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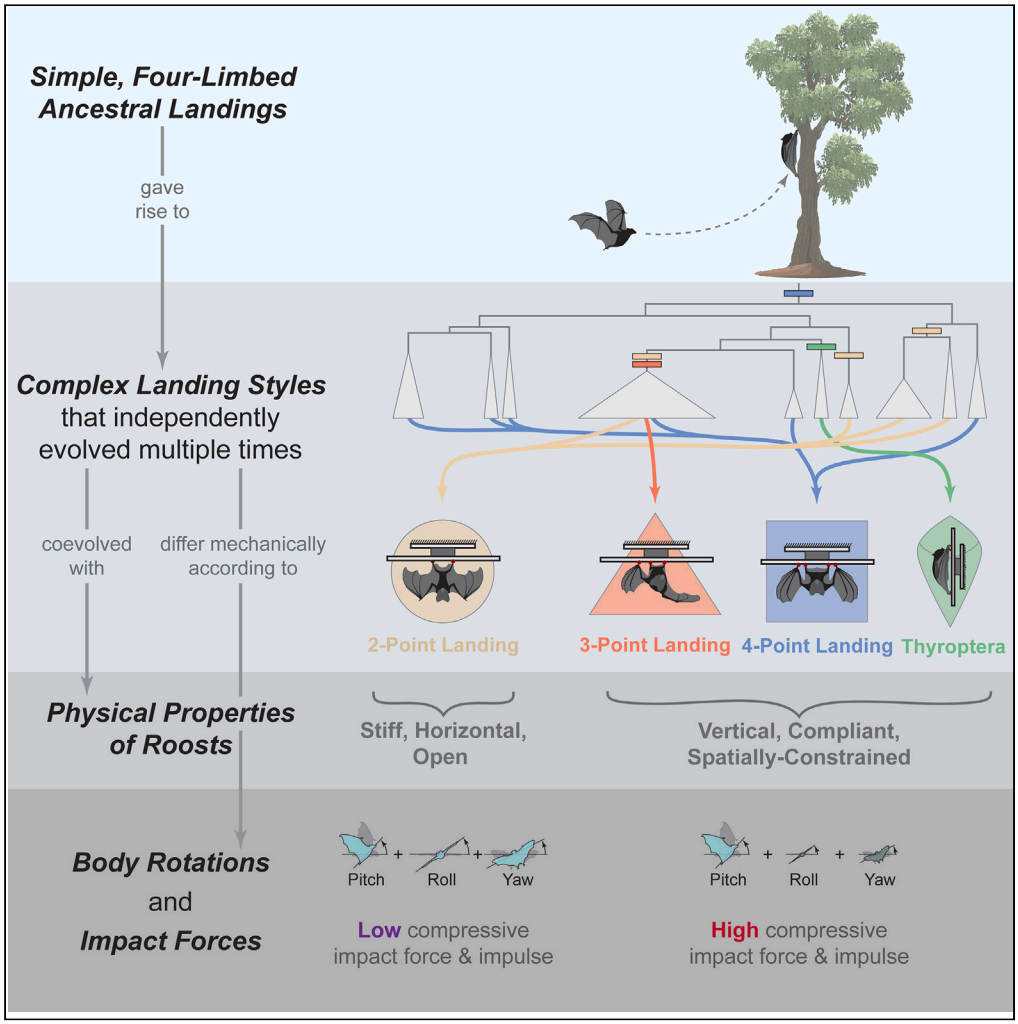

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Highlights

Specialized landings help bats achieve their iconic upside-down roosting posture

Bat ancestors likely landed with simple maneuvers similar to extant gliding mammals

Acrobatic, low-impact landings coevolved with shifts to stiff, horizontal roosts

Complex acrobatic landings evolved independently multiple times

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Roosting ecology drives the evolution of diverse bat landing maneuvers

David B. Boerma[1,2,3,5,*] and Sharon M. Swartz[3,4]

SUMMARY

Bats and birds are the only living vertebrates capable of powered flight. However, bats differ from birds in that their flight required the evolution of ascending landing maneuvers that achieve their iconic head-under-heels roosting posture. We examined the evolution of landing flight in bats and tested its association with the physical properties of roosts. Bats performed four maneuvers, each correlated with patterns of peak impact force, impulse, and roosting ecology, a critical aspect of bat biology. Our findings indicate that the common ancestor of bats performed simple, four-limbed landings, similar to extant gliding mammals, and that rotationally complex landings enhancing control over impact forces coevolved multiple times with shifts to stiff, horizontal roosts. These results suggest landing biomechanics is central to bat biology: it was critical to flight adaptation in the past, mediates roost use in the present, and may affect bats' ability to respond to deforestation in the future.

INTRODUCTION

Coordinated shifts in form, function, and ecology are necessary for the evolution of new locomotor modes, such as flight, in the lineages that gave rise to bats, birds, insects, and pterosaurs. The evolution of flight required not only the evolution of aerial locomotion itself but also the often-overlooked evolution of landing maneuvers that safely transition an animal from moving through air to resting on a solid support. For bats and many other flying animals, landing maneuvers also provide access to the structures that constitute their homes. Animals rely on these structures to provide critical functions that extend far beyond simply serving as refugia from weather and predators. For example, in many bat species, roost location determines foraging grounds; roosts serve as social spaces that facilitate access to mates, maternal care, and meal sharing; and divergent roost preferences drive niche partitioning to permit co-occurrence of closely related species.[1–4] Furthermore, roost types vary among bat species and comprise a vast range of natural and human-made structures, including bare expanses of cave ceilings, rock crevices, tree cavities, vine tangles, culms of bamboo, and even within pitcher plants to name only a subset (see studies by Kunz and Fenton,[5] and Altringham[6] for review). Roosting ecology, therefore, plays a crucial role in defining the environmental mosaic in which bats survive and evolve, providing much of the natural context that drives changes in form, function, performance, and, ultimately, diversity.[7,8]

Despite the importance of roosting ecology to extant bat diversity, we know surprisingly little about the mechanistic factors that drive roost choices or the selective pressures that roosts impart on the locomotor systems of bats. Biomechanics is situated at the intersection of organismal form, function, and ecology, and thus provides a practical lens through which to investigate the evolutionary relationships among these factors. From this perspective, we hypothesize that diversity in landing mechanics is evolutionarily linked to the physical properties of roosts. Under this framework, landing dynamics may facilitate access to specific roost types for some species and reduce access for others.

To date, research has identified two different landing maneuvers among four bat species, referred to as "landing styles": two-point and four-point landings.[9,10] Landing styles are named according to the number of points of contact a bat uses to first attach to its landing site, and are tightly correlated with (1) the required amount and nature of body reorientation to transition the bat from a head-forward, horizontal-body flight posture to the iconic head-under-heels, vertical-body roosting posture for most species, and (2) the magnitude of peak substrate reaction forces the bat sustains upon contact with the ceiling, which we subdivide into "compressive forces" directed into the ceiling and "tensile forces" directed away from the ceiling. Two-point landings require complex body rotations that fully invert a bat's body prior to contact with only the two hindlimbs, and result in low peak compressive impact forces of <1 bodyweight (BW). In contrast, four-point landings involve simpler rotations, chiefly body pitch, that do not fully invert the body prior to contact, allowing both thumbs to grasp the landing site before both hindlimbs, and result in higher peak compressive forces of >3 BW.[9,10]

Given the critical importance of landing maneuvers to the evolution of flight and the broad biological significance of roosting ecology, probing the relationship between interspecific variation in landing mechanics and roost use may reveal how the evolution of bat landing styles

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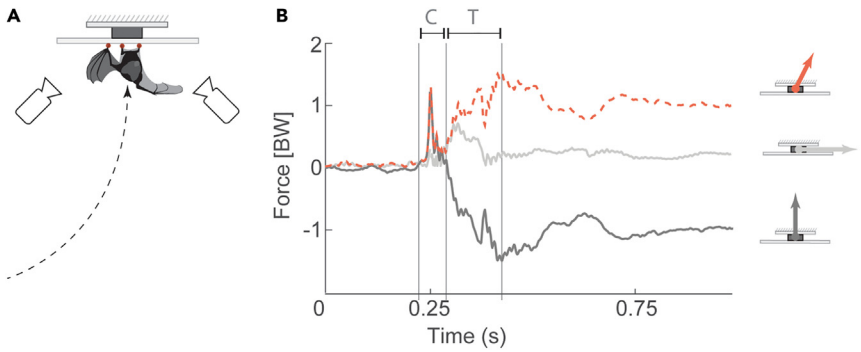

Figure 1. Experimental design

(A) Bats landed on a ceiling-mounted force plate in the view of three high speed cameras (third camera not shown).

(B) A representative force trace shows vertical (F_Z, dark gray) and horizontal (light gray) components of total 3D impact force (F_{TOT}, dashed red), along with the compression ("C") and tension ("T") phases. Peak compressive impact force (PeakF-comp) is the highest measured F_{TOT} (dashed red) during the compression phase. Peak tensile force (PeakF-tens) is the highest measured F_{TOT} (dashed red) during the tension phase. Total landing impulse (Imp-tot) is calculated as the area under F_{TOT} (dashed red) from the beginning of the compression phase to the end of the tension phase. Impulse during the compression phase (Imp-comp) is calculated as the area under F_{TOT} (dashed red) during the compression phase only. Impulse during the tension phase (Imp-tens) is calculated as the area under F_{TOT} (dashed red) during the tension phase only.

shaped the ways in which bats find refuge and disperse within their environments. In the present study, we therefore seek answers to three questions relating to landing mechanics, roosting habits, and the potential evolutionary associations between them. First, do previously documented relationships between landing style and impact forces remain consistent across a diverse sample of bats, and when sampling bat diversity more robustly, how many landing styles can be identified? Second, what is the evolutionary history of bat landing maneuvers? Lastly, did landing styles coevolve with shifts to roosts with particular physical properties, permitting certain lineages to occupy new niches?

We hypothesized that (1) landing styles requiring more body reorientation prior to contact (two-point landings) consistently result not only in lower peak impact force, but also lower impulse (time-integrated landing force), across species and body sizes; (2) four-point landings, which are high-impact and require less body reorientation, are the ancestral condition for bats from which all other landings styles must have evolved; and (3) the evolution of new landing styles is associated with the physical properties of the roosts to which they most often provide access, including qualitative roost stiffness, orientation, and spatial constraints.

RESULTS

Generalized events of a bat landing sequence

When a bat landed on a ceiling, regardless of landing style, it experienced two force peaks. First, it imparted a vertical force, F_Z, upward, into the ceiling (here defined as positive F_Z), during which time the suspending portions of the musculoskeletal system were loaded in compression and bending. During this time, the bat attached to the ceiling using two, three, or four points of contact. Gravity then began to accelerate is center of mass (COM) vertically downward, away from the ceiling (here defined as negative F_Z). This downward acceleration continued until the attached limbs began to resist motion, resulting in a second force peak in the negative vertical direction. From this point, the suspending musculoskeletal system was loaded primarily in tension.

Throughout this paper we refer to these periods as (1) the compression phase, which begins at contact, continues while F_Z remains positive, and ends when F_Z becomes negative, or (2) the tension phase, which begins when F_Z becomes negative and ends at the time of peak negative F_Z (Figure 1). For both phases of the landing, we report peak total force, which represents the highest instantaneous magnitude of force experienced by the bat, and impulse, which represents the magnitude of change in the bat's momentum as a function of force applied over time.

Landing styles across species

We recorded 637 landings from 36 species, representing ten families of Chiroptera. Of these, 17 species performed two-point landings and 16 performed four-point landings. An additional six species performed a newly discovered landing style, the three-point landing, in which individuals partially inverted their body before contacting the landing site with both hindlimbs followed by one stabilizing thumb (Figure 2). Landing style was consistent within and among individuals of the same species, with only two exceptions of species that performed multiple styles: *Artibeus jamaicensis* (two- and three-point) and *Miniopterus schreibersii* (two-, three-, and four-point). At the family-level, pteropodid, vespertilionid, molossid, and mormoopid species performed four-point landings; thyropterids performed a specialized head-up four-point landing, in which body rotation did not commence until after bats contacted the landing site by attaching with suction cups to the vertical interior surface of furled leaves (a specialized roosting ecology).[10–12] Emballonurids, rhinolophids, and hipposiderids performed two-point landings; and miniopterids and phyllostomids performed two-, three-, and four-point landings (Table 1).

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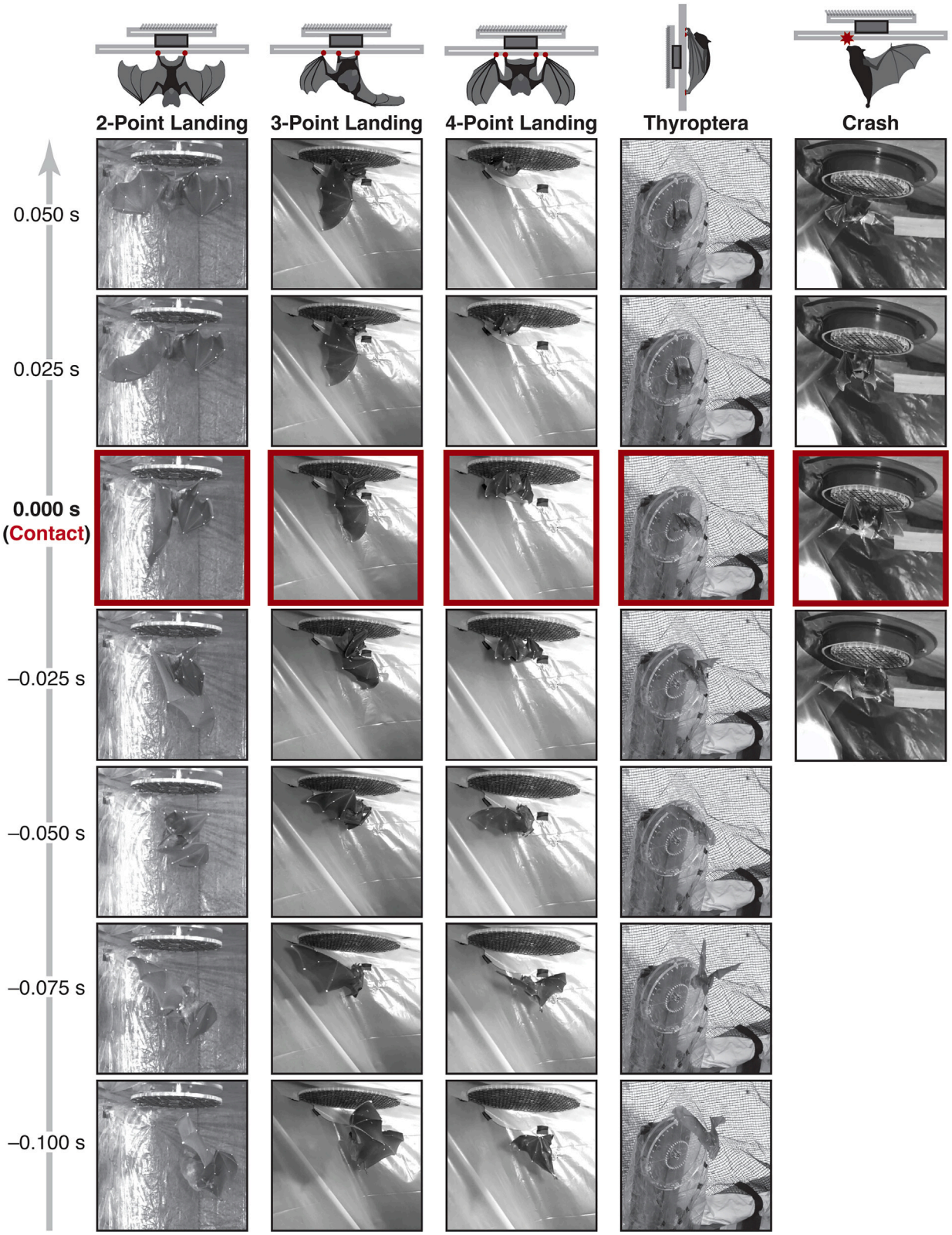

Figure 2. Image sequences for representative landing styles

Still frames from two-point (*Rhinolophus ferrumequinum*), three-point (*Artibeus jamaicensis*), four-point (*Sturnira parvidens*), specialized head-up four-point (*Thyroptera tricolor*), and crash (*S. parvidens*) landings. Images are aligned to the time of contact (t = 0.000 s, denoted by bold borders). Videos S1, S2, S3, S4, and S5 correspond with each landing pictured here.

Peak landing impact forces

Of the 36 species we sampled, we collected useable impact force data for a subset of 18 species that could be trained to land within a force-measuring target zone (Table 1). During the compression phase, peak compressive impact forces (PeakF-comp) for two-point landings were 0.99 ± 0.42 BW (mean ± standard deviation, n = 11 species). Four-point landings resulted in higher and more variable PeakF-comp of 4.01 ± 1.44 BW (n = 5 species). Three-point landings were intermediate, resulting in PeakF-comp of 3.1 ± 2.3 BW (n = 4 species). The specialized four-point landings of *Thyroptera tricolor* resulted in the highest PeakF-comp of 6.02 ± 1.11 BW (n = 13 individuals). Simulation-based phylogenetic ANOVA revealed that landing style had a significant effect on log PeakF-comp (F = 15.61, p = 0.0028). Pairwise post-hoc tests with Holm-Bonferroni corrections showed that two-point landings resulted in significantly lower PeakF-comp than four-point landings (t = −5.08, p = 0.0064) and three-point landings (t = −3.74, p = 0.0060). PeakF-comp for three-point landings was not significantly lower than four-point landings (t = −0.46, p = 0.7703) (Figure 3).

During the tension phase, peak tensile forces (PeakF-tens) were 1.94 ± 0.43 BW for two-point landings, 2.67 ± 1.43 BW for three-point landings, and 2.93 ± 1.24 BW for four-point landings (same sample sizes as above; *T. tricolor* has no tension phase because it lands on a vertical surface instead of a ceiling). Simulation-based phylogenetic ANOVA did not find a significant effect of landing style on log PeakF-tens (F = 2.11, p = 0.3378) (Figure 3).

In seven cases, under-rotation of the body during the landing maneuver caused the head or thorax to contact the ceiling before or simultaneously with the limbs, resulting in "crash landings" (Figure 2). In each case, the bat still successfully attached to the ceiling, but the impact involved compressive forces two-three times higher than typical landings (Figure 3 gray star points). Of these crashes, four instances occurred during the two-point landings of *Rhinolophus ferrumequinum* and *Rhinolophus eurayle*. In both species, failure to fully invert the body and decelerate the COM prior to attachment of the hindlimbs allowed the ventral thorax to impact the force plate during the compression phase, leading to forces of 4.06 ± 4.21 BW. We documented three additional crashes during the four-point landings of *Sturnira parvidens*. For this species, inadequate pitching rotations caused bats to strike the force plate with the head before finding purchase with one or more limbs, resulting in compressive forces of 14.12 ± 3.76 BW. Following crashes, we allowed bats to rest and move freely while we ensured their flight behavior returned to normal. No bats displayed signs of injury or impairment after these seven crash landings.

Landing impulse

Total landing impulse (Imp-tot; from time of contact to time of PeakF-tens) was 159.35 ± 57.42 BW-ms for two-point landings, 165.10 ± 73.98 BW-ms for three-point landings, and 161.91 ± 46.69 BW-ms for four-point landings. Simulation-based phylogenetic ANOVA did not find a significant effect of landing style on log Imp-tot (F = 0.482, p = 0.790) (Figure 4A).

Impulse during the compression phase (Imp-comp; from time of contact to the time at which F_Z decreases to zero) showed greater differences across landing styles. Imp-comp was 18.73 ± 10.74 BW-ms for two-point landings, 68.98 ± 56.36 BW-ms for three-point landings, and 79.3 ± 32.63 BW-ms for four-point landings. Simulation-based phylogenetic ANOVA found a significant effect of landing style on log Imp-comp (F = 12.792, p = 0.006). Pairwise post-hoc tests with Holm-Bonferroni corrections showed that, like PeakF-comp, two-point landings resulted in significantly lower log Imp-comp than three- (t = −3.590, p = 0.0102) and four-point landings (t = −4.473, p = 0.0138) (Figure 4B).

Impulse during the tension phase (Imp-tens; from the time at which F_Z becomes negative to the time of PeakF-tens) also differed among landing styles, but inversely to PeakF-comp and Imp-comp. Imp-tens was 140.63 ± 49.97 for two-point landings, 96.12 ± 32.53 for three-point landings, and 82.62 ± 22.47 for four-point landings. Simulation-based phylogenetic ANOVA found a significant effect of landing style on log Imp-tens (F = 7.966, p = 0.0239). Pairwise post-hoc tests with Holm-Bonferroni corrections showed that two-point landing tensile impulses were significantly higher than those of four-point landings (t = 3.972, p = 0.0402) and not significantly higher than those of three-point landings (t = 1.566, p = 0.445). Tensile impulses from three-point were not significantly higher than those of four-point landings (t = 1.604, p = 0.445) (Figure 4C).

Ancestral state reconstruction for landing style

We simulated 1,000 stochastic character maps of landing style on a phylogeny pruned to our sample taxa. These simulations estimated that four-point landings were the ancestral condition for bats (posterior probability, PP_4 = 0.740), and that landing style shifted an average of 10.524 times across all simulated phylogenies. The most common shift was from four- to two-point landings, which occurred an average of 2.577 times and was distributed broadly across the bat phylogeny. Additional state changes were concentrated among bats in the family Phyllostomidae, in which an average of 2.112 shifts from two- to three-point landings and 1.748 reversals from two- to four-point landings occurred.

According to the posterior probabilities, two-point landings evolved three times independently: first in the most recent common ancestor of Rhinolophidae and Hipposideridae (PP_2 = 0.754), then in the common ancestor of Emballonuridae (PP_2 = 0.950), and finally in the common ancestor of Phyllostomidae (PP_2 = 0.970) (Figure 5). Three-point landings evolved relatively recently, potentially in the common ancestor of the phyllostomid subfamily Stenodermatinae (Figure 5), which showed approximately equal posterior probability of performing two- (PP_2 = 0.486)

Table 1. Study taxa, landing style observed, peak landing impact forces, landing impulses, and roosting ecology categories

Taxon	N (Landings, individuals)	N (Force recordings, individuals)	Landing Style	PeakF$_{tot}$ Comp (Bodyweight)	Peak F$_{tot}$ Tens (Bodyweight)	Imp-total (BW ms)	Imp-Comp (BW ms)	Imp-Tens (BW ms)	Roosting Ecology[d]
				Suborder: Yinpterochiroptera					
Family: Pteropodidae									
Cynopterus brachyotis[a]	30, 3	30, 3	4-point	3.78 ± 1.20	2.39 ± 0.34	160.74 ± 26.92	81.02 ± 11.46	79.73 ± 33.01	FOL-UF, *FOL-LT*
Rousettus aegyptiacus	9, 2	–	4-point	–	–	–	–	–	R/C
Family: Hipposideridae									
Hipposideros pratti	7, 1	–	2-point[b]	–	–	–	–	–	R/C
Family: Rhinolophidae									
Rhinolophus hipposideros	33, 3	33, 3	2-point	0.64 ± 0.11	1.82 ± 0.10	125.73 ± 4.13	10.20 ± 2.47	115.53 ± 3.41	R/C
Rhinolophus mehelyi	30, 4	30, 4	2-point	0.71 ± 0.14	1.88 ± 0.22	136.32 ± 24.84	9.95 ± 3.86	126.37 ± 26.40	R/C
Rhinolophus euryale	22, 4	22, 4	2-point	1.10 ± 0.83	1.75 ± 0.21	153.04 ± 36.04	14.94 ± 13.36	138.10 ± 27.55	R/C
Rhinolophus ferrumequinum	31, 4	29, 4	2-point	1.24 ± 0.74	1.69 ± 0.06	181.48 ± 15.48	18.81 ± 13.11	162.66 ± 13.85	R/C
				Suborder: Yangochiroptera					
Family: Emballonuridae									
Rhynchonycteris naso	6, 1	–	2-point	–	–	–	–	–	*EST*, FOL-UF
Saccopteryx bilineata	2,1	–	2-point	–	–	–	–		*CST*, EST
Family: Thyropteridae									
Thyroptera tricolor	71, 16	43, 13	4-point[c]	6.07 ± 1.11	–	–	96.37 ± 32.9	–	FOL-TB
Family: Mormoopidae									
Pteronotus mesoamericanus	17, 2	–	4-point	–	–	–	–	–	*R/C*, CST
Pteronotus davyi	11, 2	–	4-point	–	–	–	–	–	R/C
Family: Phyllostomidae									
Micronycteris schmidtorum	5, 1	–	2-point	–	–	–	–	–	CST
Glossophaga soricina[a]	49, 5	49, 5	2-point	0.85 ± 0.09	1.89 ± 0.14	138.38 ± 26.48	20.73 ± 4.29	117.65 ± 27.79	CST, *R/C*
Chrotopterus auritus	3, 1	–	2-point						*R/C*
Mimon cozumelae	20, 4	19, 4	2-point	1.32 ± 0.47	2.12 ± 0.53	250.02 ± 22.19	35.87 ± 9.29	214.15 ± 18.87	*CST*, R/C
Lophostoma evotis	9, 1	–	3-point	–	–	–	–	–	TAN
Gardnernycteris crenulatum	3, 1	–	2-point	–	–	–	–	–	CST
Carollia sowelli	16, 3	14, 2	2-point	1.92 ± 0.65	1.91 ± 0.07	180.34 ± 51.12	28.52 ± 9.01	151.81 ± 42.11	*CST*, R/C
Carollia perspicillata[a]	50, 5	50,5	2-point	0.89 ± 0.17	2 ± 0.2	122.33 ± 36.72	21.94 ± 6.3	100.38 ± 30.73	*CST*, CFT, R/C
Sturnira parvidens	23, 5	20, 5	4-point	4.16 ± 2.93	4.84 ± 1.76	174.57 ± 68.03	72.91 ± 40.61	101.66 ± 63.97	*FOL-UF*, CST
Uroderma bilobatum	2, 1	2, 1	3-point	6.02±NA	4.56±NA	256.88±NA	151.79±NA	105.09±NA	FOL-LT
Dermanura phaeotis	25, 5	9, 3	3-point	3.85 ± 2.64	2.99 ± 1.62	163.96 ± 128.93	71.68 ± 60.32	92.27 ± 72.4	FOL-LT

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Table 1. *Continued*

Taxon	N (Landings, individuals)	N (Force recordings, individuals)	Landing Style	PeakF$_{tot}$ Comp (Bodyweight)	Peak F$_{tot}$ Tens (Bodyweight)	Imp-total (BW ms)	Imp-Comp (BW ms)	Imp-Tens (BW ms)	Roosting Ecology[d]
Artibeus jamaicensis	21, 3	21, 3	2-, *3-point*	1.12 ± 0.46	1.55 ± 0.17	174.47 ± 31.72	22.76 ± 11.73	151.7 ± 39.38	R/C, *FOL-LT*
Artibeus intermedius	11, 2	9, 2	2-point	1.54 ± 0.58	3.14 ± 1.64	235.73 ± 0.68	35.99 ± 16.68	199.75 ± 16	R/C, CST, FOL-UF, *FOL-LT*
Artibeus watsoni	5, 1	–	3-point	–	–	–	–	–	*FOL-LT*
Family: Molossidae									
Tadarida brasiliensis	20, 20	–	4-point	–	–	–	–	–	R/C, *CREV*
Family: Miniopteridae									
Miniopterus schreibersii	30, 4	11, 2	2-, 3-, *4-point*	1.13 ± 0.51	1.59 ± 0.16	69.88 ± 24.47	21.69 ± 14.18	48.19 ± 13.01	R/C, *CREV*
Family: Vespertilionidae									
Myotis keaysi	5, 1	–	4-point	–	–	–	–	–	R/C, *CREV*, CST
Myotis daubentonii	10, 1	–	4-point	–	–	–	–	–	R/C, *CREV*
Myotis myotis	12, 2	–	4-point	–	–	–	–	–	R/C, *CREV*
Myotis capaccinii	16, 4	4, 1	4-point	4.9±NA	3.28±NA	178.56±NA	75.82±NA	102.74±NA	R/C, *CREV*
Rhogeesa aeneus	3, 1	–	4-point	–					CST, *CREV*, FOL-UF
Eptesicus fuscus	10, 1	9, 1	4-point	5.49±NA	2.63±NA	210.64±NA	129.02±NA	81.62±NA	CST, *CREV*
Eptesicus serotinus	10, 1	–	4-point	–	–	–	–	–	R/C, *CREV*
Hypsugo savii	10, 1	–	4-point	–	–	–	–	–	R/C, *CREV*
Totals:	**637, 116**	**404, 65**							

Peak impact forces during compression (PeakF–Comp) and tension phases (PeakF–Tens) were extracted from data filtered with a 100 Hz low-pass Butterworth filter. Impulse measurements during compression (Imp-Comp) and tension phases (Imp-Tens) were extracted from data filtered with a 50 Hz low-pass Butterworth filter. Measurements are shown as mean ± SD. Roost categories are: cavity in standing tree (CST), exposed on standing tree (EST), unmodified foliage (FOL-UF), furled leaf-tube (FOL-TB), foliage modified into leaf-tent (FOL-LT), termite or ant nest (TAN), rock and/or cave (R/C), and crevice (CREV). Italicized categories indicate those used for comparative analyses; see text for further explanation.

[a]Data from Riskin et al. (2009).

[b]*H. pratti* performed landings that were qualitatively similar to two-point landings, however, following attachment with the hindlimbs, bats flexed the spine ventrally and extended the shoulder and elbow joints to lift the thumb claws ventrally toward their attachment site on the landing plate. Because the thumbs were attached only after the contact during landing, we classify landings by *H. pratti* as two-point in our analysis.

[c]*T. tricolor* performs a specialized four-point landing maneuver (see Boerma et al., 2019).

[d]See Table S1 for sources for roosting ecology designations and Datasets S2 and S3 for impact force and impulse data.

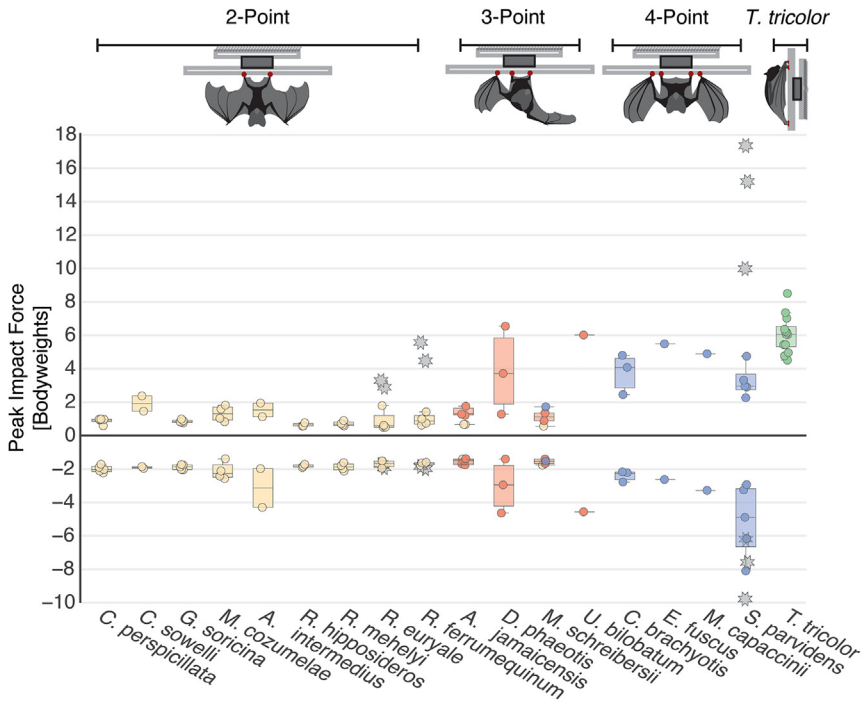

Figure 3. Peak landing impact forces

Peak 3D impact forces during the compression phase (positive values) and tension phase (negative values) for each species, grouped by landing style. Two-point landings shown in yellow, three-point landings in red, four-point landings in blue, *T. tricolor* landings in green, and crashes in gray star points. Box and whisker plots show the median and interquartile range. Yellow, red, blue, and green points represent means for each individual bat; gray points represent individual "crash" landings. See Videos S1, S2, S3, S4, and S5 for examples of each landing style.

or three-point landings ($PP_3 = 0.427$). The common ancestor of tent-making bats (stenodermatines minus *Sturnira parvidens*) likely performed three-point landings ($PP_3 = 0.925$), a landing style that also arose in the lineage giving rise to *Lophostoma evotis*. We detected a reversal from two- to four-point landings in *S. parvidens*. Four-point landings, the ancestral condition, were conserved in all other species.

Evolutionary correlations between landing style and roosting ecology

We tested for an evolutionary correlation between landing style and roosting ecology using a correlative threshold model,[13,14] in which we treated each of the traits as a binary discrete character: landing style was either high-impact/low-rotation (three- and four-point landings) or low-impact/high-rotation (two-point landings) and roosting ecology was either stiff/horizontal/spatially open or compliant/vertical/spatially constrained. Our correlational threshold model estimated a mean correlation of $r = 0.6518$ with a 95% high-probability-density (HPD) interval of 0.2197–0.9447 (lower bound–upper bound). This positive evolutionary correlation indicated that low-impact/high-rotation landings

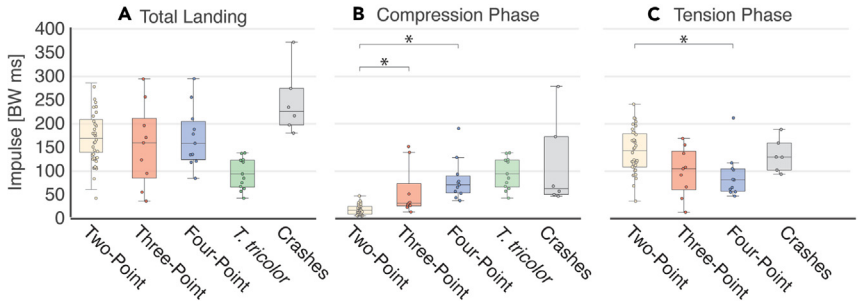

Figure 4. Landing impulse

Landing impulse is shown for the total landing (A), the compression phase (B), and tension phase (C) grouped by landing style. Post-hoc tests were calculated only for two-point landings shown in yellow, three-point landings in red, and four-point landings in blue (see STAR Methods); * denotes $p < 0.05$. For comparison, *T. tricolor* landings are shown in green and crashes in gray. Box and whisker plots show the median and interquartile range. Points represent means for each individual bat.

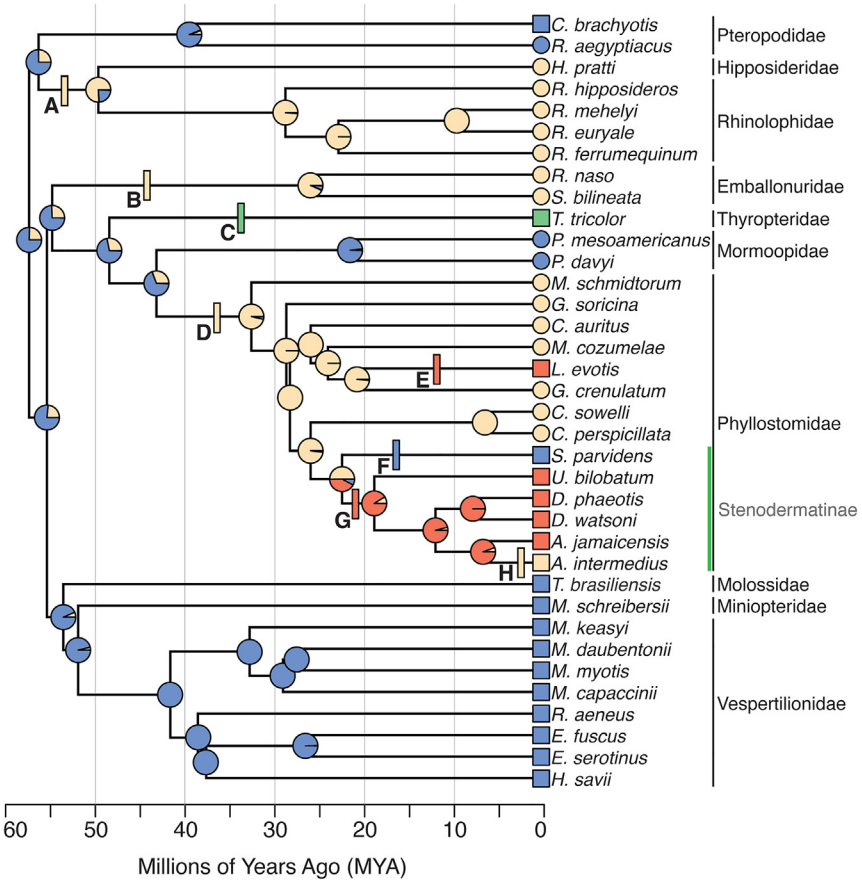

Figure 5. Ancestral state reconstruction of bat landing styles using stochastic character mapping

Pie charts at the nodes show posterior probabilities for landing style.

(A–H) mark shifts in landing style. Colors denote landing style: yellow = two-point, red = three-point, blue = four-point, and green = specialized four-point for *T. tricolor*. Tip shape denotes the roost type used in the correlational threshold model: circle = stiff, horizontal, or open roosts, whereas square = compliant, vertical, or spatially constrained roosts. Black vertical bars to the right of the species names denote families; the green line highlights the subfamily, Stenodermatinae. Phylogeny adapted from Shi and Rabosky (2015).

coevolved with roosting on stiff/horizontal/spatially open surfaces, and that high-impact/low-rotation landings coevolved with roosting on more compliant/vertical/spatially constrained surfaces (Figure S1).

DISCUSSION

Birds and bats are the only living vertebrates capable of controlled, flapping flight. However, the independent evolution of flight in each lineage resulted not only in differences in the morphology of the wings but also in the maneuvers used to safely land. Whereas birds largely evolved landings that control descent to underfoot perches, bats evolved landing maneuvers that reorient their bodies as they ascend toward roosts overhead, where they adopt their iconic head-under-heels roosting posture.[15] Using a combination of field-based high-speed videography, impact force analysis, and phylogenetic comparative methods, we investigated (1) how bats physically accomplish landings, and (2) how and (3) why this characteristic landing behavior evolved in bats.

From our sample of 36 species, we found that bats can land using one of four landing maneuvers, one of which, the three-point landing, we describe here for the first time (Figure 2). We refer to these maneuvers as "landing styles" to succinctly capture major differences in mechanics and performance. Landing styles varied along a continuum of points of contact, limb contact order, body rotations, and performance metrics such as landing impulse and peak landing impact force during both the compression and tension phases of landing (Figure 6).

Although most bat species roost by hanging from only their hindlimbs, we show that not all bats can perform a landing maneuver that immediately results in this orientation. In fact, only one of the three landing styles—the two-point landing—sufficiently inverts the body prior to contact to allow a bat to land with hindlimbs only. Furthermore, analysis based on the species we have sampled to date suggests that this landing style did not appear in bats for 10–25 million years following the diversification of modern bats, and when it did, it independently evolved at least three times in distantly related clades. We found that this rotationally complex, low-impact landing style coevolved with roosting ecologies that favored stiff, horizontal surfaces, such as cave ceilings and tree cavities (Figure 6).

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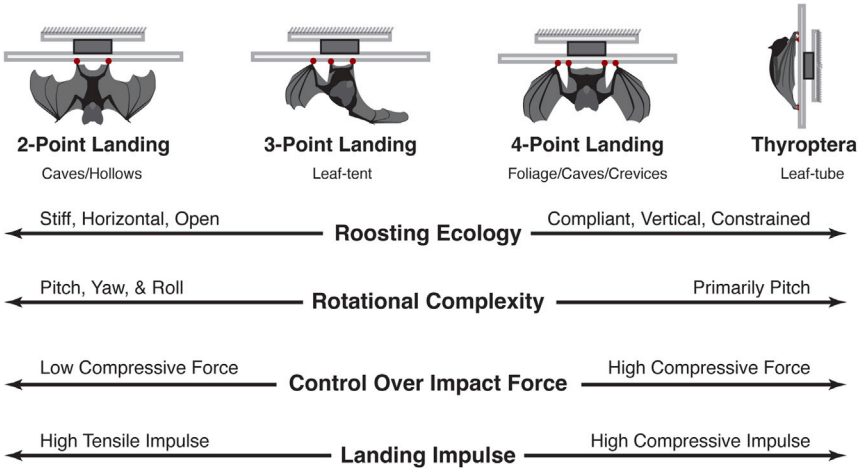

Figure 6. Continuum of landing style, roosting ecology, and landing mechanics
The mechanics of bat landings correspond with patterns of roost use among sampled bats.

Mechanics and performance across bat landing styles

Our analysis of peak landing impact force and impulse in a subset of 18 species (see Table 1) reveals that greater body rotation allows landing bats to decrease the mechanical loads experienced by the limb skeleton, particularly when considering the compressive and tensile phases of landing separately.

The two-point landing requires the most body rotation and demands that a bat to use a combination of pitch, yaw, and roll to assume a fully inverted orientation prior to contact (see Riskin et al. 2009 for full kinematic descriptions). The early timing of these rotations during landing maneuvers may allow upward vertical body velocity to decrease before the body has closely approached the landing site, thus reducing peak compressive forces and impulse that might otherwise lead to mechanical failure of the thin, elongated hindlimb long bones, especially when landing occurs on a stiff surface and is not distributed among four limbs. Two-point landings instead allow the hindlimbs to dissipate the landing forces in the horizontal and downward direction during the tension phase. This behavior applies tensile forces to the muscles, tendons, and ligaments instead of compressive forces to the hindlimb skeleton. For most bat hindlimbs, soft-tissue structures may be better suited to withstanding loads, particularly in tension, for at least three reasons. First, the flexor muscle groups at the hip, knee, and ankle can act as muscular brakes that actively lengthen (eccentrically contract) to absorb tensile forces as hindlimbs extend during the tension phase of landing.[16,17] Second, the tendons associated with these muscles, particularly those of the distal muscles such as the gastrocnemius and long digital flexors, may further absorb tensile forces and store elastic strain energy. Subsequent tendon recoil would release this energy when the bat's COM oscillates toward and away from the ceiling as it swings following a successful landing.[18] Third, most mammalian tendons are notoriously over-built for the loads they regularly sustain during locomotion,[19] and bat hindlimb tendons may thus be readily able to withstand the tensile forces they experience during two-point landings.

In contrast, the comparative under-rotation of four-point landings positions the body such that the forelimbs, specifically the thumb and wrist pad, are the first to contact the ceiling, resulting in more sustained upward vertical velocity through the time of contact. The high peak compressive forces and impulse for this landing style may thus be permissible because they are transmitted through significantly more robust bones and flight musculature, including the radius, humerus, and forelimb extensor muscle groups of the shoulder and elbow, than the case for hindlimb-only two-point landings.[20–24]

Three-point landings present an intriguing intermediate case, in part because of their high compressive forces and impulse relative to two-point landings, coupled with a hindlimbs-first contact order that could apply relatively large impact loads to the hindlimb skeleton. In practice, three-point landing bats qualitatively under-rotated their bodies compared to two-point landings, sustaining enough upward vertical velocity to allow a single forelimb, the abdomen, and the thorax to contact the ceiling almost simultaneously with the hindlimbs. This pattern mitigates the compressive forces they experience, although less than in the four-point landing case.

For both two- and four-point landing bats, the consequences of executing a landing without sufficient precision and body rotation may be dire. Our records of "crash landings" demonstrate that for either landing style, under-rotation results in peak compressive forces that are three to six times higher than normal landings. Furthermore, these higher impacts affect sensitive body regions, such as the head, neck, abdomen, and thorax, that are not equipped to use the musculoskeletal system to absorb high forces. In essence, these crash landings are the "exceptions that prove the rule": control over body orientation and compressive impact forces are linked for bat landing styles, and failure to sufficiently reorient the body prior to contact could lead to serious injury. These consequences may be especially acute for juvenile bats as they learn to fly and land. However, no studies to our knowledge have examined the ontogeny of landing performance in bats. In either case, whether adult or juvenile, selection for effective control of landings may be strong. In addition, as we discuss in the following section, substrate stiffness and orientation likely also influence the effective force on the limbs and other body regions when bats land on natural surfaces, providing a framework for exploring how landing maneuvers evolved in relation to the mechanical properties of the roosts to which they provide access.

Roosting ecology and the evolution of bat landing maneuvers

In bats, a group for which the specific origins of flight remain unresolved, the evolutionary history of landing mechanics provides a perspective that complements that of the evolution of powered flight itself. Despite a lack of fossils, most available data point to a gliding origin of bat flight in which the hypothetical bat ancestor was arboreal, possessed gliding membranes made of skin and performed locomotion similar to that of extant gliding mammals.[25–28]

If bat flight had its origins in gliding, we would expect that the landing maneuvers performed by early bats would have been comparable to those of gliding mammals. Indeed, we find that four-point landings are the ancestral condition for bats, a landing style that substantially resembles, and could plausibly have evolved from, the similarly pitch-dominated, high-impact landings of mammalian gliders.[29–33] Furthermore, the vertical tree trunks and compliant foliage of arboreal environments would have constituted the ecological backdrop for these early landing maneuvers, setting the stage for the evolution of new landing styles as early bats sought new environments throughout their ensuing global radiation. Our findings do not necessarily preclude alternative origins of bat flight, such as the "trees-down hypothesis," which posits that proto-bats used incipient wings to control their descent to capture prey on the ground. However, the transition from ground landings to ascending tree landings under this hypothesis would require additional explanation compared to the gliding origin hypothesis.

Through analysis of the shared qualitative physical properties of certain roost types, including orientation, stiffness, and spatial constraints, our ancestral state reconstruction and correlative threshold model found that four-point landings gave rise to two-point landings, which co-evolved with stiffer, more horizontal roosts, such as tree cavities or exposed cave ceilings. In contrast, higher-impact landings requiring less body rotation (three- and four-point landings) either persisted, arose, or re-evolved in association with more compliant, vertical, and/or spatially constrained roosts, such as foliage, crevices, or leaf tents.

This result contradicts our and other investigators'[9] predictions that four-point landings would be strictly associated with foliage roosting, where the compliance of the roost would mitigate the high peak compressive forces of this high-impact landing style. The foliage-roosting hypothesis is only partially supported by *T. tricolor*, which performs the highest-impact landings of any species measured to date,[10] and species in the phyllostomid subfamily Stenodermatinae. Stenodermatinae experienced a shift to foliage-roosting[34] and include species showing either evolutionary histories of reversal from two- to four-point landings (*S. parvidens*) or of three-point landings. However, most four-point landing species in our sample roost in caves, cliffs, or other stiff surfaces. In these cases, we found that the specific location of roosting was often in crevices, clefts, or corners. Field observations suggest that the location or orientation of these preferred roost microhabitats often differ from those of the initial landing site, and thus involve bats' movement along the roost surface immediately after landing (Video S6). Landing with four points of contact immediately positions the body and limbs on the substrate and thereby facilitates a rapid transition to terrestrial locomotion (crawling) along the roost surface. This likely reduces the time required to attain the eventual roosting site (e.g., a rock crevice), thus minimizing exposure to predators or adverse environmental conditions. Such decoupling of landing versus roosting locations could also closely resemble the ancestral state, which may have involved bat ancestors landing on exposed surfaces, such as tree trunks or branches, before crawling along those surfaces.[35] This kind of arboreal crawling is suggested by the presence in early bats of claws on all five forelimb digits and limb proportions that are suggestive of non-volant arboreal species,[28] which have since been lost in extant bats.

Our analyses show that two-point landings independently evolved three separate times among the taxa in our study, in lineages that we suggest began to occupy stiffer, more exposed, and/or horizontal roosts. In the suborder Yinpterochiroptera ("Old World" bats), we found that rhinolophids and hipposiderids, both of which roost in caves, likely descended from a two-point landing ancestor ($PP_2 = 0.754$). Given that these represent only two of six families in the superfamily, Rhinolophoidea, we acknowledge that two-point landings may have originated earlier in this clade. Among the Yangochiroptera, two-point landings evolved in species that roost in caves, cave-like structures, tree cavities, or exposed horizontal tree trunks or branches, as we observe in the phyllostomids and emballonurids. Two-point landings enable these bats to minimize compressive forces on the elongated hindlimb long bones while permitting them to land with precision in roosting locations without consistent requirements to subsequently move to more preferable sites. We were, however, able to sample only a small fraction of the nearly 1500 species of extant bats and recognize that further study could reveal that complex two-point landings may have evolved independently more frequently.

Three-point landings have evolved only in the phyllostomids in our sample, in close association with tent-making, a highly derived form of foliage-roosting. Tent-making refers to a behavior in which bats weaken the veins of large leaves by biting them so that portions of the leaf droop to create a tent-like shelter.[2,5,36–38] This behavior arose independently in phyllostomids (primarily within the subfamily Stenodermatinae), pteropodids (primarily among species in the genus *Cynopterus*), and at least one vespertilionid species (*Scotophilus kuhlii*).[39] Our study sample includes two groups of tent-making bats: three-point landing stenodermatine bats and *Cynopterus brachyotis*, which performs a four-point landing. This difference in landing style despite convergence in roosting ecology might be due to different evolutionary starting points for landing style in stenodermatine phyllostomids versus pteropodids. The most recent common ancestor of phyllostomids likely roosted in cavities[34] and performed two-point landings ($PP_2 = 0.970$), and thus likely used hindlimbs only for low-compressive-force landings. Under our hypothesis, the transition to roosting in spatially constrained, compliant leaf-tents would have reduced the selective pressure on low-impact landings, thus permitting a shift to higher-impact three-point landings that retained the feet-first contact order but added the thumb as a stabilizing point of contact. In contrast, the common ancestor of pteropodids likely performed four-point landings ($PP_4 = 0.923$), a landing style already amenable to roosting in compliant leaf tents able to absorb the higher compressive forces this behavior generates. The comparison of stenodermatines and *Cynopterus* shows that although three- and four-point landings differ in mechanics and evolutionary history, they result in similar functional outcomes in similar ecological contexts, suggesting many-to-one mapping of low-rotation, higher-impact landings in bats.[40]

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Broader implications: Bat conservation and adaptive radiation

Like most of the earth's biodiversity, bats are vulnerable to human disturbance, whether it is through anthropogenic climate change or more proximate issues, such as deforestation or human construction. All of these phenomena can affect the availability and quality of roosts. If landing mechanics are associated with roosting habits, then they may affect the extent to which certain species are robust to displacement via roost destruction. Bats with highly specialized roosting ecologies are generally at higher risk for extinction and are less prevalent in disturbed forest fragments.[1,41] In addition to the difficulties associated with locating suitable alternatives, species with specialized landing maneuvers, such as *T. tricolor*,[10,12] may also encounter a biomechanical barrier to establishing new roosts. In certain cases, the mechanics of bat landing maneuvers may thus mediate roost access if displaced by prohibiting certain species from successfully landing on new surfaces. Conversely, species whose landing styles are more flexible and permissive, or those that can perform multiple landing styles, such as *A. jamaicensis* and *M. schreibersii*, may be able to roost more easily on a diverse array of surfaces and thus be more robust to habitat destruction. In these latter cases, even when individuals performed multiple landing styles, the relative forces of each landing still increased or decreased with points of contact, although within a smaller range of force values (Figure 2). This pattern suggests that the ability to perform a two-point landing leads to a broader capacity to land at low impact force regardless of landing style. Analyses that probe the relationship between number of roost types used, landing style, habitat range, and tolerance of forest fragments are among the future efforts that could help evaluate this hypothesis.

Additionally, studies that integrate biomechanics with ecology and evolutionary history have the potential to reveal key morphological or behavioral innovations that changed the way lineages interacted with their environments and helped to drive adaptive radiations.[42–47] Here, we suggest that roosting ecology and landing mechanics are functionally linked. Given this relationship and the broad biological importance of roosting for bat diversity, the potential for landing mechanics to be a mediating factor during the evolution of diverse roosting habits makes this a promising system for studying how ecological opportunity (roosting ecology), form (wing morphology), and function (landing mechanics) interacted over the course of diversification in bats. The extent to which these factors acted as drivers of speciation in certain lineages is unclear, but the present study serves as a foundation for future inquiry into these evolutionary relationships.

Conclusions

Resolving the connections among form (morphology), function (mechanics), and environmental context (ecology) are central to understanding the evolutionary history of organisms. While form-function (functional morphology) and form-environment (ecomorphology) relationships are often the focus of evolutionary studies, determining linkages between mechanics and ecology is equally critical to understanding how morphological and ecological variations interact with the organismal performance on which selection acts. Our survey of landing mechanics in bats reveals that interspecific variation in landing styles follow a mechanical continuum of rotational complexity, peak landing impact forces, and landing impulse. We further demonstrate that landing styles coevolved with roosting ecology. Rotationally complex, low-impact landings (two-point) evolved in concert with use of stiff, horizontal roosts, whereas rotationally simple, higher-impact landings (three- or four-point) were conserved, arose, or re-evolved in lineages that use compliant, vertical, or spatially constrained roosts, such as crevices or leaf-tents. These results highlight the evolutionary interactions between locomotor mechanics and ecology, establish functional links between landing mechanics and roosting ecology in bats, and suggest that these interactions may be a factor both for mediating roost use and for driving diversification in certain clades. By connecting roosting ecology to the biomechanics of landing flight, we now have the potential to identify additional traits, such as aspects of limb morphology and wing architecture, that are specifically associated with a locomotor behavior of known ecological relevance. For example, given the heightened importance of wing use in inertial dynamics for two-point landings, wing moments of inertia and their morphological basis may vary between bats that use two-point and other landing styles. Our study thus lays the foundation for a broader understanding of the evolution of flight in this extraordinarily successful lineage of mammals.

Limitations of the study

The reader should consider that this study's conclusions are limited by constraints along at least three axes: (1) taxonomic sampling, (2) experimental design, and (3) phylogenetic analyses. With respect to (1), overall taxonomic sampling, we note that ten of twenty-one chiropteran families are represented in this study. Furthermore, only two pteropodid species are included, neither of which represent the largest extent of possible body sizes in bats. We also consider that limited sampling of rhinolophoid bats (represented by only the families Rhinolophidae and Hipposideridae in our study) may mask additional independent evolutionary events for landing styles within this superfamily. These taxonomic limitations are increased for impact force analyses because only a limited subset of bats was amenable to training. With respect to (2), experimental design, our study limited its scope to horizontal ceiling landings only, although many species routinely land on vertical or inclined surfaces, such as walls of caves or buildings and tree trunks. Future studies of these and landings at natural roosts may reveal additional details regarding how bats adjust fundamental landing styles in a context-dependent fashion. Finally, with respect to (3), phylogenetic analyses, a major limitation of this study is that it treats roosting ecology as a binary categorical variable. Quantitative measurements of roost material properties could offer more specific biomechanical insights regarding the interplay between landing mechanics and roosting ecology. Additionally, future advances in phylogenetic comparative methods that permit analysis of multistate categorical variables would enhance the granularity with which we can resolve the relationship between landing maneuvers and the diverse roosts to which they provide access.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2024.110381.

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AUTHOR CONTRIBUTIONS

Conceptualization, D.B.B. and S.M.S.; methodology, D.B.B. and S.M.S.; software, D.B.B.; formal analysis, D.B.B.; investigation, D.B.B.; resources, S.M.S.; writing – original draft, D.B.B.; writing – review & editing, D.B.B. and S.M.S.; supervision, S.M.S.; funding acquisition, D.B.B. and S.M.S.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Data and code for analysis	Harvard Dataverse	https://doi.org/10.7910/DVN/SCBE4W
Experimental models: Organisms/strains		
Bats (see Table 1 for species)	Wild	N/A
Software and algorithms		
MATLAB	Mathworks	https://www.mathworks.com; RRID: SCR_001622
R 4.2.2	The R Foundation for Statistical Computing	https://cran.r-project.org/mirrors.html; RRID: SCR_001905
Phantom PCC 3.9.40	Vision Research	https://phantomhighspeed.my.site.com/PhantomCommunity/s/software-downloads; RRID: SCR_021080
Other		
Phantom Miro M340 High Speed Cameras	Vision Research	https://www.phantomhighspeed.com
ATI F/T Sensor: Nano17	ATI Industrial Automation	https://www.ati-ia.com/products/ft/ft_models.aspx?id=Nano17

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, David B. Boerma (dboerma@pace.edu).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- The ceiling reaction force, landing style, and roosting ecology datasets generated during this study have been deposited at the Harvard Dataverse (https://doi.org/10.7910/DVN/SCBE4W) and in the paper's supplemental information. All data are publicly available as of the date of publication.
- All original code has been deposited at the Harvard Dataverse (https://doi.org/10.7910/DVN/SCBE4W) and in the paper's supplemental information. All data are publicly available as of the date of publication.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND STUDY SARTICIPANT DETAILS

We recorded a total of 637 landings from 116 bats (63 males, 32 females, and 22 of unknown sex), representing 36 species and 10 families, using high speed videography (Table 1). A subset of these landings also included measurements of ceiling reaction forces, totaling 404 landings from 65 bats (45 males, 20 females), representing 18 species. Landing style was consistent among individuals of each species and did not differ according to sex. We collected all measurements from wild-caught bats except for those taken from *Rousettus aegyptiacus* and those reported in Riskin et al. (2009) (*C. perspicillata*, *G. soricina*, and *C. brachyotis*), in which the study subjects were captive-bred. Although the exact ages for all bats were unknown, we collected measurements only from sexually mature adults by visually inspecting the interphalangeal joints for complete ossification. All wild-caught bats were kept only for the duration of their respective experimental trials, up to 24 h, and were housed in collapsible mesh cages (if kept for >6 h) or large cloth bags (for transport and short-term housing). We provided water via syringe *ad libitum* and gave species-appropriate nutrition (fruit, fruit juice, or meal worms). Our field sites were in Lamanai, Orange Walk, Belize (Lamanai Outpost Lodge); Barú, Puntarenas, Costa Rica (Haciénda Barú Biological Research Station); Tabachka, Bulgaria (Siemers Bat Research Station, Max Planck Institute for Biological Intelligence); and Jinan, Shandong Province, China (Shandong University). We captured bats using mist-netting, hand-netting, and harp traps. This study was approved by the Brown University IACUC and conformed to all relevant regulatory standards.

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METHOD DETAILS

Landing experiments

At each field site, we observed bat landings within a temporary flight corridor (2-4 x 1.5 × 2 m) (length x width x height). For all bats except *T. tricolor* (see study by Boerma *et al.*[10]), we covered the walls and ceiling with smooth plastic sheeting to prevent bats from landing anywhere but on a ceiling-mounted landing platform, which was covered with stiff plastic mesh that provided a favorable attachment surface for landing bats. We trained wild-caught bats to land on the platform by positively reinforcing successful landings with food rewards (fruit and juice for frugivorous bats, mealworms for insectivorous bats, and water for all bats), and recorded their landing maneuvers with a synchronized array of three high speed video cameras (Phantom Miro M340, Vision Research, Wayne, NJ, USA; 800 frames per second, 1000 μs exposure; Lenses: Sigma DC 17-50mm 1:28 EX HSM, SIGMA Corporation, Ronkonkoma, NY, USA) and three LED lights (Veritas Constellation 120, Integrated Design Tools, Pasadena, CA, USA).

Sample sizes for number of species, number of individuals per species, and number of landings per individual were subject to species availability at field sites and the extent to which wild-caught individuals were amenable to training during their brief time in our landing enclosure. Previous studies documented zero to low intraspecific variation in landing style.[9,10] We therefore accepted samples of one individual per species but required at least two landings per individual for inclusion in our study. Of the bats used in this study, we were able to train a subset of 65 individuals (representing 18 species) to land on the ceiling-mounted force plate (ATI nano17, ATI Industrial Automation, Apex, NC, USA) fitted with custom acrylic mounting and landing plates. We considered successful landings as those during which all limbs involved in the landing contacted and attached to the force plate directly, without slipping over the edge of the plate. We used a custom MATLAB script to sample impact forces at 1000 Hz and synchronize data collection between the force transducer and the high speed cameras. For bats that we could not train to successfully land on the force plate, we recorded landings on a larger patch of uninstrumented ceiling-mounted mesh to categorize landing style with high speed video alone.

Ceiling reaction forces and landing impulse

We divided the force profile of each landing into two phases: 1) a compression phase, defined as the interval of time over which the vertical component of the reaction force, F_Z, is positive (upward, into the plate), and which begins with bat-plate contact and ends when F_Z decreases back to zero; and 2) a tension phase, defined as the subsequent interval of time over which F_Z is negative, beginning when F_Z first becomes negative and ending when the total 3D force, F_{TOT}, reaches its negative peak in the vertical direction.

To extract peak impact forces during each phase, we filtered the force profiles using a zero-phase 2nd order low-pass Butterworth filter with a cutoff frequency of 100 Hz, which attenuates high-frequency oscillations and electrical noise while preserving the primary peaks associated with landing impact. Although filtering slightly diminishes the absolute magnitude of peak forces, accurate comparisons among individuals for all force components are preserved as long as they have been filtered using the same parameters (Boerma et al., 2019; Riskin et al., 2009). Our filtering parameters match those used by previous investigations of bat landing impact forces (Riskin et al., 2009 and Boerma et al., 2019), to allow direct comparison of the measurements reported here with previous analyses. We normalized landing impact forces to each individual's BW, measured using a hand-held spring scale before each experiment (Pesola Micro-Line, Pesola AG, Schindellegi, Switzerland), then extracted peak 3D impact during the compression (PeakF-comp) and tension (PeakF-tens) phases for each landing. We averaged peak compressive and tensile impact forces for each individual prior to computing species means for statistical tests.

We calculated landing impulse as the area under the total 3D force curve (F_{TOT}) after filtering the force profiles using a zero-phase 2nd order low-pass Butterworth filter with a cutoff frequency of 50 Hz by using the trapz function in MATLAB.[48] We performed this calculation over three domains: the compression phase (Imp-comp), the tension phase (Imp-tens), and the total landing (Imp-tot), which was defined as the interval from the beginning of compression phase to the end of tension phase. We repeated statistical tests for peak force and impulse data filtered at 100, 50, and 25 Hz cutoff frequencies and found no meaningful differences in the results (see Supplemental Software S1).

Definitions of categorical variables

We used high speed videography to categorize bat landings according to the convention established in Riskin et al. 2009, which named landing styles according to the number of limbs that make initial contact at landing impact with the roost. Landing styles included two-point landings (both hind limbs), three-point landings (both hind limbs plus one thumb claw), and four-point landings (both thumb claws plus both hind limbs) (Figure 1, landing style insets, Figure 2, Videos S1, S2, S3, and S4).

We classified the roosting habits of each species according to published observations (Table 1), using categories for roosting guilds outlined in Voss et al. 2016 and Garbino & Tavares 2018, with modifications. Our roosting categories included: cavity in standing tree (CST), exposed on standing tree (EST), unmodified foliage (FOL-UF), furled leaf-tube (FOL-TB), foliage modified into leaf-tents (FOL-LT), termite or ant nests (TAN), rocks and/or caves (R/C), and rock crevices (CREV).

QUANTIFICATION AND STATISTICAL ANALYSIS

We used a published time-calibrated molecular phylogeny,[49] pruned to our focal taxa, for all phylogenetic analyses.[50,51] *Artibeus watsoni* was not included in the Shi & Rabosky tree; we therefore substituted the phylogenetic position of its congener, *Artibeus aztecus*, for analyses. For all analyses, sample sizes can be found in the corresponding figure legends.

We conducted a simulation-based phylogenetic ANOVA (10000 iterations) with Holm-Bonferroni corrected post-hoc tests using the phylANOVA function in the R package phytools[50,51] to test for pairwise differences in log-peak landing impact forces and log-impulse among landing styles for each landing phase (compression and tension). Peak impact force or impulse was the response variable and landing style was the factor. We omitted two species from these analyses due to an inability to unambiguously designate them as a two-, three-, or four-point landing: *M. schreibersii*, which displayed a high degree of behavioral variability and *T. tricolor*, which performed a specialized landing maneuver to alight head-up on a vertical substrate,[10] rather than beneath a horizonal roost as in the landing experiments for our other sampled taxa.

We then conducted an ancestral state reconstruction for landing style using stochastic character mapping,[52] as implemented in the make.simmap function of the R package phytools.[50] We first assigned one landing style as a discrete character to each taxon according to its most-often observed landing style (Table 1). We then used the fitDiscrete function in the R package Geiger[53] to compare the fit of four different models for the transition matrix of the stochastic character mapping procedure: equal rates (ER), symmetric (SYM), all rates different (ARD), and meristic (MER). The ER model yielded the lowest AICc score, thus we selected this model, which gave all state changes equal probability. We used the make.simmap function to compute 1000 simulations of landing style evolution, using a Bayesian Markov chain Monte Carlo (MCMC) to sample the transition rate of the ER model, Q, from its posterior distribution. We set the prior probabilities for each landing style to be estimated empirically from their observed frequencies in our dataset.

We tested for evolutionary correlation between landing style and roosting ecology using a correlational threshold model as implemented in the threshBayes function of the R package phytools.[13,14,54] This method determines the state of a discrete trait at any time along the phylogeny according to the value of an unobserved continuous trait called a "liability". When the liability crosses certain thresholds, the state of the discrete trait shifts. Correlation between discrete traits is thus determined by the correlation of their liabilities. This method requires binary discrete traits, so we assigned landing style to each species as either low-impact/high-rotation (two-point) or high-impact/low-rotation (three- and four-point). We assigned roosting ecology to each species according to the physical properties of their preferred roosts as either stiff/horizontal/spatially open (CST, EST, and R/C) or compliant/vertical/spatially constrained (FOL-LT, TAN, FOL-UF, and CREV). We ran the model for 4,000,000 generations and extracted the post-burn-in (20% burn-in) values of the posterior distribution of the correlation coefficient, r. We then computed a 95% HPD (high-probability-density) interval around this correlation using the HPDinterval function as implemented in the R package coda.[55] The ordination of our discrete traits was: 1) high-impact <–> low-impact and 2) compliant/vertical/constrained <–> stiff/horizontal/open, indicating that a positive value for r implies that higher values of the liability for low-impact landings tend to coevolve with higher values of the liability for stiff, horizontal roosts and vice-versa.