Testing the hindlimb-strength hypothesis: non-aerial locomotion by Chiroptera is not constrained by the dimensions of the femur or tibia

Daniel K. Riskin[1,*], John E. A. Bertram[2] and John W. Hermanson[1]

[1]*Department of Biomedical Sciences, College of Veterinary Medicine, Cornell University, Ithaca, NY 14853, USA* and
[2]*Department of Cell Biology and Anatomy, Faculty of Medicine, University of Calgary, Calgary, AB T2N 4N1, Canada*

*Author for correspondence (e-mail: dkr8@cornell.edu)

Summary

In the evolution of flight bats appear to have suffered a trade-off; they have become poor crawlers relative to terrestrial mammals. Capable walking does occur in a few disparate taxa, including the vampire bats, but the vast majority of bats are able only to shuffle awkwardly along the ground, and the morphological bases of differences in crawling ability are not currently understood. One widely cited hypothesis suggests that the femora of most bats are too weak to withstand the compressive forces that occur during terrestrial locomotion, and that the vampire bats can walk because they possess more robust hindlimb skeletons. We tested a prediction of the hindlimb-strength hypothesis: that during locomotion, the forces produced by the hindlimbs of vampire bats should be larger than those produced by the legs of poorly crawling bats. Using force plates we compared the hindlimb forces produced by two species of vampire bats that walk well, *Desmodus rotundus* (*N*=8) and *Diaemus youngi* (*N*=2), to the hindlimb forces produced during over-ground shuffling by a similarly sized bat that is a poor walker (*Pteronotus parnellii*; *N*=6). Peak hindlimb forces produced by *P. parnellii* were larger (ANOVA; *P*<0.05; *N*=65) and more

variable (93.5±36.6% body weight, mean ± S.D.) than those of *D. rotundus* (69.3±8.1%) or *D. youngi* (75.0±6.2%). Interestingly, the vertical components of peak force were equivalent among species (*P*>0.6), indicating similar roles for support of body weight by the hindlimbs in the three species.

We also used a simple engineering model of bending stress to evaluate the support capabilities of the hindlimb skeleton from the dimensions of 113 museum specimens in 50 species. We found that the hindlimb bones of vampires are not built to withstand larger forces than those of species that crawl poorly. Our results show that the legs of poorly crawling bats should be able to withstand the forces produced during coordinated crawling of the type used by the agile vampires, and this indicates that some mechanism other than hindlimb bone thickness, such as myology of the pectoral girdle, limits the ability of most bats to crawl.

Key words: terrestrial locomotion, bat, hindlimb, femur, tibia, *Desmodus rotundus*, *Diaemus youngi*, *Pteronotus parnellii*, *Natalus tumidirostris*.

Introduction

When opposing selective pressures have acted on an anatomical trait the result can be an evolutionary trade-off, whereby the current ability of an organism to perform one task is hindered by requirements for some other aspect of its life history (Vanhooydonck and Van Damme, 2001). This appears to have been the case in the evolution of locomotion by the bats (Mammalia: Chiroptera). All bats possess capable powered flight, but most are poor terrestrial locomotors relative to ground-dwelling mammals of similar size (Lawrence, 1969).

Compared to similarly sized terrestrial mammals, the bones of a bat's forearm are long and curved, the radius is large relative to the ulna (with which it is often fused), and the digits are elongated as a supporting frame for the membranous wings. The hindlimb skeleton is also extensively modified: The fibula is reduced or absent, the femur and tibia are long and slim

relative to those of similarly sized terrestrial mammals, and these bones are rotated 90–180° from the typical mammalian pattern. As a result, the femora extend laterally or caudally, and the flexor surfaces of the knees face ventrally. This combination of specializations is presumed to adapt bats to flight (Simmons and Geisler, 1998; Strickler, 1978; Swartz et al., 1992; Vaughan, 1959). They are not seen together in any of the terrestrial mammals, and most likely underlie the general trend of poor walking ability seen in bats.

While the vast majority of the >1,100 species of bats crawl poorly, coordinated terrestrial locomotion does occur in a few phylogenetically disparate bat species (Teeling et al., 2002, 2003). Several molossid bats walk well (Dietz, 1973; Strickler 1978), most notably *Cheiromeles* spp. These animals possess distinctive subaxillary pouches where the tips of the folded

wings are held during walking (Schutt and Simmons, 2001). In addition, the short-tailed bats (Mystacinidae: *Mystacina tuberculata*) forage terrestrially and even burrow (Daniel, 1979), having invaded a terrestrial niche in New Zealand that is more typically occupied by insectivoran mammals elsewhere. The most studied of the walking bats are the vampires (Phyllostomidae: *Desmodus rotundus*, *Diaemus youngi*, *Diphylla ecaudata*). These bats constitute a monophyletic group of obligate blood-feeders (Baker et al., 1989). All three species are known to approach their prey by walking over a substrate, either over ground or along the surface of a branch (Greenhall and Schmidt, 1988).

It is not clear whether the walking ability of different bat species can be predicted by any morphological differences among them. Strickler (1978) observed that in bats that walk well, several muscles of the shoulder (m. pectoralis abdominis, m. subscapularis, m. supraspinatus, m. triceps brachii and m. rhomboideus) are enlarged, and suggested distinct roles for those muscles during crawling. However, he did not provide a predictive model of crawling ability based on muscle dimensions. A more numerical approach was taken by Howell and Pylka (1977), who observed the ratio of femur length to diameter in bats and found that the allometry of this ratio differs from the typical mammalian pattern; the femora of bats are longer and more gracile than those of terrestrial mammals. They hypothesized that this morphological difference meant that the legs of bats could not support the body's weight during crawling. Howell and Pylka noted that the femora of vampire bats were more robust than those of other bats, and suggested that the improved walking ability of vampires was due to their improved ability to support weight with the legs.

The Howell and Pylka study has been cited widely in the popular (Why bats hang upside down: *Omni*, vol. 1(2), p. 38, 1978) and scientific literatures (Jungers, 1979, 1984; Norberg, 1981; Schutt, 1993; Simmons and Geisler, 1998; Smith et al., 1995; Swartz, 1997; Swartz et al., 2003), but the hindlimb-strength hypothesis has not yet been experimentally tested. We do this by directly measuring the forces produced by the hindlimbs of walking vampire and non-vampire bats.

The hindlimb-strength hypothesis has two components: that the skeletons of most bats are too weak to withstand the ground reaction forces associated with terrestrial locomotion, and that the vampire bats walk well because their hindlimbs are stronger than those of other bats. If these components of the hypothesis are both correct, the legs of vampires are predicted to withstand forces during walking that the legs of other bats cannot. Therefore the hindlimb ground reaction forces produced during terrestrial locomotion by vampire bats will be larger in magnitude than those of poorly crawling species. If the forces transmitted by the hindlimbs of poorly crawling bats are as large as those of vampires, the hindlimb-strength hypothesis would be rejected. Even then, however, robustness could reflect some other capacity, such as manoeuverability or speed, which lends vampires their improved terrestrial ability over other bats. We examine the dimensions of femora and tibiae in a broad range of bat species, to verify that the limbs

of vampires are more robust than those of other bats, and comment on how the allometric relationships among external limb dimensions might relate to function in the bats.

Materials and methods
Force platform and video analysis
Study animals

To represent bats with the ability to walk terrestrially we chose two species of vampire bats, *Desmodus rotundus* Wied 1826 (*N*=8) and *Diaemus youngi* (Jentink 1893; *N*=2). These were compared to a poorly crawling insectivorous bat of similar size, *Pteronotus parnellii* (Gray 1843; Mormoopidae; *N*=6). We also made behavioural observations of *Natalus tumidirostris* Miller 1900 (Natalidae; *N*=5), which are not known to crawl. The subject animals were caught using mist nets at various locations in Trinidad, West Indies, during August 2003 and July 2004. Some animals were also collected directly from their roosts with hand nets. In all cases, locomotion studies were conducted within 24 h of capture. All animals were handled in accordance with permits issued by the Ministry of Agriculture (Forestry Division) of Trinidad and Tobago, and protocols were approved by the Institutional Animal Care and Use Committee at Cornell University.

Platform construction

Following improvements on Heglund's original design (Heglund, 1981) by Biewener and Full (1992), we constructed two force-sensitive platforms, serially set in a runway, to measure the ground reaction forces of the hindlimbs as animals walked or crawled sequentially across their surfaces. We designed and built the platforms to be highly sensitive, but also so that they could be easily transported to field locations. In further reference to these measurements, the axis parallel to the direction of travel is denoted as *x*, the orthogonal horizontal axis as *y*, and the vertical axis as *z*.

Each of our platforms consisted of a 74.6 mm (*x*) by 155.0 mm (*y*) honeycomb fiberfoam plate, supported at either end by two hollow aluminum box beams oriented parallel to the *y* axis. These beams rested at their ends on short box beams glued to a heavy aluminum base plate. We used Trubond Clear 2-ton Epoxy (Devcon, Danvers MD, USA) to attach the fiberfoam plate to the beams, and specialized epoxy (J-B Weld, Sulphur Springs TX, USA) for all aluminium–aluminum joints. At certain sites the aluminum box beams were milled to form a series of double cantilevers (Biewener and Full, 1992), each oriented so that they were perpendicular to one of the three orthogonal axes. A force applied to the surface of a plate caused bending in the cantilevers, which was measured *via* strain gauges bonded to them (Micromeasurements Corp., Raleigh, NC, USA).

The strain gauges were wired into four 3.3 V Wheatstone bridge circuits. Each bridge input and output was connected to one channel of a multi-channel strain-conditioning isolation amplifier (National Instruments, Austin, TX, USA; SCXI 1000 chassis containing two SCXI 1121 modules with SCXI 1327

terminal blocks). The analog data were digitized (National Instruments DAQCard-1200) and saved to a laptop computer (Apple Macintosh PowerBook) running a custom-made acquisition program (LabVIEW 6.1). Forces in the *z*-direction were measured separately at the front and rear supporting beams of each plate so that the position of the centre of pressure along the *x*-axis could be determined from the relative output of the two channels (Heglund, 1981). Horizontal channels were monitored with one output each because horizontal forces can only be applied at the surface of the plate.

Platform performance verification and calibration

The functional capabilities of the platforms were evaluated on the basis of resonant frequency response and repeatability of load response (calibration). The former determines the minimum reliable response time of the plate and indicates the loading-rate limit at which useful data can be observed using the instrument.

We measured the resonant frequency of each axis by applying a sharp blow to the plate surface with the tip of a pen, and measuring the rate of oscillation after contact (Biewener and Full, 1992). One platform had a resonant frequency at 457 Hz (*x*), 128 Hz (*y*), 458 Hz (*z*), and the other at 480 Hz (*x*), 156 Hz (*y*), 480 Hz (*z*). Using the lowest of these values, the platforms allowed reliable event records on the order of 7.8 ms.

Both platforms were calibrated on each day that measurements were taken, using the methodology described by Biewener and Full (1992). Briefly, horizontal location of force along the *x*-axis was determined by placing a 100 g mass at a series of different locations on a force plate. From the relative difference in output between the front and rear vertical circuits, the voltage output could be related to the known positions of force application. Force magnitude–voltage relationships of each channel were determined using a series of known loads calibrated against the voltage output in each direction. For this calibration the front and rear *z*-oriented channels were summed to represent total vertical load. Regressions of force to voltage were linear on all channels, with $r^2>0.999$. Electronic drift in the baseline output was determined separately for each individual trial by sampling the signals from each channel of an unloaded plate (zero force) within 10 s of data collection.

Because our platforms were designed to measure relatively small forces, they were also susceptible to noise generated by small vibrations in the environment and stray electrical interference. These artifacts were removed through digital filters; a Butterworth band-stop of 58–62 Hz eliminated AC-generated noise, and a 100 Hz Butterworth low-pass filter eliminated all higher-frequency noise.

Force records were successfully collected from all three force plate axes in the 2004 field season. Calibration problems for the horizontal axes made these records unreliable in 2003, so only vertical forces from that field season were included in our analyses.

Video recordings and synchronisation with force measurements

A Plexiglas cage, 0.48 (*x*) by 0.15 (*y*) by 0.11 (*z*) m, was used to contain the animals while we observed their locomotion. The force plates comprised the centre of the cage floor. We placed a MotionMeter 250 digital high-speed camera (Redlake Systems, San Diego CA, USA) ca. 2 m from the cage, level with the surface of the plate. A mirror above the cage that was tilted 45° from horizontal permitted simultaneous views of the plates from the side (*y*) and above (*z*).

A square-wave signal from the master/slave port of the video camera was sent to both an LED next to the plate in the camera view, and to the laptop (*via* the SCXI strain gauge amplifier). In each trial the signal was interrupted briefly by means of a hand-held switch. This event was clearly visible on the computer files as a change in the shape of the square wave, and on the video recordings as the interruption of the LED emission. These signals were used to synchronize the video sequences with force-plate output, to a resolution of 4 ms.

Trials and analyses

To record the forces produced by the hindlimbs during locomotion, an individual bat was placed at one end of the Plexiglas enclosure. We encouraged it to walk across the force plates by blowing on it through a straw. As the animal crossed the force plates, video (250 Hz) and force plate data (1000 Hz) were recorded simultaneously.

From each trial where a bat moved at a relatively steady speed across the force plate, we isolated the span of time where only the hindlimbs were in contact with a plate. The first and last 10 ms of the selected interval were eliminated to account for the time resolution of our force plate outputs. From each trial we recorded the magnitude and direction of the peak ground-reaction force, calculated as the vector sum of forces in the *x*, *y*, and *z* directions. Jumps and stationary standing were omitted from analyses.

We measured the total force experienced by the hindlimb skeleton in every trial, regardless of how many feet were in contact with the ground. In all three species tested, several of the peak hindlimb forces occurred when only one of the hindlimbs was in contact with the force plate, while others occurred while both feet were in contact. Our methods did not permit us to determine the relative contributions of two feet in simultaneous contact with a single force plate.

In order to understand how the limb bones of the poorly crawling bat, *P. parnellii*, were loaded during locomotion, we recorded the angle θ between the net ground reaction force vector and the long axis of the tibia. Since the force contributions of each leg could not be isolated in most trials, this analysis was restricted to those trials in which peak force occurred as a single limb contacted the plate. We were unable to perform similar measurements for the femur, as there were too few trials in which its orientation could be clearly discerned.

Museum specimens

Hindlimb measurements

We measured the greatest lengths and least diameters (to 0.1 mm) of right femora and tibiae of 113 museum specimens

spanning 50 species in 12 of the 17 currently recognized chiropteran families (Teeling et al., 2002). We examined specimens from as many families as possible from the museums we visited and did not choose our specimens with regard to any criteria other than availability. We obtained body-mass estimates for each species from the literature. Where only a body-mass range was available, we took the midpoint of the range as our estimate. Our sample ranged in body mass across three orders of magnitude, and approximates an unbiased sample of chiropteran hindlimb diversity.

Both internal and external dimensions will influence the stress developed within a long bone due to an applied bending load. When evaluating the structural capacity of long bones based primarily on external dimensions, it is important to verify the underlying assumption that relative cortical thicknesses remain consistent between groups compared. We were unable to make direct measurements of cortical thickness for all species included in the dimensional analysis. In order to evaluate the potential for differences between cortical dimensions of terrestrially active and non-ambulatory species we compared the cortical thickness of femora and tibiae of *D. rotundus* and a non-vampire bat species, *Myotis lucifugus* (Vespertilionidae). Measurements were taken from radiographs of five right hindlimb skeletons of each species in mediolateral and dorsoventral views. The percentage of a bone's diameter that was occupied by cortex in each of the two views was averaged, and these measurements were compared between species.

Comparison of vampire bats with non-vampire bats

We applied the external femur and tibia dimensions of bats to two models. First, we repeated the procedures of Howell and Pylka (1977), using least-squares regressions of log–log plots to compare the allometric relationship of length to diameter found in the femora and tibiae of vampire and non-vampire bats. Since ordinary least-squares regression is no longer generally considered an appropriate tool for studies of allometry (LaBarbera, 1989), we also applied reduced major axis regressions (RMA) to the same data. Second, we applied the same limb dimensions to an engineering-based bending model of bone stress. If the bones of vampire bats really are built to withstand the forces of walking better than those of other bats, they should be subject to smaller stresses during walking than those of other bats.

For simplicity, we modeled each bone as a cylinder of uniform diameter δ and length λ. When a force F is applied at some angle to the end of a cylinder, it can be separated into components parallel and perpendicular to the cylinder's long axis. The relative magnitude of each depends on the angle θ between the force vector and the long axis of the cylinder. The total stress (σ) can be calculated as follows (Gere, 2001):

$$\sigma_{estimated} = \frac{4F}{\pi\delta^2} \cdot \left(\cos\theta + \frac{8\sin\theta\lambda}{\delta} \right). \qquad (1)$$

Because stress is unevenly distributed across the diameter of a cylinder when it is loaded in bending, stresses imposed by bending will greatly exceed those from compression. This is especially true for long, thin cylinders. Therefore, the greatest stresses for the femora and tibiae of bats are generated when a force acts perpendicular to the long axis of the bone ($\theta=90°$). In this case, the equation simplifies to a single term:

$$\sigma_{estimated} = \frac{32F\lambda}{\pi\delta^3} . \qquad (2)$$

If we assume that the forces applied to the hindlimbs scale with body mass (M_b) across species, we can obtain a relative estimate of bone stress as follows:

$$\sigma_{relative} \propto \frac{M_b\lambda}{\delta^3} . \qquad (3)$$

Relative stress does not provide an absolute estimate of the stresses endured by bat bones, but provides a means by which the strengths of bat limbs can be compared among species. Because the numerical values of relative stress are arbitrary, we assigned a value of 1.0 to the $\sigma_{relative}$ of the tibia in the more thin-legged of the two vampires in this study, *D. youngi*. If, as the hindlimb-strength hypothesis predicts, the legs of vampires are more robustly built than those of other mammals, it follows that $\sigma_{relative}$ values of all non-vampire bats should be significantly greater than 1.0.

Our model assumes that the forces exerted by a bat during terrestrial locomotion are proportional to its body mass, and that the stresses vary among species as a result of bone dimensions. Alternatively, it is possible that the stresses experienced by the hindlimbs of all bats are similar during terrestrial locomotion, and that the magnitudes of the forces vary according to bone dimensions. However this distinction is unimportant, as the two models have numerically equivalent predictions and conclusions.
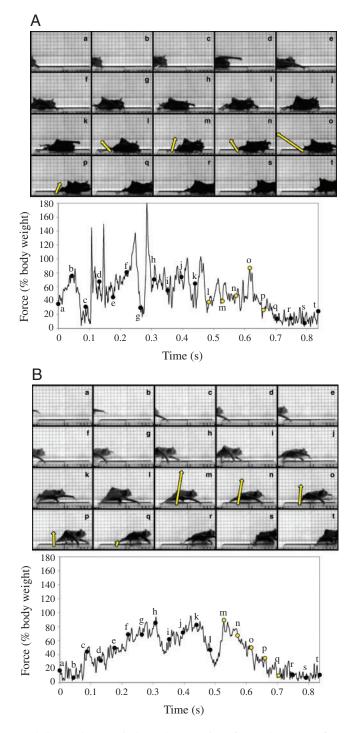
Results
Force platform and video analysis
Kinematics of non-aerial locomotion

Pteronotus parnellii exhibited no consistent gait across trials (Fig. 1A). During crawling, limb movement patterns were highly variable, with kinematics similar to those described for several vespertilionid and phyllostomid bats (Dietz, 1973; Lawrence, 1969). Typically, the body rested in contact with the substrate, with the limbs in a sprawling position. To initiate forward motion the body was lifted by adduction of the forelimbs. The head and torso moved anteriorly 0.25–0.5 body lengths as the forearms rotated dorsoventrally and the legs shuffled forward. The bat then lifted its wings dorsally and the thoracic region collapsed to the ground. The forearms generally moved together, but their motions were not symmetrical, and animals frequently tilted or fell to one side during crawling.

During forward crawling, the femora were directed dorsolaterally and held roughly horizontal. The tibiae pointed

A

B

C

Fig. 1. Typical locomotory sequences for (A) *P. parnellii*, (B) *D. rotundus* and (C) *D. youngi*. Images are at 44 ms intervals. In those images for which only the hindlimbs are in contact with the left plate, the normal force for that plate is shown as a yellow arrow. The graph below each image shows the magnitude of the force on the left plate over the course of the image sequence. Open yellow circles indicate the timing of images with force vectors. Solid circles give the times of all other frames. Note that the magnitude of the force vector for both vampire species decreases gradually as the animal shifts its weight forward, but that the forces are highly variable for the poorly crawling bat, *P. parnellii*.

caudally and occupied angles ranging from 5 to 40° from horizontal. We did not observe contact between the floor and any part of the hindlimbs other than the pelvic girdle and the plantar surfaces of the feet. Peak hindlimb forces typically occurred while the torso was not in contact with the ground, suggesting that the hindlimbs played a role in supporting body weight.

We do not describe the gaits of *D. rotundus* and *D. youngi* in detail here because they did not differ from detailed descriptions available in the literature (Altenbach, 1979; Schutt et al., 1999). Both species used a latera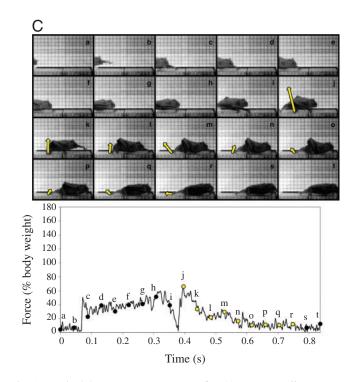l-sequence symmetrical walking gait (Hildebrand, 1985), in which only the plantar surfaces of the feet and the carpi and pollices of the forelimbs made contact with the substrate (Fig. 1B,C). Animals held their abdomens above the ground at all times. The ventral surface of the abdomens of *D. youngi* were ca. 1 cm from the floor and those of *D. rotundus* were ca. 2.5 cm. Peak hindlimb forces typically occurred just after a forearm was lifted from the plate. Ground reaction forces at the hindlimbs decreased as the bat placed its forelimb on the ground and shifted the centre of mass anteriorly. Forces declined to zero as the bat lifted its feet to take the next step.

We also introduced bats of a fourth species, *Natalus tumidirostris,* to the enclosure, but none conducted crawling locomotion. Instead, individuals initiated flight by leaping vertically from the plate by means of strong downward thrusts of the wings, and flew to the end of the enclosure. We did not use the trials from this species in any of our analyses, but present them here as an example of a species that does not crawl.

Hindlimb forces

The body masses of bats in this study were similar, though *D. youngi* were slightly larger (27.0 g and 36.0 g; *N*=2) than

D. rotundus (23.1±2.4 g; *N*=8) or *P. parnellii* (19.1±1.2 g, *N*=6). To account for differences in body size among individuals, we report all forces as a percentage of body weight.

Contrary to the predictions of the hindlimb-strength hypothesis, we found that at the time of peak hindlimb force production the legs of the poorly crawling insectivore, *P. parnellii*, were loaded with significantly larger forces (93.5±36.6% of body weight; mean ± S.D.) than those of *D. rotundus* (69.3±8.1%) or *D. youngi* (75.0±6.2%; ANOVA with Tukey–Kramer; *N*=65; *P*<0.05). The magnitudes of maximum forces were also most variable in *P. parnellii* (Levene test; *N*=65; *P*<0.0001), reflecting the highly variable movements performed by that species (Fig. 2A).

The directions of peak hindlimb ground reaction forces were nearly vertical in *D. rotundus* (73.6±10.8°) and *D. youngi* (75.5±6.7°), while forces produced by *P. parnellii* (61.7±16.7°) were less vertically directed (Kruskal–Wallis; *N*=65; *P*<0.01). The vertical component of peak hindlimb force did not differ significantly among the three taxa studied (ANOVA; *N*=84; *P*>0.6), even though the maximum force applied by the hindlimbs was greater in *P. parnellii* (Fig. 2B). This occurred due to the larger horizontal force component of *P. parnellii*. The similar vertical force contribution likely indicates that the hindlimbs of all three species contributed equally to support of body weight against gravity.

In those *P. parnellii* trials in which a single hindlimb contacted the ground at peak force, we were able to measure the angle θ between the force vector and the long axis of the tibia. The sine of this angle, which is proportional to the bending stress of the tibia (Equation 1), was highly variable (0.68±0.26; *N*=10). No correlation existed between the magnitude of the force and sine θ (*F*-test, *N*=10; *P*>0.9; Fig. 3).

Museum specimens

Allometry of limb bones

Across species, femur length scaled to $M_b^{0.30}$ (r^2=0.78; *N*=50) (RMA: $M_b^{0.38}$), while tibia length scaled to $M_b^{0.32}$

(r^2=0.73; *N*=49) (RMA: $M_b^{0.43}$). The exponents of these least-squares regressions are comparable to values reported for femora (0.18–0.36) by Howell and Pylka (1977) and for tibiae (0.27–0.42) by Norberg (1981), suggesting that our sample of museum specimens was representative of the group and not biased by the availability of specimens for this study.

Our least-squares regressions of length to diameter in the long bones of bat limbs also closely match those of Howell and Pylka (1977). Excluding vampire bats from the analyses, femur lengths of bats scaled to diameter$^{0.78}$ (r^2=0.81; *N*=48) (RMA: $M_b^{0.97}$), while tibia lengths scaled to diameter$^{0.63}$ (r^2=0.44; *N*=45) (RMA: $M_b^{1.43}$).

The lengths of vampire bat femora in our study were proportional to diameter$^{0.18}$ and the lengths of tibiae were proportional to diameter$^{0.21}$. These results are similar to those of Howell and Pylka (1977). The r^2 values of our least-squares regressions were 1.0, since they each consisted of only two species. We recognize that two data are clearly not sufficient for an allometric study (which is why we do not report the RMA regression values), but the Howell and Pylka (1977) study included only three data in the vampire bat regression, and our purpose was to compare their results to our own.

Despite these differences of allometric function exponent between vampire and non-vampire bats, the hindlimb bones of vampire bats did not fall outside the least-squares 95% confidence interval of the length-diameter ratio prescribed by the other bats in this study (Fig. 4). In other words, the length to diameter ratio of vampire bats does not fall outside the range of variation that exists among non-vampire bats.

We found that cortical thickness was greater in *M. lucifugus* (*N*=5) than in *D. rotundus* (*N*=5), for both femora (*t*-test, *P*<0.001, *N*=10) and tibiae (*t*-test, *P*<0.001, *N*=10). Although the cortex was not uniform along the length of any bone, we found that in mid-point femoral cross-sections, cortex occupied 66.7±3.3% of radius in *M. lucifu*gus and 41.3±1.8% in *D.*
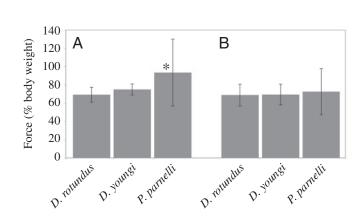
Fig. 2. Magnitudes of hindlimb force in *D. rotundus*, *D. youngi*, and *P. parnellii*: (A) total force, calculated as the vector sum of forces in the *x*, *y* and *z* directions; (B) vertical component of peak force. Asterisk denotes significance at *P*<0.05.
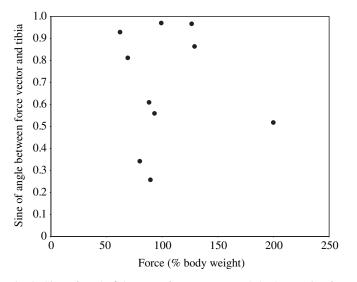
Fig. 3. Sine of angle θ between force vectors and the long axis of a tibia *vs* magnitude of peak force in *P. parnellii* trials, where peak force occurred as a single leg was in contact with the plate.
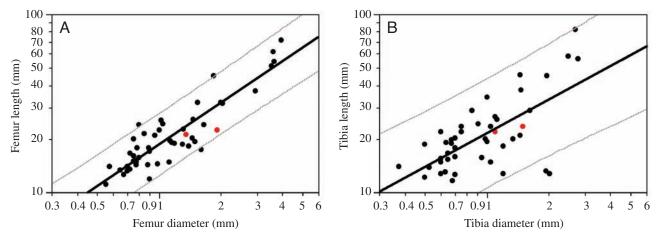
Fig. 4. Log–log plots of length to diameter for bat (A) femora (B) and tibiae. Red circles denote vampire bats. Other bat species are black. Bold line represents best fit and grey lines indicate 95% confidence interval from least squares regression of non-vampire bat data only.

rotundus. For tibiae, cortical thickness was 71.0±10.1% in *M. lucifugus* and 35.3±6.0% in *D. rotundus*.

Estimation of relative bone stresses

There was a slight trend for $\sigma_{relative}$ to increase with $\log M_b$ for femora (r^2=0.25) and tibiae (r^2=0.36). Vampire bats did not possess more structurally stable hindlimbs than those of all other bats in our study (Fig. 5). The values of $\sigma_{relative}$ for *D. rotundus* and *D. youngi* femora were first and sixteenth lowest respectively among all species (*N*=50), while relative tibia stresses were fourth and eighteenth lowest respectively (*N*=47). The lowest $\sigma_{relative}$ we calculated among tibiae was that of *Molossus molossus* (Molossidae). The highest predicted bone stresses in our study were those of the tibiae of *Hipposideros commersoni*, a large-bodied (0.13 kg) predatory species, and the frugivore *Pteropus vampyrus*, the largest bat (1.08 kg) in our sample.

Discussion

Inference of hindlimb strength from external bone dimensions
The hindlimb-strength hypothesis rejected

The legs of *P. parnellii* were loaded with larger forces than those of vampires, but did not break. It is therefore clear that the bones of *P. parnellii* would be able to withstand the forces associated with coordinated non-aerial locomotion. However, *P. parnellii* are poor walkers relative to *D. rotundus* and *D. youngi*. This is reflected by their inability to hold the abdomen above the floor during crawling, and by the higher variation in magnitudes and directions of force vectors applied by the hindlimbs. These results demonstrate that some mechanism other than frailty of the hindlimb skeleton prevents *P. parnellii* from walking smoothly.

The hindlimb-strength hypothesis inferred differences in hindlimb strength from the allometric relationship between length and diameter in the femora of bats. This approach was flawed in two ways. First, although the exponents of the allometric relationships of vampire and non-vampire bats

differ, the vampire bat data points fall within the non-vampire regression. The argument that vampire bats are built differently than other bats would only have structural consequences beyond the body sizes of the vampire bats. Second, the ratio of length to diameter in a bone does not necessarily determine strength. A simple model of bone strength suggests that the leg bones of vampires are not significantly stronger than those of non-terrestrial bats.

Comments on our model of bone stress

Our treatment of bones as fixed cantilever beams oversimplifies the complexity of *in vivo* quadruped bone stresses (Blob and Biewener, 2001), but is useful for contrasts of bending stress among species. These comparisons are appropriate if the magnitude of hindlimb force is a constant proportion of body weight across species, as has been shown for terrestrial mammals (Biewener, 1991), and if forces are exerted at a consistent angle (θ) to the long axis of the bone across species. The latter assumption can only be tested through measurements from a broad range of species. Our measurements of θ in the poorly crawling *P. parnellii* indicate that this species does not employ the advantage that could be gained by aligning large forces with the long axis of the tibia. Bats would be able to drastically reduce the stresses on their hindlimb bones by adjusting the positions of their limbs during locomotion. As a result, differences in kinematic strategies among species could influence the relative magnitudes of hindlimb stresses.

The difference in cortical thickness between the hindlimb bones of *D. rotundus* and *M. lucifugus* demonstrates that internal structure varies among bat species, and may therefore be an important component of hindlimb strength. Because we do not have data on more species, we do not know whether cortical thickness differs in vampire bats compared with all other species, or whether the cortical thickness of vampire leg bones is within the range of values demonstrated by other bats. However, since we assumed that relative cortical thickness is constant when it appears to be less in *D. rotundus*, our model
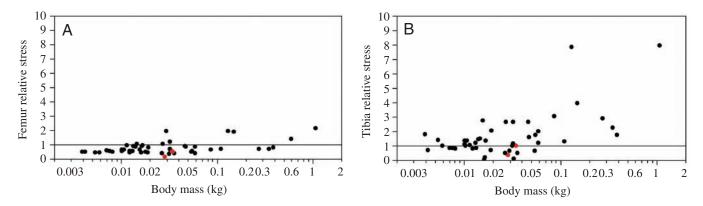
Fig. 5. Relative hindlimb bone stresses for femora (A) and tibiae (B) across the range of body masses in this study. Red circles represent vampire bats (*D. rotundus*, *D. youngi*), black circles represent other species. According to the hindlimb-strength hypothesis, the non-vampires should have relative bone stress values greater than that of *D. youngi* tibiae (1.0).

Table 1. *Mean hindlimb bone dimensions and predicted stresses of museum specimens in 50 species*

	N	M_b (kg)	λ_f (mm)	δ_f (mm)	σ_f	λ_t (mm)	δ_t (mm)	σ_t
Emballonuridae								
Rhynchonycteris naso	2	0.0039[a]	14.0	0.6	0.50	13.9	0.4	1.81
Saccopteryx bilineata	2	0.0075[a]	16.5	0.7	0.57	19.6	0.7	0.84
Megadermatidae								
Lavia frons	1	0.0320[a]	24.2	1.1	1.18	29.0	0.9	2.65
Macroderma gigas	1	0.1500[b]	45.3	1.9	1.89	45.6	1.5	3.94
Molossidae								
Eumops perotis	2	0.0590[c]	25.8	1.5	0.83	19.3	1.0	2.00
E. underwoodi	1	0.0540[d]	24.1	1.7	0.51	20.9	1.5	0.65
Molossus ater	1	0.0317[e]	18.1	1.4	0.37	15.6	1.0	1.01
M. bondae	2	0.0179[f]	11.9	0.9	0.51	10.6	*	*
M. molossus	4	0.0161[a]	14.5	1.0	0.43	12.8	2.0	0.04
Mops condylurus	2	0.0330[g]	14.8	1.1	0.60	13.1	2.0	0.10
Tadarida brasiliensis	3	0.0122[a]	14.3	0.9	0.44	11.6	0.7	0.78
Mormoopidae								
Mormoops megalophylla	2	0.0155[e]	25.5	1.0	0.64	21.8	0.6	2.75
Pteronotus parnellii	5	0.0191[e]	20.9	1.0	0.79	18.9	0.7	2.06
Natalidae								
Natalus stramineus	1	0.0054[g]	20.0	0.8	0.45	18.6	0.5	1.40
Noctilionidae								
Noctilio albiventris	11	0.0356[e]	20.2	1.5	0.41	19.9	1.3	0.52
N. leporinus	2	0.0590[a]	32.1	2.0	0.42	37.7	1.5	1.22
Nycteridae								
Nycteris macrotis	1	0.0115[a]	24.1	0.8	0.95	21.8	0.8	1.04
Phyllostomidae								
Artibeus jamaicensis	5	0.0470[a]	22.6	1.3	0.83	19.3	1.0	1.59
A. phaeotis	2	0.0104[a]	14.9	0.8	0.58	13.1	0.6	0.98
A. toltecus	1	0.0165[e]	15.6	0.8	0.88	12.7	1.2	0.21
Desmodus rotundus	7	0.0285[a]	22.5	1.9	0.16	23.4	1.5	0.35
Diaemus youngi	1	0.0347[e]	21.1	1.4	0.52	21.9	1.1	1.00
Glossophaga soricina	1	0.0146[a]	13.9	0.7	1.04	12.8	0.6	1.51
Macrotus californicus	1	0.0141[a]	21.4	0.9	0.86	20.2	0.7	1.46
Phyllostomus hastatus	6	0.1100[a]	31.8	2.1	0.71	28.7	1.6	1.31
Uroderma magnirostrum	1	0.0294[e]	16.0	0.8	1.95	14.8	1.1	0.66
Vampyrops helleri	1	0.0133[a]	13.2	0.7	0.90	12.6	0.7	0.86

likely overestimates the strength of vampire bat limb bones. A more thorough survey of cortical thickness among bats would permit an improved model, where leg bones could be modeled as hollow beams of known thickness. *In vivo* stresses on the bones of bats are complex during flight (Swartz et al., 1992), and are likely also complex when bats crawl. To understand how stresses in bones compare among species, a detailed analysis should be made of bone structure from micro CT-scans, and then combined with kinematic and muscle activation data from each species. This would permit analyses to include stresses that result from internally produced forces, which are not considered in this study.

Form and function in the non-aerial locomotion of bats
Why are some bats better at walking than others?

As suggested by Strickler (1978), the proportions of the shoulder muscles may be important determinants of walking ability. Also, the fine motor control associated with the slow movements of walking may require specific muscle fibre types that are absent from most bats. The pectoralis muscles of *D. rotundus* and *D. youngi* contain four fibre types, including three fast-twitch types (IIa, IIb, IIe) and one slow-twitch type (I; Hermanson et al., 1993, 1998). The pectorialis of all other bats studied to date possess between one and three fibre types, and none possess type I fibres (Hermanson et al., 1993; Brigham et al., 1990). Such an array of fibre types in terrestrially adept species may provide the functional capacity to coordinate support and movement while meeting the power requirements of flight (Hermanson et al., 1993). Although the pectoralis muscles of bats like *P. parnellii* can supply the power necessary for flight, they might be incapable of the slow, coordinated contractions necessary to hold the body steady above the ground.

The hypothesis that type I fibres facilitate non-aerial locomotion by bats is supported by the fact that the type I fibres of *D. rotundus* are present in the m. pectoralis abdominis

Table 1. *Continued*

	N	M_b (kg)	λ_f (mm)	δ_f (mm)	σ_f	λ_t (mm)	δ_t (mm)	σ_t
Pteropodidae								
Cynopterus brachyotis	1	0.0321[e]	19.0	1.2	0.70	23.4	1.1	1.14
C. sphinx	1	0.0465[h]	18.8	1.2	0.91	24.3	0.9	2.64
Eidolon helvum	2	0.2740[a]	37.2	3.0	0.69	44.9	2.0	2.90
Eonycteris spelaea	3	0.0549[e]	19.4	1.5	0.56	25.6	1.1	1.77
Epomorphorus wahlbergi	1	0.0870[a]	17.4	1.6	0.65	26.6	1.1	3.05
Pteropus alecto	1	0.5950[e]	61.5	3.6	1.38	*	*	*
P. giganteus	1	0.3470[a]	54.2	3.7	0.68	57.9	2.5	2.26
P. hypomelanus	2	0.3900[e]	51.4	3.5	0.80	55.9	2.8	1.76
P. vampyrus	1	1.0781[e]	71.2	4.0	2.17	82.4	2.7	7.93
Rhinolophidae								
Hipposideros commersoni	1	0.1300[a]	32.1	1.6	1.97	34.3	1.0	7.83
Rhinopomatidae								
Rhinopoma microphyllum	1	0.0271[e]	22.3	1.0	1.06	23.4	0.8	2.64
Vespertilionidae								
Antrozous pallidus	11	0.0189[i]	19.6	1.1	0.45	19.9	1.0	0.69
Corynorhinus rafinesquii	3	0.0101[j]	17.9	0.8	0.66	19.1	0.6	1.33
Eptesicus fuscus	2	0.0166[a]	15.2	0.8	0.95	15.9	0.7	1.35
Lasionycteris noctivagans	1	0.0106[a]	14.9	0.8	0.66	15.4	0.6	1.33
Lasiurus borealis	1	0.0131[a]	17.1	0.9	0.54	17.7	0.7	1.19
L. seminolus	2	0.0122[k]	17.8	0.9	0.55	17.6	*	*
Myotis griescens	2	0.0102[a]	14.3	0.8	0.55	16.7	0.7	1.09
M. keeni	1	0.0070[a]	13.4	0.7	0.60	14.8	0.6	0.84
M. lucifugus	2	0.0081[a]	13.6	0.7	0.51	15.3	0.7	0.79
M. nigricans	1	0.0042[a]	11.2	0.6	0.49	12.1	0.5	0.71
Nyctalus noctula	1	0.0265[a]	18.6	1.3	0.39	18.2	1.2	0.49
Pipistrellus subflavus	2	0.0059[a]	12.7	0.7	0.43	13.8	0.5	0.99

Stress estimates are calculated using Equation 3, as explained in the text. Symbols used are as follows: M_b=body mass, λ_f=femur length, δ_f=femur diameter, σ_f= relative femur stress, λ_t=tibia length, δ_t=tibia diameter, σ_t=relative tibia stress. Relative stresses are dimensionless values based on the estimated stress of *D. youngi* tibiae, which we arbitrarily assigned a value of 1.0. Those specimens with broken or missing tibiae are denoted by an asterisk.

Sources used for body-mass estimates are denoted by superscripts ([a]Norberg, 1981; [b]Hudson and Wilson, 1986; [c]Best et al., 1996; [d]Kiser, 1995; [e]Jones and MacLarnon, 2004; [f]Burnett et al., 2001; [g]Hosken et al., 2001; [h]Storz and Kunz, 1999; [i]Hermanson and O'Shea, 1981; [j]Jones, 1977; [k]Wilkins, 1987).

(Hermanson et al., 1993). Strickler (1978) listed this muscle as a major humeral retractor, important to non-aerial locomotion. The presence or absence of type I fibres from bats that crawl well but which are not closely related to the vampire bats will help to resolve the importance of that character to walking. It should be noted that many shrews (Insectivora) walk and run without any type I fibres at all (Hermanson et al., 1996; Suzuki, 1990; Savolainen and Vornanen, 1995), but that the type II fibres of insectivorans may differ in their contractile speed and rate of fatigue from those of bats (Goslow, 1985).

The terrestrial abilities of the vampire bats are impressive. *D. rotundus* are known to walk or hop forward, sideways, backward (Altenbach, 1979), and perform unique flight-initiating jumps during which vertical forces equal to 9.5 times body weight are exerted by the forelimbs in under 30 ms (Schutt et al., 1997). Comparable kinematic observations are lacking for other walking species, including the highly terrestrial New Zealand Short-tailed Bats (*M. tuberculata*), which diverged from *Desmodus* 47 mya, and almost certainly evolved their terrestrial habits independently of the vampires (Teeling et al., 2003). Comparative studies have not been performed to determine whether these convergent taxa perform coordinated locomotion in the same ways. The lack of such data makes it difficult to isolate the mechanisms that enable walking in some bats, or prevent it in others, but our experimental results demonstrate that the apparent strength of the hindlimb bones does not determine walking ability.

Ecological and behavioural correlates of walking ability

Our data (Table 1) reveal that among the bats included in this study the tibiae of *P. vampyrus* and *H. commersoni* are likely to be the most susceptible to breaking from non-aerial locomotion. If either of these species is able to walk, we predict that they do so by carefully restricting the orientation of force applied to the tibia, or by avoiding higher-level load application to the hindlimbs, perhaps by dragging them passively behind. *H. commersoni* roost in caves and trees, and take large flying insects by hawking (Vaughan, 1977), while *P. vampyrus* roost and forage in trees (Goodwin, 1979). *P. vampyrus* have been observed in captivity to crawl quickly to a vertical surface when placed on a concrete floor (M. O'Brien, personal communication), and similar observations have been made of this species in the wild (J. Epstein, personal communication). Since the tibiae of *P. vampyrus* are less robust than all other bones included in this study, and since non-aerial locomotion has been observed in this species, we can be certain that a slender hindlimb skeleton does not, in itself, prevent crawling by bats. Those bats that do not crawl at all must be limited by some other factor.

The inability to crawl occurs in several bat species. For example, it has been reported that adult *Leptonycteris* sp. and *Macrotus* sp. (Phyllostomidae) are incapable of crawling, although juveniles of both species do crawl (Dietz, 1973). The fact that *N. tumidirostris* did not attempt to crawl in our enclosure suggests that adults of this species may also be incapable of terrestrial locomotion. *N. tumidirostris* frequently alighted from the floor of our cage in a single jump, so terrestrial locomotion may not be necessary for this species. Vaughan (1959) made similar observations of *Macrotus californicus*, which would not attempt to crawl, but instead launched into flight directly from the ground. The ability to initiate flight from a horizontal surface is probably a prerequisite for loss of crawling ability, although this ability in itself does not restrict crawling, as is demonstrated by *D. rotundus*.

We did not observe successful flight-initiating jumps by *P. parnellii*. Vaughan (1959) similarly observed that free-tailed bats (Molossidae) could only initiate flight once they had climbed to a suitable height. *P. parnellii* roost in large colonies within caves and mines, where individuals can number in the thousands (Herd, 1983). Each night they fly close to the ground through cluttered environments at speeds averaging 4.9 m s^{-1} to regions where they feed aerially on insects (Bateman and Vaughan, 1974; Kennedy et al., 1977). When bats accidentally strike an obstacle, such as another bat in the cave or a branch in their foraging territory, they are likely to fall to the ground. Since *P. parnellii* do not take flight from the ground, the ability to shuffle, however awkwardly, provides a distinct advantage for bats of this species.

There is a broad diversity in crawling ability represented by Chiroptera. The terrestrial abilities of *P. parnellii* represent a mid-way point between the complete absence of crawling by *N. tumidirostris* and the agility of *D. rotundus and D. youngi*. Whatever the advantages of long, thin legs to bats, it appears from our data that in the majority of species reduction of the hindlimb robustness has not exceeded the mechanical requirements of non-aerial locomotion. Perhaps the requirements of crawling have constrained their reduction in those species that cannot initiate flight from the ground.

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