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MATERIALS AND METHODS
Flight enclosure and animal training

We investigated the landing behaviour of three bat species, *Cynopterus brachyotis* (Muller), *Carollia perspicillata* (Linnaeus) and *Glossophaga soricina* (Pallas) (Table 1). Although there is some breadth in the roosting habits of all three species, *C. brachyotis* most often roost in foliage (Boon and Corlett, 1989; Campbell et al., 2006; Tan et al., 1997) whereas the other two species typically roost in caves (Alvarez et al., 1991; Cloutier and Thomas, 1992; Fleming, 1988). Bats of all three species hang head-down by their toes from their roosts. For the present study, we used bats that had been raised in captivity and were housed at the Concord Field Station of Harvard University (Bedford, MA, USA) (*C. brachyotis*) and at the University of Maryland (College Park, MD, USA) (*C. perspicillata* and *G. soricina*).

Experiments were performed in flight enclosures measuring $8.3\,m \times 1.0\,m \times 2.4\,m$ (L×W×H) for *C. brachyotis* and $1.6\,m \times 1.3\,m \times 2.3\,m$ (L×W×H) for the other two species. The highest point in each enclosure was the horizontal surface of a ceiling-mounted force-measuring platform, where landings were recorded in our experiments. To discourage bats from landing in locations other than the force platform, we covered other parts of the ceiling with plastic sheets and cardboard.

For training, a bat was introduced to the enclosure and allowed to fly freely for several minutes. When it landed on a part of the enclosure other than the surface of the force platform, we gently touched it to encourage flight or captured it and placed it on the plate surface. This was repeated until the bat ended a free flight by landing on the force platform. As a general rule, once a bat landed a single time on the force platform, and was subsequently left there for a few minutes, it returned to that site after almost every flight. Training required 3–4 daily sessions for *C. brachyotis* and a single training session lasting 10–30 min for the other two species.

Kinematics and Euler rotation sequences

We recorded 11, 10 and eight landings from each of three individuals of *C. brachyotis* and 10 landings each for five individuals of *G. soricina* and five individuals of *C. perspicillata*. Landings were recorded at 250 or 1000 Hz with three phase-locked Photron 1024 PCI digital high-speed cameras (Photron USA, San Diego, CA, USA). Three-dimensional reconstructions from camera images were performed using the Direct Linear Transformation method (Hedrick et al., 2004), based on a $0.35 \times 0.35 \times 0.28\,m$ (L×W×H), 40-point calibration cube held adjacent to the surface of the force plate immediately before experiments were performed.

For each landing, we determined the time of peak impact force from the force plate recordings (see below). We referred to this time as $t=0$ and aligned all other events relative to this time. For this experiment, we were not concerned with the time varying motions of different parts of the body but with the overall changes in the orientation of the body itself over time. For this reason, we did not follow a specific set of kinematic markers throughout the landing sequences, as is typically done in kinematics studies (Riskin et al., 2008). Instead, we measured the orientation of the bat relative to

the ceiling at 11 time steps, from –0.2 s to 0.2 s, using a right-handed body-referenced coordinate system (x_b, y_b, z_b) and a right-handed global coordinate system (x_g, y_g, z_g).

The body-referenced coordinate system moved with the bat. At each time step, we measured the position of the base of the skull and the position of the torso between the legs; x_b was defined as the line through those points, with positive x_b toward the head. We measured two positions on opposite sides of the body (left and right points) and defined the y_b axis as the projection of this line onto the plane normal to x_b, with positive y_b to the bat's right. The z_b axis pointed ventrally and was defined as the cross product of x_b and y_b. The global reference frame consisted of x_g and y_g in the plane orthogonal to gravity, with x_g lined up with the horizontal projection of the initial x_b value of the trial (0.2 s before peak impact). We defined z_g as vertical, positive down.

We used different anatomical landmarks for the sides of the body over the course of a landing sequence because bats approached the ceiling with time-varying body postures that obscured almost any given anatomical location from view for at least part of the approach. When possible, we used the wingtips or wrists of the symmetrically outstretched wings. In frames where the wings were not easily digitized or the wings were not held symmetrically, we used the sides of the rib cage as left and right points. We tested whether the use of wingtips or ribs influenced our measured angles (when wings were symmetrical) and found no significant effect.

We describe the orientation of the bat at each time step relative to the global reference frame in terms of a three-part Euler axis rotation sequence, consisting of the pitch angle (θ), yaw angle (ψ) and roll angle (ϕ) required to align the (x_g, y_g, z_g) with the (x_b, y_b, z_b). For most readers, it will be sufficient to note that for a bat flying with its ventral surface facing downward, a positive pitch causes the head to be raised above the feet, a positive yaw causes the head to turn to the right and a positive roll causes the right wing to drop and the left wing to rise. For the detail-minded reader, pitch angle (θ) is the rotation angle around y_g required to line z_g up with the projection of z_b onto the x_g–z_g plane. After the global frame is rotated through θ, it occupies a new orientation (x'_g, y'_g, z'_g). Yaw angle (ψ) is defined as the angle around z'_g required to align x'_g with x_b. After the (x'_g, y'_g, z'_g) frame is rotated through ψ, it occupies a new orientation (x''_g, y''_g, z''_g). The roll angle (ϕ) is defined as the angle around x''_g necessary to align (x''_g, y''_g, z''_g) with (x_b, y_b, z_b).

The values of θ, ψ and ϕ will differ depending on the order in which they are calculated but when all three are reported, along with the order in which they were calculated, their result is unambiguous. Traditionally, these values are calculated in the order ψ, θ, then ϕ (Stengel, 2004). However, this order resulted in discontinuities in our measured angles. We therefore used the sequence order outlined above (θ, ψ, then ϕ).

Design, calibration and use of the force platform

To record the magnitudes and orientations of ceiling reaction forces during landing, we used a custom-built force-measuring platform. Its surface consisted of a stiff $0.28\,m \times 0.28\,m$ honeycombed fiberfoam surface with a $0.12\,m \times 0.12\,m$ area of plastic webbing at

Table 1. Descriptions of the three bat species used in the present study

	Cynopterus brachyotis	*Carollia perspicillata*	*Glossophaga soricina*
Family	Pteropodidae	Phyllostomidae	Phyllostomidae
Body mass (g)	31.6, 34.9, 40.8 (*N*=3)	19.3±3.1 (*N*=5)	10.0±1.4 (*N*=5)
Preferred roost type	Foliage (Tan et al., 1997)	Cave (Cloutier and Thomas, 1992)	Cave (Alvarez et al., 1991)

Body masses are shown as means ± one standard deviation, except where *N*<5.

its center. Bats were unable to grasp the flat surface of the fiberfoam so, instead, all bats landed by grabbing the central webbing. This arrangement prevented bats from using the edges of the platform or making contact with features of the ceiling adjacent to the platform when landing. The webbing was also stiff and glued to the surface to minimize the dampening of impulses that passed through it during a landing event.

The force platform measured forces in all three dimensions and was constructed and calibrated in the same manner as in previous studies (Riskin et al., 2005; Riskin et al., 2006). The platform had resonant frequencies >290 Hz in all three directions. On days in which landings were recorded, the force–voltage relationship of each channel was calibrated by suspending weights (10 g–200 g) directly from the surface or through a series of pulleys so as to apply forces in different directions. A separate linear force-to-voltage regression slope was calculated for forces into the ceiling, down from the ceiling and in four horizontal directions at 90 deg. intervals. The platform demonstrated linear force–voltage relationships in each of these six directions (R^2>0.999). Electronic drift in the baseline output was corrected in each trial by sampling the signal of the unloaded force plate for several seconds immediately before a landing event.

For each landing, we recorded forces at 1000 Hz and synchronized force plate recordings with videos by recording the camera trigger signal alongside the force plate's voltage signals. All forces were scaled to the body weight of the individual that produced them and are reported in units of body weights.

Force profile descriptions

The force profiles associated with landing events were similar for all trials (see Results) and several descriptive parameters could be systematically recorded from them. In each trial, a landing bat first struck the ceiling, imparting a three-dimensional force to the plate that included an upwards vertical component. We designate the total magnitude of this force in three dimensions ($\mathbf{F}_{peak-up}$) and define $\alpha_{peak-up}$ as its angle from vertical up (negative z_g). Next, as a result of the ceiling reaction force plus gravity, the bat's COM began to move away from the ceiling and this separation from the ceiling was arrested when the attached limbs were placed in tension, causing another local peak in the net force vector, this time with its vertical component directed downward. We refer to the magnitude of total force at this time as $\mathbf{F}_{peak-down}$ and define $\alpha_{peak-down}$ as its angle from vertical down (positive z_g). Afterward, the vertical component of the ceiling reaction force oscillated near –1 body weights as the bat hung from the ceiling.

Statistical analyses

Values of body pitch that were recorded for the body at the beginning of the approach (t=–0.2 s) were compared among species using an analysis of variance (ANOVA) with *post-hoc* pairwise *t*-tests. $\mathbf{F}_{peak-up}$ and $\mathbf{F}_{peak-down}$ values were not normally distributed, thus, we used statistical procedures that are robust against deviations from normality. To determine whether each of these differed among species, we used one-way ANOVA tests on rank-transformed values for all 129 landings [i.e. Kruskal–Wallis tests (Zar, 1999)]. *Post-hoc* pairwise comparisons were made using *t*-tests of the rank-transformed data (Mann–Whitney *U*-tests). To avoid pseudoreplication for the ANOVAs, we used two degrees of freedom (number of species – 1) in the numerator and 12 degrees of freedom (number of individuals – 1) in the denominator and similarly adjusted the degrees of freedom to reflect the number of individuals in each *post-hoc* comparison.

Signal filtering

We improved the signal-to-noise ratio of the force plate signals by filtering them with a 100 Hz low-pass Butterworth filter. However, even after filtering, oscillations in voltage due to background noise alone (an unloaded plate) were equivalent to voltage changes that would result from *ca.* 0.04 N of force, around 40% of the weight of our smallest bats. This noise may have prevented the resolution of small-magnitude impact forces, as any rapidly applied force smaller than *ca.* 0.04 N would be masked by electrical noise. Because forces were scaled to the weight of the organisms, this issue could have potentially led to the false conclusion that small-bodied animals produce larger peak forces than large-bodied ones when, in fact, all organisms simply applied equivalent forces (in units of body weights) but noise concealed the peak for small bats. One way to further decrease the magnitude of the electrical noise would be the use of a lower (<100 Hz) Butterworth low-pass cutoff frequency; however, stronger filtering of this kind has the additional effect of decreasing the apparent magnitudes of the brief force peaks associated with landing – the very peaks we sought to measure in the present study. Thus, we used the 100 Hz cutoff frequency but to ensure that the statistical trends we report are not artifacts of this choice, we repeated our analyses using Butterworth low-pass filter cutoff frequencies of 50 Hz, 25 Hz and 10 Hz and using unfiltered data.

RESULTS
Kinematics of landing

We observed two different landing strategies among the bats in this study: one where the wrists and feet struck the surface simultaneously (four-point landing) and one where only the hindlimbs contacted the ceiling (two-point landing). *C. brachyotis* always used four-point landings and the other two species always used two-point landings.

Four-point landings

In a four-point landing, a bat arrived at the ceiling with the wings partially folded, the forelimbs extended laterally and anteriorly and the hindlimbs extended laterally and caudally from the body (Fig. 1A) (t=0.00 s). After making contact with the ceiling, the bat dragged the thumbs and toes toward the body, across the ceiling, until the claws of one or more limbs had interlocked with a part of the surface webbing (Fig. 1A) (t=0.04 s). Thereafter, the bat suspended itself by the limbs that grasped the ceiling. The four-point landing ended with a ventral belly-up posture. Subsequently, the bat let go with its thumbs to assume a typical, head-down roosting posture.

Four-point landings were characterized by large changes in pitch, with negligible yaw or roll rotations throughout the sequence (Fig. 2A). At the beginning of the landing sequence (t=–0.2 s), pitch angle averaged 59.8±9.7 deg. (means ± s.d.; N=29), yaw angle was zero by definition and body roll was near zero (3.8±10.0 deg.). As bats approached the ceiling, they increased body pitch until their ventral surfaces faced the ceiling upon impact (Fig. 3A). At the time of peak impact, pitch angle averaged 144.0±33.4 deg. and yaw angle and roll angle remained near zero (4.1±7.8 deg. and –1.6±7.0 deg., respectively).

In some four-point landings, the bat's head struck the ceiling simultaneously with, or immediately before, the wrists and feet. Head-strikes were common for one *C. brachyotis* (7 out of 10 landings) but less common for a second individual (3 out of 7 landings) and they did not occur (0 out of 12 landings) for the third individual of that species. Other than the contact of the head with

Fig. 1. Continued on next page.

Two-point landings

Individual bats performing a two-point landing did so by moving the left and right sides of their bodies asymmetrically. These bats either brought their hindlimbs anteriorly along the right side of their body (which we refer to as right-handed two-point landing) (Fig. 1B,D) or along the left side of the body (left-handed two-point landing) (Fig. 1C,E). Some individuals alternated between right-handed and left-handed landings whereas others consistently used one landing type; the five *C. perspicillata* individuals used right-

the ceiling, these 10 landings did not generally differ from the other 19.

handed landings in 3/10, 4/10, 7/10, 9/10 and 9/10 trials and the five *G. soricina* individuals used right-handed landings in 0/10, 0/10, 3/10, 4/10 and 8/10 trials.

For eight of the 100 two-point landings, we were unable to accurately measure Euler rotation angles because the bat was not visible in two cameras at $t=-0.2$ s (one trial), because of camera problems that caused the field of view to be too dark (three trials), or because of coincidental alignment of body axes with global ones during the landing sequence that interfered with the accuracy of our calculations (four trials). Video recordings of these landings were similar to the other two-point landings but these trials were omitted from our summaries of Euler rotation angles.

Fig. 1. Landing sequences of bats: (A) a four-point landing by *Cynopterus brachyotis*, (B) right-handed and (C) left-handed two-point landings by *Carollia perspicillata*, and (D) right-handed and (E) left-handed landings by *Glossophaga soricina*. Peak impact force into the ceiling occurs at $t=0.00$.

For two-point landings, body pitch angles at $t=-0.2$ s were 54.7 ± 12.5 deg. ($N=45$) for *C. perspicillata* and 48.6 ± 8.5 deg. ($N=47$) for *G. soricina.* These values were similar to those of *C. brachyotis* that used four-point landings (59.8 ± 9.7 deg.) but were slightly lower (ANOVA: $F=10.7$, d.f.=2,7, $P=0.002$). Body yaw was zero (by definition) and, like those of bats that used four-point landings, the body roll angles were near zero (*C. perspicillata*, 1.5 ± 19.0 deg.; *G. soricina*, 0.64 ± 11.1 deg.).
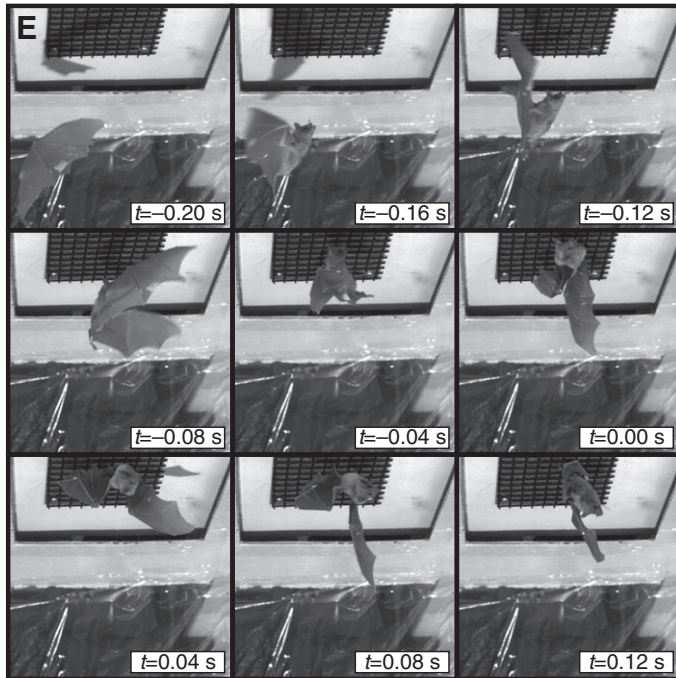
In a right-handed two-point landing (Fig. 2B,F), body pitch increased first, then continued to increase while the body began a negative yaw rotation, bringing the feet up next to the right side of the body. Yaw rotation continued until the feet were above the head (*ca.* -180 deg.) and was accompanied by a slight negative body roll. The result of these rotations was that at the end of the landing sequence, bats hung from the force platform by their hindlimbs with their ventral surfaces (z_b) facing toward negative y_g (Fig. 3B). Left-handed two-point landings (Fig. 2C,G) were similar to right-handed ones but with the pitch and roll values changing in the opposite direction (both positive), resulting in final head-down roosting postures with the ventral surfaces (z_b) oriented toward positive y_g. In some landings, only one foot attached during the landing sequence and some time later, the second foot became interlocked with the ceiling. In most two-point landings, the bat swung from side-to-side for several seconds after landing. We did not observe swinging of this kind with four-point landings.

Some two-point landings did not fit the typical pattern of pitch, roll and yaw changes, even though their kinematics were very similar to those of typical two-point landings. Most plots of pitch, roll and yaw (Fig. 2) were easily assigned to left-handed, right-handed or four-point categories. However, 10 of the 45 plots for *C. perspicillata* revealed an alternative pattern that did not conform to any of these three categories (Fig. 2D,E). The kinematics of the 10 alternative landings were very similar to typical two-point landings but with

the change in yaw initiated later. In these situations, changes in pitch throughout the landing sequence were larger and changes in yaw were smaller than in typical two-point landings. As in typical two-point landings, this alternative landing strategy resulted in a head-down roosting posture with the body facing in the same direction, as it would have in a typical landing event. This alternative landing strategy was performed by three individuals, all of which also performed typical two-point landings. We interpreted the alternative landing strategy as a variant of the typical two-point landing and did not assign it to a different category because it was almost indistinguishable from typical two-point landings in the videos.

Ceiling reaction forces

When a bat landed on the ceiling, regardless of kinematic category, there was an initial peak in vertical force associated with the first impact of the body with the ceiling. As the ceiling began to support the bat's weight, a second peak in force occurred with a vertical component directed away from the ceiling. After landing, *C. perspicillata* and *G. soricina* swung back and forth by their toes, causing periodic oscillations in ceiling reaction forces (Fig. 4).

We observed a significant difference in $F_{peak-up}$ among species ($F=62.9$, d.f.=2,12, $P<0.0001$) (Fig. 5A). Peak impact forces were larger for *C. brachyotis* than for the other two species (*G. soricina*, $t=9.73$, d.f.=7, $P<0.0001$; *C. perspicillata*, $t=10.42$, d.f.=7, $P<0.0001$). We found no significant difference between the impact force magnitudes of *G. soricina* and *C. perspicillata* ($t=0.80$, d.f.=9, $P=0.20$). The magnitudes of $F_{peak-down}$ values also differed among species ($F=13.9$, d.f.=2,12, $P=0.0007$) (Fig. 5B). Impact forces observed from *C. brachyotis* were larger than those of *G. soricina* ($t=5.20$, d.f.=7, $P=0.0006$) and *C. perspicillata* ($t=3.94$, d.f.=7, $P=0.003$) but no significant difference existed between $F_{peak-down}$ values of *G. soricina* and *C. perspicillata* ($t=1.45$, d.f.=9, $P=0.09$).

Peak force was directed 14.9 ± 12.5 deg. (median ± interquartile range) from vertical for *C. brachyotis*. This was closer to vertical and less variable than $\alpha_{peak-up}$ values of *C. perspicillata* (20.9 ± 73.1 deg.) or *G. soricina* (24.2 ± 26.2 deg.). Values of $\alpha_{peak-down}$ averaged 16.0 ± 12.9 deg. for *C. brachyotis*, 49.4 ± 23.8 deg. for *G. soricina* and 51.0 ± 46.8 deg. for *C. perspicillata*.

Filtering artifacts

As expected, using lower filter cutoff frequencies decreased the apparent magnitudes of peak forces. For example, $F_{peak-up}$ for *C. brachyotis* was 3.7 ± 2.4 body weights (median ± interquartile range) when a 100 Hz cutoff frequency was used but only 2.9 ± 1.5 body weights when a 25 Hz cutoff frequency was used or 6.4 ± 7.5 body weights when unfiltered data were used. The lower the cutoff frequency used, the smaller the apparent force peaks. However, the pattern of significant differences among our statistical tests was the same for unfiltered data and at all Butterworth low-pass cutoff frequencies used: 100 Hz, 50 Hz, 25 Hz and 10 Hz. As excess filtering would diminish the magnitudes of peak forces relative to their actual values and because 100 Hz is a commonly used cutoff frequency for kinematics studies, we have chosen to report the 100 Hz-filtered data. We caution, therefore, that the actual magnitudes of peak impact force are influenced by our filtering protocols and thus emphasize that it is the relative difference in peak impact force among species that is of most value.

DISCUSSION

We found that the kinematics of landing differed among bat species and that these gross differences in landing kinematics were associated with differences in impact force. Bats that used two-point
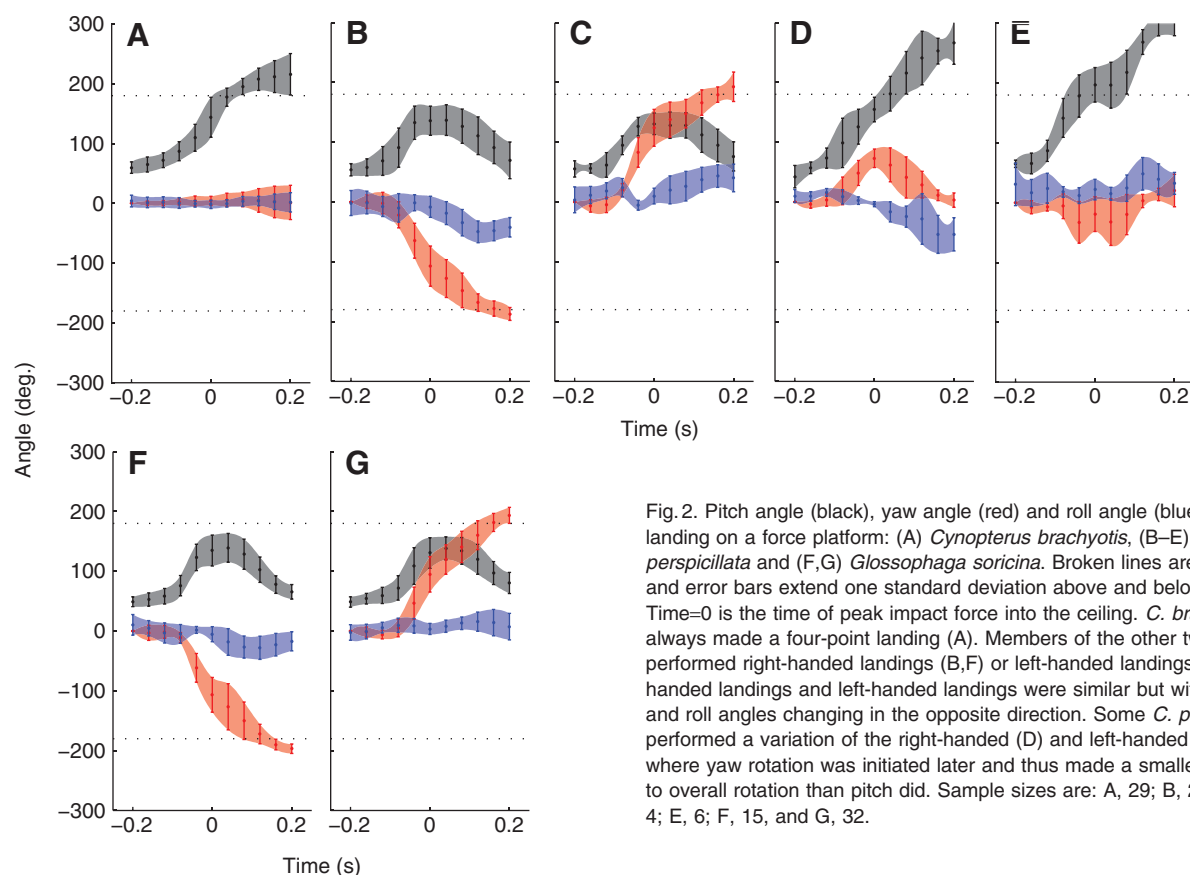
Fig. 2. Pitch angle (black), yaw angle (red) and roll angle (blue) of bats landing on a force platform: (A) *Cynopterus brachyotis*, (B–E) *Carollia perspicillata* and (F,G) *Glossophaga soricina*. Broken lines are at ±180 deg. and error bars extend one standard deviation above and below the mean. Time=0 is the time of peak impact force into the ceiling. *C. brachyotis* always made a four-point landing (A). Members of the other two species performed right-handed landings (B,F) or left-handed landings (C,G). Right-handed landings and left-handed landings were similar but with the yaw and roll angles changing in the opposite direction. Some *C. perspicillata* performed a variation of the right-handed (D) and left-handed (E) landings where yaw rotation was initiated later and thus made a smaller contribution to overall rotation than pitch did. Sample sizes are: A, 29; B, 22; C, 13; D, 4; E, 6; F, 15, and G, 32.

landings (*C. perspicillata* and *G. soricina*) impacted the ceiling gently whereas bats that made four-point landings (*C. brachyotis*) impacted more forcefully. The kinematics of both landing types were consistent across individuals. Two-point landings were asymmetrical, such that a landing bat chose between a right-handed or left-handed variant, and individuals were able to alternate between right-handed and left-handed landings over the course of our experiments.

Explaining interspecific variability in landing strategy

It is plausible that the differences in impact force that we observed among species reflect a larger pattern among species associated with roosting habits, wherein cave-roosting bats land more gently than foliage-roosting taxa. A surface such as foliage that bends in response to a landing bat can absorb impact energy and dissipate it slowly therefore the time course over which landing forces are transmitted through the skeleton is increased, thereby reducing peak forces and stresses. This hypothesis is supported by the observation that the cave-roosting bats in our study landed more gently (with smaller peak impact forces) than foliage-roosting bats did.

Alternatively, differences in landing style might be an artifact of phylogeny; our four-point landing species is a pteropodid (Suborder Yinpterochiroptera, formerly Megachiroptera) and the other two species are phyllostomids [Yangochiroptera, formerly Microchiroptera (Teeling et al., 2005)]. Differences in thumb-use during feeding between these groups have been documented previously (Vandoros and Dumont, 2004), so differences between them in the use of thumbs during landing is perhaps not surprising. The vast majority of pteropodids are foliage roosters but yangochiropterans use a diverse array of roost types (Kunz, 1982). Resolution of the relative influences of phylogeny and roosting

ecology on landing performance would therefore require investigation of landing performance in a more disparate and much larger group of bat species than that presented in the current study.

At first glance, a third possible explanation for our results would be that bats larger than *ca*. 25 g employ a four-point strategy and smaller bats use a two-point one. However, high-speed videos of five *Artibeus jamaicensis*, a cave-roosting phyllostomid similar in body mass to *C. brachyotis* (38.1±1.7 g; D.K.R. and J.M.R., unpublished data), revealed that, like the smaller bat species in the present study, *A. jamaicensis* perform a two-point landing that results in relatively small impact forces (*ca*. 0.3 body weights, *N*=1). Body size is therefore not the sole determinant of landing strategy.

Hindlimb stresses during landing

It is not surprising that for bats performing two-point landings, peak impact forces were small as all force was transmitted to the ceiling through the hindlimbs. Because the diameters of the hindlimb bones of bats are reduced compared with those of terrestrial mammals, bat hindlimb long bones are better able to accommodate tensile loading than compression or bending (Riskin et al., 2005). The hindlimbs of landing bats are most probably at their greatest risk of mechanical failure at *t*=0.00, when peak force is applied into the ceiling. Bats that make two-point landings are therefore required to land gently.

We were unable to measure hindlimb stresses directly because both hindlimbs (two-point landings) or all four limbs (four-point landings) contacted the ceiling together, masking the relative contributions of each limb. Bats landing with their wrists and hindlimbs simultaneously might be able to afford larger impact forces by applying the majority of the force with their forelimbs.
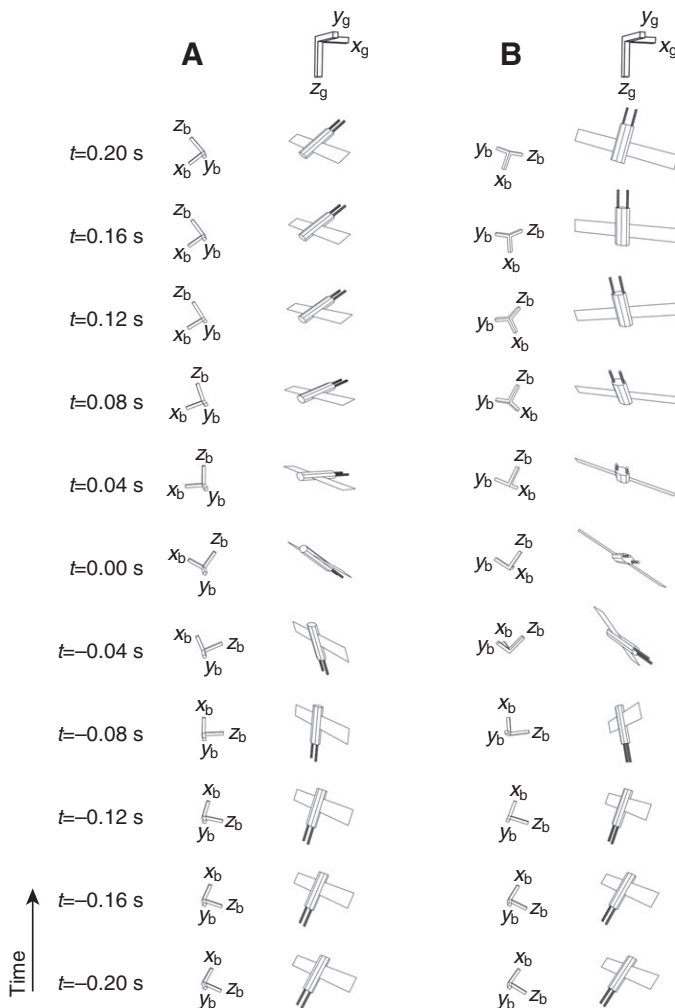
Fig. 3. Schematic of (A) a four-point landing and (B) a right-handed two-point landing, based on the mean kinematic data from Fig. 2A and 2B, respectively. As the bat landed on the ceiling, we used the difference between the body-referenced coordinate system (x_b, y_b, z_b) and the global coordinate system (x_g, y_g, z_g) to describe the orientation of the bat. The x_b vector points anteriorly, y_b points laterally to the bat's right and z_b points ventrally. The x_g vector is the horizontal projection of x_b at t=–0.2 s, z_g is vertical down and y_g is the cross product of z_g and x_g.
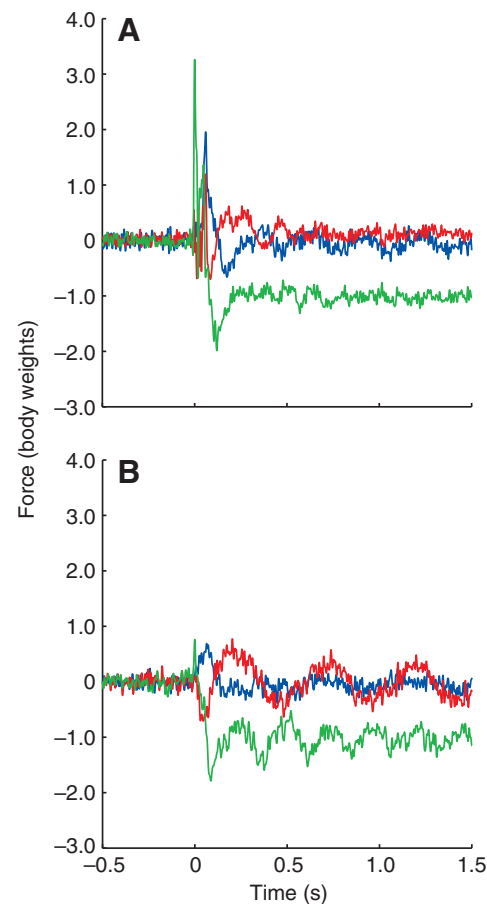

Fig. 4. Typical force profiles for (A) a four-point landing *Cynopterus brachyotis* and (B) a two-point landing *Carollia perspicillata*. The green line shows vertical force, with positive numbers representing forces into the ceiling and negative numbers away from the ceiling. Red and blue lines are forces in two orthogonal horizontal axes. Force profiles for *G. soricina* were very similar to those of *C. perspicillata* and are therefore not shown. The magnitude of the peak impact force (into the ceiling and, later, away from the ceiling) for four-point landing bats was typically larger than those of bats using two-point landings. The oscillations in horizontal force that occur after landing in B are the result of the bat swinging from side to side as it hangs from its toes after landing.

Based on our examination of the high-speed videos, the hindlimbs appear to strike the ceiling with considerable momentum but we cannot adequately compare hindlimb stresses between four-point and two-point landing bats with the data we collected.

Aeromechanics of landing

Immediately before landing, a bat's body has both translational momentum and rotational momentum that will together bring the claws in contact with the ceiling. During landing, a bat must stop both the rotation and translation of its body using some combination of gravitational forces, ceiling reaction forces and aerodynamic forces. Although a great deal could be learned by quantifying the relative contributions of these forces to changes in translational and rotational momentum, there are too many unknowns for that accounting to be performed at present.

First, the location of the COM is difficult to calculate, owing to the changing body posture throughout the landing sequence. Without knowledge of its position and of the body's moment of inertia around its axes of rotation, the translational momentum of the COM and rotational momentum of the body around the COM cannot be computed. Second, quantification of aerodynamic forces is even more daunting. These would need to be inferred using computational fluid dynamics models based on wing kinematics and this is most likely to be near the limit of the abilities of the most modern computational methods (Mittal and Iaccarino, 2005). Moreover, the ceiling would cause wall effects (unfortunately named in this case) that introduce solid–fluid interactions, which further complicate the use of such models.

Ecological implications of landing performance

The implications of mid-flight manoeuvrability for feeding ecology are obvious. For example, differences in turning ability influence the kinds of environments in which all bats can forage for food, and insectivorous bats must be able to make the tight turns necessary
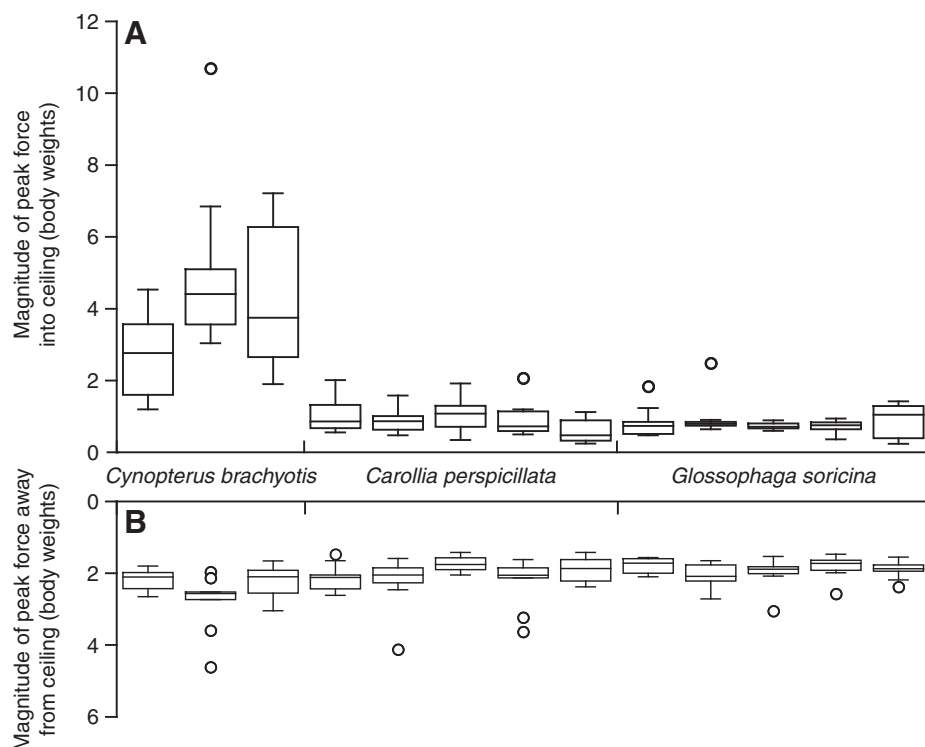
Fig. 5. Box plots of (A) peak impact force into the ceiling ($F_{peak-up}$) and (B) peak pulling force down from the ceiling ($F_{peak-down}$) over the course of each trial for all 13 individuals tested in this study. Each individual occupies its own position on the x-axis. N=10 trials for all individuals except *C. brachyotis* for which sample sizes are (from left to right in figure) N=11, N=10 and N=8. $F_{peak-up}$ and $F_{peak-down}$ were larger in magnitude for *C. brachyotis* than they were for either of the other two species ($P<0.0001$ and $P<0.005$, respectively). Circles represent outliers.

for intercepting prey (Ghose and Moss, 2006; Ghose et al., 2006; Triblehorn et al., 2008). If landing performance is considered to be a component of aerial manoeuvrability, our results expand the implications of flight performance to include roosting ecology as well.

The mastery of landing upside down by bats has permitted their exploitation of an extremely diverse assemblage of roost types. Bats roost in caves and tree hollows, under bark, against leaves, among branches and in human-made structures, to name a few (Fenton et al., 2001; Fenton et al., 2000; Kunz, 1982; Kunz and Lumsden, 2003; Riskin and Fenton, 2001; Riskin and Pybus, 1998). Although a generalized landing strategy could permit bats to land on any substrate, our results indicate that there are species-specific differences that may make different kinds of roosts accessible to different species. In a broader survey, we might expect to find a correlation between foraging habitat and roost type and a complementary correlation between flight performance and landing mechanics. Conversely, the biomechanics of landing and steady flight might interfere with one another and result in species-specific trade-offs that ultimately have influenced the evolutionary ecology of foraging behaviour and roost use.

Because terrestrial locomotion results in mechanical loading of the hindlimbs, we might also find a correlation between landing kinetics and locomotor performance, with terrestrially agile bats such as *Desmodus tumidirostris* or *Mystacina parnellii* able to withstand greater compressive stresses during landing than those that cannot walk well such as *Natalus rotundus* or *Pteronotus tuberculata* (Riskin and Hermanson, 2005; Riskin et al., 2005; Riskin et al., 2006).

Vaughan noted correlations between flight performance and roost type among bats and considered these in the context of flight initiation (Vaughan, 1959). Our discovery that the kinematics and kinetics of landing can vary among species adds another dimension to the link between flight performance and roosting ecology. Bats that can land gently at a small target might have a competitive

advantage over other bats for roosting on hard or sharp roost surfaces such as the ceilings of caves.

Landing performance and the evolution of flight
The ability to land safely at the end of a flight is a functional constraint on locomotor performance for any flying vertebrate. Because nearly all bats hang head down, it appears that the ability to land at an overhead roost has been conserved since the appearance of bats over 50 million years ago (Jepsen, 1966; Simmons et al., 2008; Teeling et al., 2005). Our results demonstrate that there are interspecific differences among bat species in the kinematics and kinetics of landing. Future investigation of the way in which bats end their flights will shed new light on the evolution of flight manoeuvrability and roosting ecology in the Chiroptera.

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