three distinct phases were identified in the launch sequence of individuals from all taxa investigated (Figs 3, 4). The first phase was termed the preparatory phase. It was characterized by a preliminary hop that transported the hindlimbs forward to

Table 1. *Results of a repeated-measures analysis of variance of launch kinematics in chipmunks, red squirrels and flying squirrels*

|  | Chipmunk | Red squirrel | Flying squirrel | *P* |
|---|---|---|---|---|
| **Joint timing and angles** |  |  |  |  |
| Knee minimum angle (degrees) | 49.7±1.4 | 52.5±2.0 | 40.5±1.4 | 0.031 |
| Knee maximum angle (degrees) | 110.0±1.7 | 114.1±3.7 | 104.0±2.9 | 0.300 |
| Knee excursion angle (degrees) | 60.3±1.7 | 61.7±3.8 | 63.4±3.3 | 0.906 |
| Ankle minimum angle (degrees) | 23.6±1.9 | 33.1±2.0 | 16.8±1.7 | 0.019 |
| Ankle maximum angle (degrees) | 127.2±15.7 | 133.5±5.4 | 133.3±2.9 | 0.716 |
| Ankle excursion angle (degrees) | 103.6±2.6 | 100.4±5.3 | 116.6±2.9 | 0.144 |
| Tail minimum angle (degrees) | 126.7±8.6 | 103.7±4.4 | 70.9±3.8 | 0.001* |
| Tail maximum angle (degrees) | 193.5±6.4 | 118.1±5.9 | 139.5±3.2 | 0.001* |
| Protraction angle at hand-off (degrees) | 46.9±1.0 | 43.0±0.8 | 47.2±1.1 | 0.142 |
| Protraction angle at toe-off (degrees) | 57.5±11.9 | 60.3±9.7 | 59.8±2.0 | 0.746 |
| Abduction angle at hand-off (degrees) | 67.6±2.1 | 54.1±1.8 | 64.4±2.6 | 0.172 |
| Abduction angle at toe-off (degrees) | 56.5±2.3 | 41.3±2.8 | 71.5±2.1 | 0.001* |
| Time to hand-off (ms) | 30 ±2.0 | 20±1.9 | 60±5.0 | 0.001* |
| Elbow angle at hand-off (degrees) | 156.6±5.6 | 168.1±4.6 | 133.7±7.2 | 0.197 |
| Elbow angle at toe-off (degrees) | 70.5±3.1 | 68.5±5.6 | 71.9±4.0 | 0.947 |
| Wrist angle at hand-off (degrees) | 145.6±3.5 | 156.9±2.7 | 153.1±2.8 | 0.195 |
| Wrist angle at toe-off (degrees) | 131.1±5.1 | 138.1±3.8 | 110.9±3.9 | 0.084 |
| **Performance variables** |  |  |  |  |
| Take-off velocity (m s$^{-1}$) | 2.3±0.05 | 3.0±0.08 | 2.5±0.06 | 0.001* |
| Horizontal range (m) | 1.6±0.04 | 2.3±0.07 | 1.9±0.05 | 0.002* |
| Take-off angle (degrees) | 9.7±2.5 | 21.0±2.2 | 12.0±2.6 | 0.402 |
| Preparatory duration (ms) | 60±4.0 | 70±4.0 | 70±0.005 | 0.808 |
| CM+propulsive duration (ms) | 60±2.0 | 50±2.0 | 90±0.01 | 0.377 |
| Total duration (ms) | 120±4.0 | 130±5.0 | 160±0.006 | 0.061 |

Values are means ± S.E.M. (*N*=5 trials per individual, 5 individuals per species; thus *N*=25 for each mean).

CM, counter movement.

Significance following sequential Bonferroni correction is indicated by an asterisk.

the edge of the platform. The preliminary hop resulted from extension of the knee and ankle (pooled means ± S.E.M., $N$=75, knee 72.3±1.9°; ankle 67.8±2.2°), flexion during the swing phase (knee 48.5±1.9°; ankle 36.8±2.2°) and extension as the toe made contact with the platform (knee 71.1±1.5°; ankle 56.3±2.1°). In contrast, the tail and forelimbs remained relatively stationary during the preparatory phase (Figs 3, 4). As mentioned above, forelimb movement was not quantified until approximately the onset of the propulsive phase because of the difficulty of discerning the landmarks. In general, the preparatory phase was remarkably stereotyped in all sciurid launches.

The second phase was termed the countermovement phase and was initiated immediately following the preparatory phase

(Fig. 3). This phase began at toe-down and was characterized by flexion of the knee and ankle (knee 47.6±1.6°; ankle 24.5±1.9°) producing a countermovement important for maximizing take-off velocity (Zajac, 1993). The countermovement was followed by a propulsive phase characterized by rapid extension (knee 109.4±2.8°; ankle 131.3±8.0°; means ± S.E.M., $N$=75), until the animal lost contact with the platform (Fig. 4). The propulsive phase was typified by dorsiflexion of the tail and protraction of the forelimbs (Fig. 3).

### *Kinematic patterns of the hindlimb and tail*

In general, hindlimb kinematic profiles are virtually identical in all three species. The remarkable similarities observed in the kinematic profiles of the knee and ankle (Fig. 4) are further
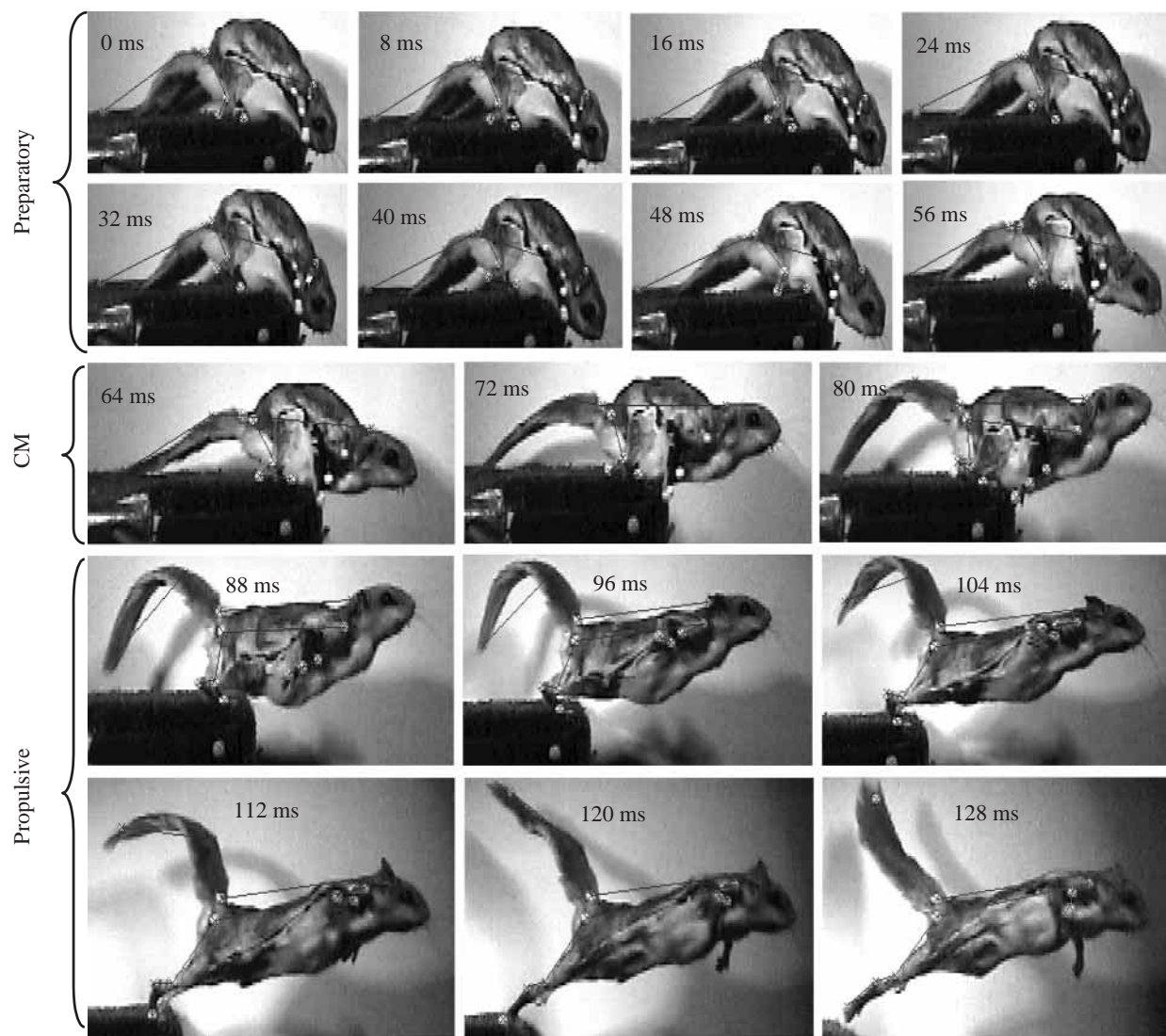


Fig. 3. Representative video frames portraying a single take-off sequence during a launch in the flying squirrel. Three distinct phases were identified: (i) the preparatory phase is characterized by a stereotyped preliminary hop that transports the hindlimbs forward to the edge of the platform; (ii) the countermovement (CM) phase is characterized by flexion of the knee and ankle, producing a countermovement that increases take-off velocity; (iii) the propulsive phase immediately follows the countermovement phase and is characterized by rapid extension of the knee and ankle until the animal loses contact with the platform. Note that, during the propulsive phase, the tail is dorsiflexed and the forelimbs are protracted. Landmarks (cotton pom-poms)=5 mm.

reinforced by the absence of significant differences among species in the hindlimb joint angle variables included in the repeated-measures analysis of variance (Table 1).

In contrast to the hindlimb kinematics, the profile of the tail during the propulsive phase indicates a divergence among the three species with respect to tail dorsiflexion. Chipmunks dorsiflex the tail to the greatest extent (mean 193.5 °), followed by flying squirrels (mean 139.5 °) and red squirrels (mean 118.1 °; means ± S.E.M., $N$=25; Table 1). In addition, the three species differ with respect to minimum tail angle during the propulsive phase. Flying squirrels initiate the propulsive phase with the tail still in contact with the platform (Fig. 3), resulting in a low minimum tail angle (mean 70.9 °), compared with red squirrels (mean 103.7 °) and chipmunks (mean 126.7 °; Table 1). Analysis of variance revealed that minimum and maximum tail angles differ significantly among the three taxa (both $P$<0.001; Table 1).

### Kinematic patterns of the forelimb

Forelimb protraction during the propulsive phase is similar in all three taxa. They all gradually bring the forelimbs forward from approximately 45 ° of protraction at the onset of hand-off to approximately 65 ° at toe-off (Fig. 5). In contrast, there is a divergence among taxa with respect to forelimb abduction. The angle of forelimb abduction at hand-off does not differ significantly ($P$=0.172) but, by toe-off, there is a significant difference among the taxa ($P$<0.001; Table 1). Flying squirrels were the only species that abducted the forelimb prior to becoming airborne, indicated by an increasing forelimb abduction angle (from 64.4 ° at hand-off to 71.5 ° at toe-off; mean values; Table 1; Fig. 5). The other two species show a decrease in the abduction angle (mean 67.6–56.5 ° in chipmunks; mean 54.1–41.3 ° in red squirrels), indicating adduction.

Besides forelimb abduction, the timing of hand-off is the only other significant difference involving the forelimb. The time from the onset of the countermovement phase (toe-down) to the point when the hands are lifted from the platform was significantly longer in flying squirrels (mean 60 ms) than in red squirrels (mean 20 ms) or chipmunks (mean 30 ms; Table 1).

### Launch performance

All three species differed significantly with respect to take-off velocity ($P$=0.001; Table 1). The mean take-off velocity for chipmunks was 2.3 m s$^{-1}$, followed by flying squirrels with a mean take-off velocity of 2.5 m s$^{-1}$. Red squirrels exhibited the best performance, with a mean take-off velocity of 3.0 m s$^{-1}$ (Table 1). Similarly, all three species differed significantly with respect to horizontal range. The mean range for chipmunks was only 1.6 m, while flying squirrels and red
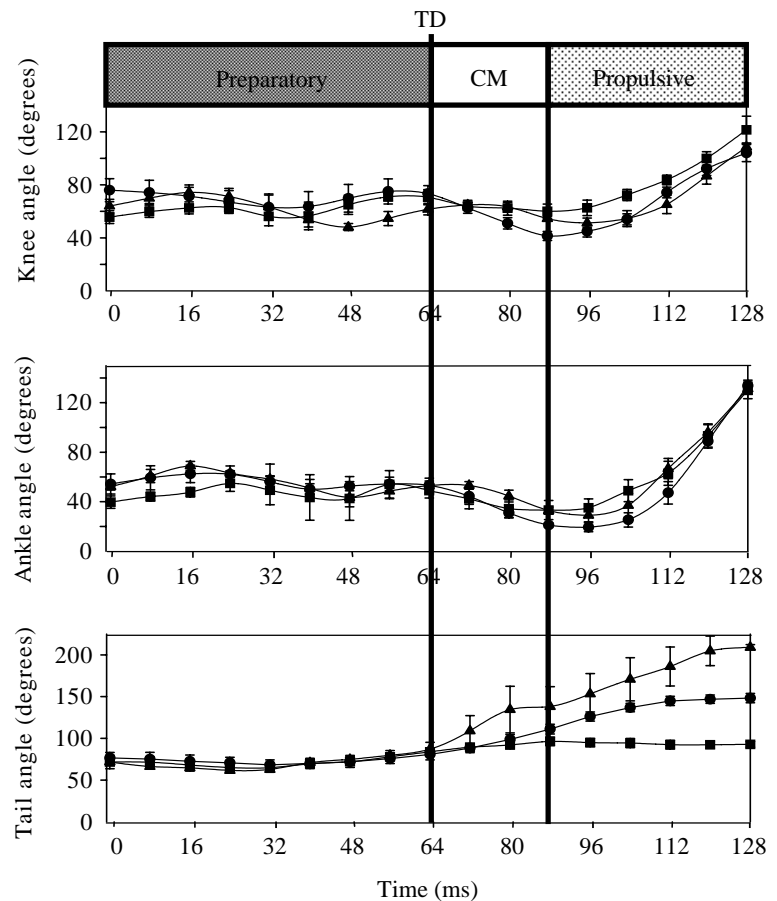


Fig. 4. Mean kinematic profiles of the hindlimb and tail in chipmunks (triangles), red squirrels (squares) and flying squirrels (circles). All three species exhibit similar hindlimb kinematics and share a preparatory phase with a preliminary hop. The foot is initially extended during the preliminary hop, then flexed during transport and extended once again as it is set back down. Toe-down (TD) marks the beginning of the countermovement (CM) phase characterized by flexion of the knee and ankle. This is followed by extension during the propulsive phase. Tail kinematic profiles indicate a divergence among the three species, with chipmunks exhibiting the greatest amount of dorsiflexion, followed by flying squirrels and red squirrels. Values are means ± S.E.M., $N$=5 trials per species.

squirrels performed better, with mean ranges of 1.9 and 2.3 m, respectively. In contrast, take-off angles, although higher in red squirrels (mean 21.0 °), were not significantly different from those of flying squirrels (mean 12.0 °) or chipmunks (mean 9.7 °; Table 1) because of a strong interaction effect between species and individual. No significant differences were found in any of the remaining performance variables.

## Discussion
### Hindlimb kinematics

Despite relying upon different locomotor modes and considerable ecological and morphological differences, the three species in this study do not differ with respect to hindlimb kinematics during the launch phase. This suggests that propulsion is relatively unspecialized in sciurids, irrespective
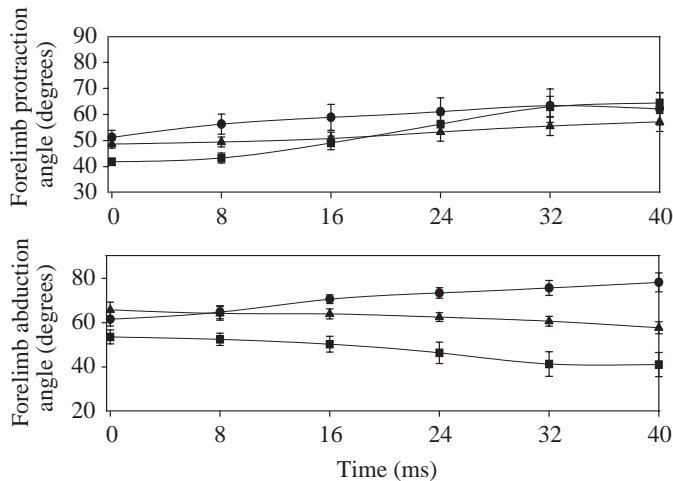
Fig. 5. Mean kinematic profiles of the forelimb in chipmunks (triangles), red squirrels (squares) and flying squirrels (circles). Protraction brings the forelimbs closer to the head and is indicated by an increasing angle. A protraction angle of 90° indicates that the forelimbs have been brought forward to the level of the occiput. All three species exhibit similar values for forelimb protraction, bringing the forelimbs from approximately 45° at the onset of hand-off to approximately 65° at toe-off. Forelimb abduction moves the forelimbs away from the midline of the body and is indicated by an increasing angle. Forelimb adduction moves the forelimbs closer to the midline of the body and is indicated by a decreasing angle. An abduction angle of 90° indicates that the forelimbs are fully abducted to the level of the occiput, while an angle of 0° indicates that the forelimbs are fully adducted to the midline. Flying squirrels abduct to approximately 72° before losing contact with the platform. The other two species show a decrease in the abduction angle, indicating that they are adducting the forelimbs during the propulsive phase. Values are means ± S.E.M., *N*=5 trials per species.

of locomotor mode. While it is possible that one or more of the taxa included in this study have converged upon identical patterns for generating propulsion, the most parsimonious explanation is that the three species investigated have retained this pattern from a common ancestor. Given that chipmunks, tree squirrels and flying squirrels are thought to have diverged in the late Oligocene (Black, 1963), the high degree of conservatism seems especially remarkable and indicates considerable constraint on the launch.

Despite variation in limb proportions among chipmunks, red squirrels and flying squirrels, they are classified as small-bodied leapers compared with the range of size variation that has been examined in primates (e.g. Demes et al., 1996). In general, small-bodied leapers are limited by hindlimb length, while large-bodied leapers are limited by force-generating capacity (Bennet-Clark, 1977; Emerson, 1985; Demes and Günther, 1989; Demes et al., 1996; Preuschoft et al., 1996). This scaling phenomenon has resulted in a dichotomy in the leaping kinematics of small-bodied *versus* large-bodied primates based upon a differing reliance on proximal *versus* distal limb segments for generating propulsion (Demes et al., 1996). On the basis of the limb kinematics presented in the

present study, squirrels appear to be launching like small-bodied primates, relying more upon the ankle (mean ankle excursion 106.8°) than the knee (mean knee excursion 61.8°) for propulsion. More studies are needed over a range of body masses to determine the degree to which generalized arboreal mammals, and squirrels in particular, fit this allometric pattern. Nevertheless, it is noteworthy that the differences in hindlimb morphology over the subset of sciurid size ranges (approximately 100–200 g) used in this study were not substantial enough to have an effect on hindlimb kinematics.

### Morphologically based kinematic differences

Both the variables describing movement of the tail were significantly different. Tail dorsiflexion is frequently observed in leaping animals and is an inherent response that balances the angular momentum generated by counterclockwise rotation (when viewed from the right) of the pelvis during the launch (Emerson, 1985; Günther et al., 1991). However, the degree of response of the tail is dependent on its moment of inertia [mass×(radius of gyration)$^2$]. Thus, a longer tail with the center of mass located farther from the axis of rotation will respond less than a shorter tail with the mass concentrated closer to the axis of rotation (Hall, 1995). Consistent with this principle, red squirrels have the longest tails, followed by flying squirrels and then chipmunks (R. L. Essner, personal observation). This fits the pattern identified by Scheibe et al. (1990) that arboreal non-gliding forms generally have the longest tails, followed by gliding and ground-dwelling forms.

In general, the tail movement in flying squirrels was more stereotyped than in the other taxa. This probably explains their significantly lower minimum angle for the tail. Flying squirrels always began the propulsive phase with the tail in contact with the platform and in line with the long axis of the body. In contrast, chipmunks and red squirrels often began the propulsive phase with the tail elevated or directed to one side. This is illustrated by the greater standard errors associated with their tail movements (Table 1). A possible explanation may be that flying squirrels are constrained to move in a more controlled manner since their dorsoventrally flattened tails have aerodynamic properties that could initiate detrimental rotations of the body during the initial airborne phase. More data are needed to determine the exact role of the tail in leaping and gliding.

The significant difference in the timing of hand-off can also be explained by morphological variation. This variable discriminates flying squirrels from the two non-gliding taxa. In contrast to the more subtle differences in hindlimb proportions, the forelimbs are extremely elongated in flying squirrels. Forelimb elongation is undoubtedly a gliding-related trait that acts to increase the width of the airfoil during the glide (Rayner, 1981; Thorington and Heaney, 1981). The delayed timing of hand-off in flying squirrels probably results from their relatively long forelimbs maintaining contact with the platform for an extended period.

### Behaviorally based kinematic differences

While tail kinematics and the timing of hand-off are

probably attributable to morphological variation, forelimb abduction is best considered as a behavioral difference. Forelimb abduction is a gliding-related behavior that brings the forelimbs into the appropriate position to form an airfoil during the airborne phase. The process of abduction during the launch in flying squirrels appears to be relatively uncomplicated. In general, the wrists and elbows are flexed as the limbs are brought forward in all three species. Since the wrist and elbow angles are statistically indistinguishable among the three species at both hand-off and toe-off (Table 1), we can conclude that assuming an abducted posture during the launch in flying squirrels only involves abduction of the forelimb at the shoulder and no reorientation of the forelimbs themselves.

The precise three-dimensional description of take-off kinematics in this study has demonstrated conclusively that forelimb abduction in flying squirrels begins prior to the animals becoming airborne. This is probably to initiate gliding sooner. To accomplish this, flying squirrels provide angular momentum to the forelimbs while still in contact with the platform. Forelimb abduction is still possible in the absence of angular momentum; however, it undoubtedly takes longer and is of greater complexity since it must be accompanied by rotations about other body axes for angular momentum to be conserved (Frohlich, 1979, 1980; Dunbar, 1988). In general, mid-air rotations are minimized in all but the most specialized arboreal leapers (e.g. prosimians) because of the danger of initiating detrimental rotations that could result in an improper landing posture (e.g. Dunbar, 1988).

There are a number of advantages to be gained from an early onset of gliding in flying squirrels. For example, beginning a glide early produces a flatter trajectory with less initial vertical drop, resulting in a more energetically efficient glide (Pennycuick, 1986; Scholey, 1986; Scheibe and Robins, 1998). In addition, it allows gliding over relatively short distances. For example, the animals in the present study reached stable glides over distances as short as 1 m. Finally, an early onset of gliding enables maneuverability sooner within the glide phase. Early maneuverability, in turn, allows for quicker changes in direction to avoid predators or obstacles and even to choose a different landing site.

Curiously, chipmunks and red squirrels adduct the limbs prior to becoming airborne. Observations of the airborne phase indicate that at some point red squirrels reverse this trend and begin to abduct the limbs in mid-air, while the limbs of chipmunks remain adducted. It is not clear why red squirrels do not abduct their limbs prior to becoming airborne in the same manner as flying squirrels. One possibility is that mid-air abduction of a flexed 'parachuting' limb, possessing a relatively low moment of inertia, is less problematic than mid-air abduction of an extended 'gliding' limb with a relatively high moment of inertia. Another possibility is that the advantages gained by an early onset of gliding are not relevant to parachuting.

### Performance-based kinematic differences

The high take-off velocities and horizontal ranges of red squirrels are consistent with previous observations of their leaping proficiency. Contributing to their launching ability are their absolutely longer hindlimbs (mean femur plus tibia length, red squirrel, 8.1 cm; flying squirrel, 6.4 cm; chipmunk, 5.6 cm). The observation that take-off velocities are significantly different between the similarly sized flying squirrels and chipmunks suggests that flying squirrels are taking advantage of their longer hindlimbs to increase take-off velocity substantially. This, combined with the ability to glide, even over short distances, allows flying squirrels to increase their horizontal range significantly compared with chipmunks.

Generally, sciurid take-off angles were lower than expected. The optimum take-off angle for maximizing horizontal range depends upon the vertical difference between take-off and landing sites (Lichtenberg and Wills, 1978). In the present study, where squirrels launched from an elevated platform to the ground, the optimal take-off angle is not the 45° expected for level take-off and landing sites. Instead, the 1.5 m vertical differential reduces the optimal angle well below 45° as a result of an increased flight time. For example, the mean optimal take-off angle for a ballistically moving chipmunk, determined using the approach of Lichtenberg and Wills (1978), which takes into account the relative height of take-off and landing sites, is 23.4° compared with an observed angle of 9.7° (Table 1). The low take-off angles used by squirrels in the present study differ dramatically from those reported for arboreal leaping primates, which generally approach optimum take-off angles (Crompton et al., 1993; Demes et al., 1996).

It is unclear why the take-off angles preferred by primates should differ from those used by squirrels. One possibility is that quadrupedal squirrels are not able to raise their center of mass as high as are bipedally leaping primates. Another explanation would be the existence of a differing trade-off between take-off angle and take-off velocity between the two groups. The trade-off between angle and velocity has been well documented in human athletes: attempts to optimize take-off angles in jumping or throwing events result in significantly reduced horizontal velocities (Hall, 1995). Consistent with this, Keith et al. (2000) found a similar relationship during the launch in flying squirrels. Future research should attempt to determine whether the trade-off between take-off angle and take-off velocity in quadrupedal leapers, such as squirrels, is more substantial than it is in bipedally oriented primate leapers.

Another possible explanation for the disparity between squirrels and primates is that animals making an escape response (e.g. present study) launch in a different manner from animals taking off for a food reward (e.g. many primate studies). Low take-off angles may be preferred during escape responses since they place a greater horizontal distance between a predator and its prey in a given time, despite higher take-off angles resulting in greater overall distance. Nevertheless, observations of squirrels launching in the wild as well as inside an enclosure used for studying locomotor behavior and habitat use suggest that low take-off angles are the norm for sciurids (R. L. Essner, in preparation).

*Evolutionary implications*

While this study investigated only a subset of sciurid diversity and more taxa are undoubtedly required before definitive conclusions can be drawn, it may be fruitful to explore some of the evolutionary implications of the launch in this group. The evolution of gliding in squirrels is generally perceived as having progressed through intermediate leaping and parachuting stages (e.g. Bock, 1965). While it is impossible to test such a model directly, inferences may be drawn on the basis of extant forms that exhibit these stages. On the basis of the three species investigated in the present study, it appears that the demands of hindlimb propulsion have resulted in a single mechanism for generating thrust during horizontal take-off. Furthermore, the absence of variation in hindlimb kinematics implies that launch propulsion played a relatively minor role during the evolution of parachuting and gliding locomotion in squirrels, since no specialization appears to be necessary to enter the airborne phase. In contrast, we cannot infer this for the other morphological elements, since some degree of specialization related to gliding was evident in the tail and forelimb kinematics.

In conclusion, it is surprising to find that only six out of 23 kinematic variables investigated differed among the three species. While there are key differences that discriminate gliders from non-gliders, none of these fundamentally affects the launch itself. Undoubtedly, movement patterns during the latter phases of leaping, parachuting and gliding (e.g. airborne and landing phases) will prove to be more complex. A detailed investigation of these phases may reveal additional distinguishing characteristics that will further elucidate the functional importance of locomotor variation in this group.

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