

Terrestrial locomotion of the New Zealand short-tailed bat *Mystacina tuberculata* and the common vampire bat *Desmodus rotundus*

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Summary

Bats (Chiroptera) are generally awkward crawlers, but the common vampire bat (*Desmodus rotundus*) and the New Zealand short-tailed bat (*Mystacina tuberculata*) have independently evolved the ability to manoeuvre well on the ground. In this study we describe the kinematics of locomotion in both species, and the kinetics of locomotion in *M. tuberculata*. We sought to determine whether these bats move terrestrially the way other quadrupeds do, or whether they possess altogether different patterns of movement on the ground than are observed in quadrupeds that do not fly. Using high-speed video analyses of bats moving on a treadmill, we observed that both species possess symmetrical lateral-sequence gaits similar to the kinematically defined walks of a broad range of tetrapods. At high speeds, *D. rotundus* use an asymmetrical bounding gait that appears to converge on the bounding gaits of small terrestrial mammals, but with the roles of the forelimbs and hindlimbs reversed. This gait was not performed by *M. tuberculata*.

Many animals that possess a single kinematic gait shift

with increasing speed from a kinetic walk (where kinetic and potential energy of the centre of mass oscillate out of phase from each other) to a kinetic run (where they oscillate in phase). To determine whether the single kinematic gait of *M. tuberculata* meets the kinetic definition of a walk, a run, or a gait that functions as a walk at low speed and a run at high speed, we used force plates and high-speed video recordings to characterize the energetics of the centre of mass in that species. Although oscillations in kinetic and potential energy were of similar magnitudes, *M. tuberculata* did not use pendulum-like exchanges of energy between them to the extent that many other quadrupedal animals do, and did not transition from a kinetic walk to kinetic run with increasing speed. The gait of *M. tuberculata* is kinematically a walk, but kinetically run-like at all speeds.

Key words: terrestrial locomotion, independent evolution, biomechanical trade-off, Chiroptera, *Desmodus rotundus*, *Mystacina tuberculata*.

Introduction

Trade-offs in locomotion

In many animals, morphology matches the mechanical requirements of locomotion to produce an effective movement system. For example, whales have body shapes that generally minimize drag in water over a broad range of swimming speeds, and choose fluke beat frequencies that maximize efficiency while swimming (Rohr and Fish, 2004). Similarly, the bodies of dogs are well-suited to long-distance travel over land, and they use walking and running gaits that minimize the metabolic cost of locomotion for their body plans (Goslow et al., 1981). In both of these cases, evolution has resulted in morphology and behaviour that function efficiently in a single mode of locomotion. This is, however, not always the case. For example, consider the sea lion (Carnivora: Otariidae) that

spends much of its time in the water, but must also manoeuvre on land. As the result of having a body well-suited to swimming after elusive prey (Fish et al., 2003), sea lions are less agile on the ground than typical terrestrial mammals, and thus move quite differently from them (Chechina et al., 2004).

In instances where animal morphology simultaneously meets the requirements of more than one form of movement, studies of form and function take on another dimension of complexity. Additionally, the issue of trade-offs and compromise may be enlightening to investigations of morphological adaptation. Organisms that perform more than one type of locomotion offer insight into how animals might transition between modes of transportation over the course of their evolution, like the sarcopterygian fish that gave rise to tetrapods, the theropod dinosaurs that gave rise to flying birds,

and the ungulates that gave rise to whales (Ashley-Ross, 1995; Dial, 2003; Gingerich, 2005).

These issues have been addressed previously in studies of tetrapods that move terrestrially and aquatically (Ashley-Ross and Bechtel, 2004; Biewener and Corning, 2001; Biewener and Gillis, 1999; Fish et al., 2001). In this study, we explore such compromises using bats (Chiroptera) as a model. Unlike walking birds, that use the forelimbs for flight and the hindlimbs for walking, bats use all four limbs for both modes of locomotion. Bats are extremely agile in the air, but compared to other mammals most bats move awkwardly on the ground (Schutt and Simmons, 2006; Vaughan, 1959; Vaughan, 1970), suggesting biomechanical trade-offs between aerial and non-aerial locomotion.

Origins of terrestrial agility in two bat species

There are more than 1100 currently recognized species of bat (Simmons, 2005), and the majority of these spend very little time traveling on the ground. Typically, when a bat accidentally falls to the ground, having struck an obstacle in flight or fallen from an overhanging roost, it either immediately launches itself directly back into flight by pressing its wings on the substrate, or shuffles to a vertical feature of the environment, climbs it, then drops into flight (Vaughan, 1959). Those bat species that forage for terrestrial prey typically do so by landing directly on their prey, rather than by chasing them down on foot (Johnston and Fenton, 2001; Ratcliffe and Dawson, 2003). A few bats move fairly well on the ground, most notably molossids and vespertilionids, but they generally fall short of the rapid bounding and hopping locomotion performed by terrestrial mammals of similar size (Biewener et al., 1981; Biewener and Blickhan, 1988; Hatt, 1932). However, the common vampire bat (Phyllostomidae: *Desmodus rotundus*) and the New Zealand short-tailed bat (Mystacinidae: *Mystacina tuberculata*) are extremely agile crawlers, even though they are also fully capable of flight (Schutt and Simmons, 2006).

Desmodus rotundus are obligate blood-feeders, found in Mexico, Central and South America, and two Caribbean islands, where they primarily parasitize domestic livestock, such as cattle (Turner, 1975). Terrestrial locomotion permits them to approach their hosts stealthily, and to escape if the prey animal or some other danger threatens them while feeding (Altenbach, 1979). *D. rotundus* also initiate flight with rapid and powerful jumps that enable them to attain a vertical velocity of 2.4 m s^{-1} in less than 30 ms (Schutt et al., 1997). This type of rapid escape is necessary in habitats where terrestrial predators of bats are plentiful, and is especially needed by a bat that sometimes feeds with its tongue against the foot of an animal that outweighs it 14 000-fold (Greenhall, 1988).

Mystacina tuberculata are restricted to New Zealand, where they also frequently utilize terrestrial locomotion, but their ecology and behaviour are quite different from those of vampire bats. New Zealand is well known for its flightless birds (most famously kiwis, *Apteryx* spp.) that became highly

terrestrial in the absence of snakes or predatory mammals, prior to the arrival of invasive species with humans. Similarly, *M. tuberculata* expanded their niche from the aerial hawking and/or gleaning that typifies most bats, to include significant terrestrial foraging. *M. tuberculata* spend some 30% of their foraging time crawling, even burrowing, while searching for arthropods, fruit, nectar and pollen (Daniel, 1976; Daniel, 1979).

Common vampire bats are more closely related to poorly crawling bats (e.g. phyllostomids, mormoopids) than they are to New Zealand short-tailed bats (Teeling et al., 2003; Teeling et al., 2005), suggesting that these taxa evolved their terrestrial behaviours independently. Both move quadrupedally, as do the majority of mammals, but the bats do so using limbs that are specialized for aerial locomotion. We were therefore interested to know whether their movement patterns are similar to those of other quadrupeds, or whether they involve altogether different patterns. Because *D. rotundus* and *M. tuberculata* manoeuvre terrestrially so well compared with other bats, their anatomy has been the subject of several investigations (Altenbach, 1979; Dwyer, 1960; Dwyer, 1962; Howell and Pylka, 1977; Riskin et al., 2005; Schutt, 1998; Schutt and Altenbach, 1997; Strickler, 1978). However, while previous studies provided descriptions and photographs of locomotion in *D. rotundus* (Altenbach, 1979; Riskin and Hermanson, 2005), they did not include many of the kinematic parameters useful for comparing their gaits with those of other tetrapods. We report several such parameters here. Also, this is the first study to report the kinematics of locomotion in *M. tuberculata*.

Describing locomotion

There are several different ways to classify gaits so that they can be compared among species, and most of these movement taxonomies include a distinction between walking and running (Ahn et al., 2004; Cavagna et al., 1976; Hildebrand, 1985; Ruina et al., 2005). As a result, there are several criteria by which to distinguish the two. In this study, we make use of kinematic and kinetic distinctions between walks and runs.

Kinematic definitions of gait

To make our observations of both bat species comparable with those of as many organisms as possible, we follow kinematic definitions of gait that have been applied to >150 genera of quadrupeds (e.g. Hildebrand, 1985). By one kinematic definition, a run is characterized by the presence of an aerial phase, where all four limbs are off the ground at some point during the stride cycle, while in a walk at least one limb touches the ground at all times. By another definition, a gait in which a limb spends more than 50% of the stride cycle in contact with the ground (duty factor >0.5) is considered a walk, while one in which the duty factor is less than 0.5 is defined as a run (Ahn et al., 2004; Hildebrand, 1985; Hutchinson et al., 2003; Rubenson et al., 2004).

Since the footfall patterns of quadrupedal animals are largely governed by stability (Alexander, 1977; Cartmill et al., 2002), which is a biomechanical constraint that operates

independently of evolutionary origins, we expected the footfall patterns of bats to fall within the range that has been described for quadrupedal animals that do not fly. Also, if bats walk the way that other tetrapods do, we would expect that bats using a single kinematic gait over increasing speeds will increase their stride frequencies and decrease their duty factors (Ahn et al., 2004; Dutto et al., 2004; Fish et al., 2001; Heglund and Taylor, 1988).

Kinetic definitions of gait

In many recent studies, force plates have been used to apply kinetic (or energetic) distinctions between walking and running to a broad range of animals, including mammals, birds, reptiles, amphibians and arthropods (Ahn et al., 2004; Blickhan and Full, 1987; Cavagna et al., 1976; Farley and Ko, 1997; Goslow et al., 1981; Griffin and Kram, 2000; Minetti et al., 1999). Specifically, a gait where kinetic energy (E_K) and gravitational potential energy (E_P) of the centre of mass (COM) oscillate out of phase is considered a kinetic walk, while one in which E_K and E_P oscillate in phase is considered a kinetic run (Cavagna et al., 1977). These kinetic definitions are motivated by ideas about the mechanisms of energy conservation employed by moving animals. In a gait where E_K and E_P oscillate out of phase, energy can be cycled between them in a pendulum-like manner (Cavagna et al., 1977; Ruina et al., 2005). In a kinetic run, exchanges of energy between E_K and E_P (here defined as gravitational potential energy) are decreased, so more energy must either be supplied by muscles or be stored in spring-like tendons and muscles, making the energetics of running analogous to that of a bouncing ball or pogo-stick (Cavagna et al., 1977).

Confusingly, a gait that meets the criteria of a kinetic walk might be classified as a run by kinetic nomenclature. For example, it has been observed (Gatesy and Biewener, 1991; Rubenson et al., 2004) that the single kinematic gait of a bipedal bird can transition from a kinetic walk at low speeds to a kinetic run at higher speeds. Similar trends have also recently been noted for quadrupedal frogs (Ahn et al., 2004). Because *M. tuberculata* in this study exhibited only one kinematically distinguishable gait (see Results), we sought to determine whether a range of kinetic gaits exists within that single kinematic gait. We expected that *M. tuberculata* would transition from a kinetic walk to a kinetic run with increasing speed.

Materials and methods

Capture and handling of bats

In July 2004, we captured *Desmodus rotundus* Weid 1826 (five males; body mass 23.1 ± 2.0 g, mean \pm s.d.) from ranches in Southwestern Trinidad. In November 2004 we caught *Mystacina tuberculata* Gray 1843 (three males, three females; 13.9 ± 0.9 g) in Fiordland, New Zealand. Each bat was used in only one sequence of force plate trials, and one subsequent sequence of treadmill trials. All experiments were performed within 24 h of capture. Protocols for capture and

experimentation were approved by the Cornell University Institutional Animal Care and Use Committee, the University of Auckland Animal Ethics Committee, the Ministry of Agriculture (Forestry Division) of Trinidad and Tobago, and the Department of Conservation of New Zealand.

Gait kinematics: treadmill trials

Treadmill design

To observe the terrestrial gaits of animals over a broad range of speeds, we placed each bat inside a custom-built PlexiglasTM enclosure 0.48 m long, 0.15 m wide, and 0.11 m high, with a floor consisting of a variable-speed treadmill. In a trial, the treadmill was accelerated smoothly to a constant speed. Once the bat had matched its crawling velocity to that of the treadmill, we recorded images at 250 Hz using a MotionMeter 250 digital high-speed camera (Redlake Systems, San Diego, CA, USA). The camera was positioned ca. 2 m from the enclosure, and a mirror above the cage, angled 45° from horizontal, permitted us to record simultaneous lateral and dorsal views of the bat in each camera frame. Up to 8 s of video were recorded, then the treadmill was stopped and the bat permitted to rest for ca. 60 s before the next trial. We conducted trials over increasing speeds until either the subject appeared fatigued, or we were unable to further increase its speed.

Analyses

To measure speed and stride frequency, we recorded the time taken to complete the largest possible integer number of stride cycles in a trial. Stride frequency was calculated as the number of stride cycles divided by this period. We measured speed by adding the change in position of the bat's nose to the change in position of markers on the treadmill surface, both relative to a stationary object, and dividing their sum by the same period.

To see how gaits changed kinematically with speed, we selected a single stride cycle sequence from each trial, beginning and ending with left hind footfall. From it, we observed the timing of footfall and foot lift events, and recorded whether or not an aerial phase occurred. Duty factors of the two forelimbs were averaged in the cycle, as were those of the hindlimbs. The two kinematic gaits of *D. rotundus* (walking and bounding) were easily distinguished by sight, and analysed separately. *M. tuberculata* used only one kinematically distinguishable gait (walking), so all trials for that species were analysed together.

It is possible that *M. tuberculata* do bound at high speeds, and did not do so in our study because the treadmill moved too slowly. To ensure that we observed locomotion by *M. tuberculata* at sufficiently high velocities, we compared the greatest speeds of *M. tuberculata* on the treadmill to the range of speeds at which *D. rotundus* used the walking and bounding gaits. To correct for the nearly twofold difference in body mass between the two species, we compared them using a dimensionless descriptor of movement called Froude number (Fr). Animals with similar body plans transition between gaits

at equivalent Froude numbers across broadly varying body sizes (Alexander and Jayes, 1983). Therefore if *M. tuberculata* walked at Froude numbers for which *D. rotundus* exclusively bounded then we would infer that the bounding gait is not used by *M. tuberculata* at any speed.

Froude number is defined as $Fr = v^2 g^{-1} l^{-1}$, where v is velocity, g is the gravitational constant ($g = 9.81 \text{ m s}^{-2}$), and l is hip height (Alexander and Jayes, 1983). We use the mean tibia lengths of animals in our study as a proxy for l (26.8 mm in *D. rotundus* and 16.9 mm in *M. tuberculata*), since when walking quadrupedally, bats hold the femora somewhat horizontally and the tibiae roughly vertical (Schutt and Simmons, 2006). In most tetrapods, shoulder height is roughly equivalent to hip height, but in *D. rotundus* and *M. tuberculata* the shoulder joint is much higher than the hip. We therefore only use Froude analysis to compare these bat species to one another, and do not assume dynamic similarity between the gaits of bats and those of other tetrapods.

Gait kinetics of New Zealand short-tailed bats: force plate trials

Force plate design, calibration and use

Recordings of COM energetics in *M. tuberculata* were made in the same Plexiglas™ enclosure as that used for the treadmill trials, but the treadmill was replaced with two serially set force platforms in the centre of the enclosure, flush with Plexiglas™ over the rest of the floor. The Plexiglas™ floor and the honeycombed fiberfoam surfaces of the force plates both appeared to provide sufficient friction for quadrupedal locomotion. We only observed the feet of bats slipping in a few instances where bats jumped, and these events were not included in our analyses.

Each force plate was 74.6 mm long, and spanned the width of the enclosure (155 mm). The plates independently measured the ground reaction forces of crawling bats in three directions, to which we refer throughout this paper as fore–aft (the axis parallel to the long-axis of the cage), mediolateral (the orthogonal horizontal axis) and vertical.

The force plates used in this study were built based on designs by Heglund, and Biewener and Full (Heglund, 1981; Biewener and Full, 1992). A design and construction of our plates have been described in detail previously (Riskin et al., 2005). Each plate had resonant frequencies $\geq 128 \text{ Hz}$ in all three directions, permitting reliable event records on the order of 7.8 ms. On each recording day the force plates were calibrated for load response in each direction, and demonstrated linear correlations of force to output voltage over a range of forces threefold greater than the body weights of our largest animals ($r^2 > 0.999$). Electronic drift in the baseline output of the force plates was corrected in each individual trial by sampling the signal of unloaded plates (zero force) within 10 s of data collection. Crosstalk was $\leq 7\%$ between vertical and horizontal channels, and $\leq 16\%$ between horizontal channels. Force plate recordings were filtered with a 50–54 Hz Butterworth bandstop filter to remove AC noise (ca. 52 Hz in New Zealand), and with a Butterworth lowpass filter of 25 Hz

to improve the signal-to-noise ratio overall. Signals from the two plates were summed for all calculations.

In a trial, we encouraged a bat to cross the force plates by blowing on it through a straw. As the bat crossed the plates, we recorded ground reaction forces at 1000 Hz in each of three directions, and simultaneously recorded video at 250 Hz in lateral and dorsal views. Video and force plate signals were synchronised in the manner used previously (Riskin et al., 2005). The 250 Hz square wave emitted by the master/slave port of the video camera powered an LED visible in the camera frame, and was simultaneously recorded to a computer with the force recordings. The manual interruption of that signal by means of a hand-held switch during each trial permitted us to synchronise video sequences to force plate output with a resolution of 4 ms.

Calculations of COM energetics

From each force plate trial, we isolated a single stride cycle, beginning and ending with a hind footfall, where the bat's body weight was completely supported by the force plates. From it, we calculated the energetics of the COM. Only one stride cycle was used from each trial.

Forces in fore–aft and mediolateral directions, and vertical force minus the product of mass and the gravitational constant (g), were divided by the animal's body mass to obtain instantaneous acceleration of the COM in three dimensions. Acceleration in each direction was then integrated with respect to time to calculate instantaneous velocity, and vertical velocity was integrated to determine the height of the COM throughout the trial.

To obtain constants for the integrations of acceleration (initial velocity values), we used a custom-made program in Matlab 7.0.1 (MathWorks Inc., Natick, MA, USA) to digitize the movement of the nose tip over the 10 camera frames (0.04 s) prior to the beginning of the stride cycle. A linear least-squares best-fit line was calculated for both the fore–aft and mediolateral movements over time, to produce initial velocity estimates for that trial. Unfortunately, changes in the pitch of the body did not allow reliable estimates of initial vertical velocity in the same manner. Therefore, we selected an initial vertical velocity such that the calculated net change in height of the COM based on force recordings would match the observed change in the height of the nose from the beginning to the end of the trial. To ensure accuracy, calculated patterns of increase and decrease in calculated COM height over the course of the entire trial were checked against changes in the height of the bat's body in videos. The constant for integration of vertical velocity (initial height) was chosen as zero.

Kinetic energy in the fore–aft direction was calculated using the equation $E_{KF} = 0.5mv_F^2$, where m is the mass of the animal and v_F is forward velocity. Mediolateral and vertical kinetic energies (E_{KL} and E_{KV} , respectively) were calculated analogously. We defined total kinetic energy as $E_K = E_{KF} + E_{KL} + E_{KV}$, and gravitational potential energy as $E_P = mgh$, where h is the height of the COM. Total energy was defined as $E_{TOT} = E_K + E_P$.

Descriptions of COM energetics

Where E_K and E_P of the COM oscillate in serial sinusoidal patterns of similar frequency, the 'phase shift' between them reveals information about the degree to which energy might be exchanged in a pendulum-like manner. Although this statistic is frequently reported in studies of this kind (Ahn et al., 2004; Cavagna et al., 1977; Farley and Ko, 1997), we do not present it here because we did not observe clear sinusoidal changes of E_K or E_P from trial to trial in *M. tuberculata*.

'Percent congruity' (%congruity), calculated as the percentage of time taken to complete the stride cycle for which E_K and E_P increased together or decreased together, to the exclusion of time where the product of their slopes was negative (Ahn et al., 2004), was calculated for all trials. If animals use a pendulum-like exchange of E_K and E_P , %congruity should be near zero. If instead the kinetics are similar to those of a bouncing ball, %congruity should approach 100%.

Percent recovery (%recovery), has been widely used as a descriptive statistic of the potential for exchange between E_K and E_P for the stride cycle of an animal (e.g. Zani et al., 2005), so we recorded it for *M. tuberculata*. Percent recovery was calculated as

$$\%recovery = \left(\frac{\Sigma\Delta E_K + \Sigma\Delta E_P - \Sigma\Delta E_{TOT}}{\Sigma\Delta E_K + \Sigma\Delta E_P} \right) \times 100,$$

where $\Sigma\Delta E$ is the sum of positive increments in a given component of energy over the course of the stride cycle (Cavagna et al., 1977). Percent recovery for a pendulum-like kinetic walk should approach 100%, since $\Sigma\Delta E_{TOT}$ should

approach zero if energy is tightly recycled between E_K and E_P . Percent recovery for a bouncing ball-like kinetic run should approach zero. If *M. tuberculata* use a kinetic walk at low speeds and kinetic run at high speeds, %congruity would increase with increasing speed, while %recovery would decrease.

Results

Treadmill trials: common vampire bats

Behaviour

All *D. rotundus* used in this study took only a matter of minutes to train on the treadmill. When the treadmill belt began moving, they quickly learned to move against its direction, and to sustain constant speed until it was stopped. In later trials, bats would make long leaps toward the front of the treadmill, stand on the moving floor until they came close to the back of the cage, then jump again. We interpreted this pattern of behaviour as the result of fatigue, and ceased trials with a given individual once it was observed. We recorded 61 treadmill trials (31 walking, 30 bounding) from five individuals over speeds ranging from 0.12 to 1.14 m s⁻¹. The speed-to-stride-frequency relationship for those trials was reported elsewhere (Riskin and Hermanson, 2005). We were only able to resolve footfall patterns in 28 walking and 21 bounding trials, but the speeds and kinematic gaits from all 61 trials were used in this study for comparison to the velocities of *M. tuberculata*.

Lateral-sequence walking gait

At low speeds, *D. rotundus* used a lateral sequence gait, to a maximum speed of 0.56 m s⁻¹. As the left forelimb moved

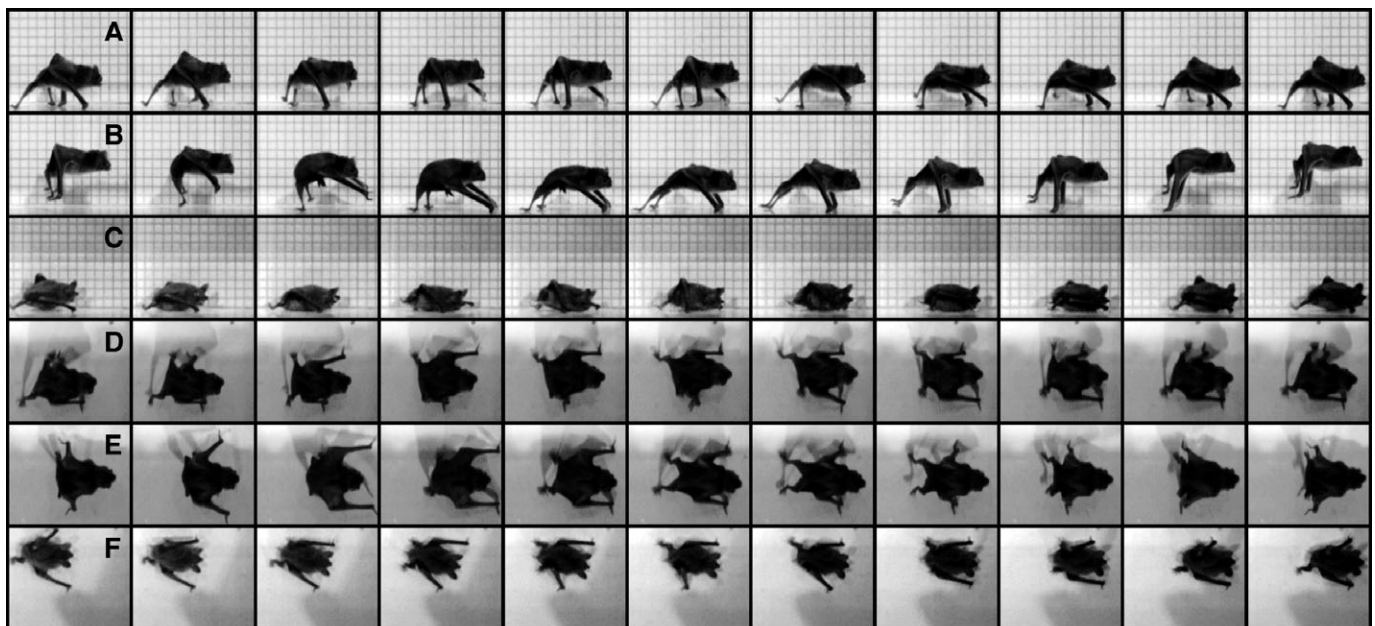


Fig. 1. Representative stride cycles on the treadmill of *D. rotundus* in lateral view (A) walking at 0.12 m s⁻¹ and (B) bounding at 0.60 m s⁻¹; (C) *M. tuberculata* moving at 0.35 m s⁻¹. The time between frames differs in the three sequences (40, 24 and 16 ms, respectively). The background is a 1 cm² grid. Dorsal views of the same three sequences are shown in D, E and F, respectively.

forward, so did the right hindlimb, and *vice versa* (Fig. 1A,D). Walking *D. rotundus* kept the body at a relatively constant height, so that it did not bounce, but instead moved cat-like in a straight horizontal line, as has been reported previously (Altenbach, 1979).

During the lateral sequence gait, at least one limb remained in contact with the ground at all times. Forelimb duty factors (0.72 ± 0.07 , mean \pm s.d.) were significantly greater (paired- $t=6.09$, d.f.=27, $P<0.0001$) than those of the hindlimbs (0.62 ± 0.06), and duty factors of the forelimbs and hindlimbs both exceeded 0.5 ($t=15.86$ and 10.68 , respectively, d.f.=27, $P<0.0001$). Duty factor decreased with speed in the forelimbs ($t=-2.72$, $P=0.012$; $r^2=0.22$), but only very slightly, and hindlimb duty factor decreased with speed, but not significantly ($t=-1.88$, $P=0.07$, $r^2=0.12$; Fig. 2A).

Bounding gait

At speeds of $0.28\text{--}1.14\text{ m s}^{-1}$ on the treadmill, *D. rotundus* used a bounding gait that included a dramatic aerial phase (Fig. 1B,E). This range of speeds overlaps with the upper 50% of speeds at which lateral-sequence walks were used in other trials, and extends into a range of speeds at which walking was not observed. During bounding, duty factors were greater than 0.5 ($t=7.00$, d.f.=20, $P<0.0001$) in the forelimbs (0.62 ± 0.08), less than 0.5 ($t=-4.56$, d.f.=20, $P<0.0001$) in the hindlimbs (0.40 ± 0.10), and decreased with increasing speed in both the forelimbs ($t=-3.27$, $P=0.004$, $r^2=0.36$) and hindlimbs ($t=-4.71$, $P=0.0002$, $r^2=0.54$; Fig. 2B).

Treadmill trials: New Zealand short-tailed bats

Behaviour

In general, we were unable to train *M. tuberculata* to move predictably against the motion of the treadmill within the single testing period to which each was subjected, and were unable to extend the training period due to their endangered status. When the floor began moving, bats typically sat still, forcing us to stop the treadmill before the bat reached the end of the enclosure. In those instances where the bat did travel on the moving treadmill, it seemed as likely to move with the direction of floor movement as against it. Nevertheless, we were able to glean 10 trials in which a bat moved at constant speed for at least three sequential stride sequences, from among five bats over speeds ranging from 0.20 to 0.59 m s^{-1} . Although *M. tuberculata* sometimes made single jumps similar to the flight initiating jumps of vampire bats, we never observed any individuals jumping sequentially like bounding *D. rotundus* did.

Lateral-sequence gait

At all treadmill speeds, *M. tuberculata* (Fig. 1C,F) used a lateral-sequence walk in which stride frequency increased with increasing speed ($t=4.38$, $P=0.002$; $r^2=0.71$; Fig. 3). In general, the patterns of limb movement were consistent between trials. However the vertical movements of the body varied tremendously in frequency and amplitude from trial to trial, and did not appear to change in a predictable pattern with the movement of the limbs.

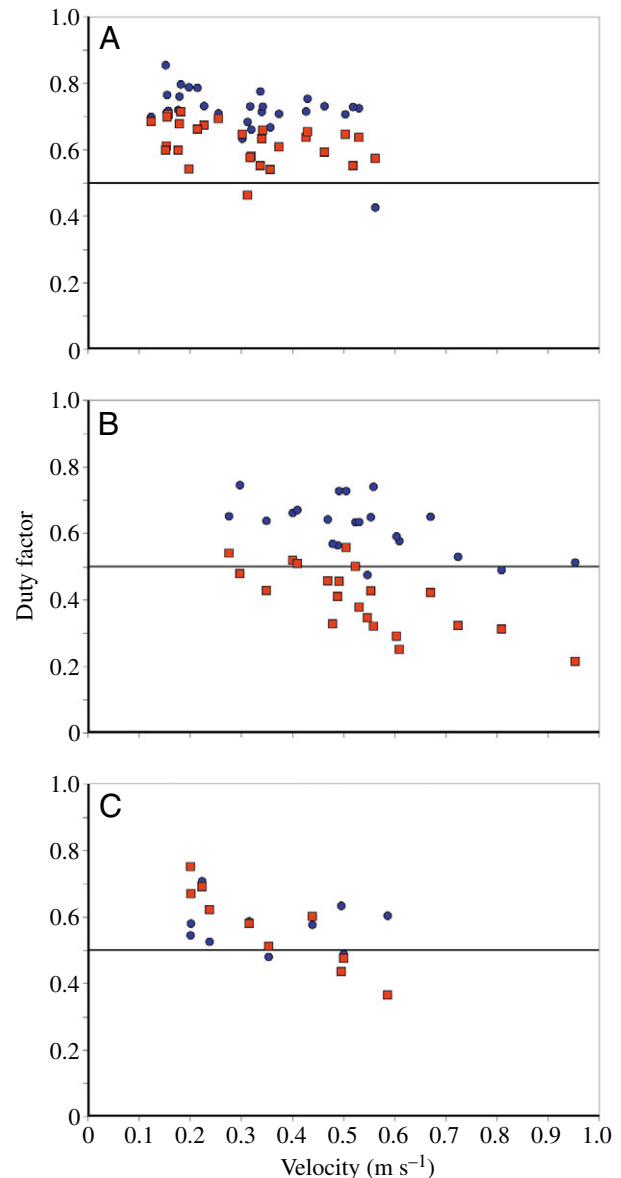


Fig. 2. Duty factor (the proportion of a stride cycle for which a given limb is in contact with the ground) of treadmill trials for (A) walking *D. rotundus*, (B) bounding *D. rotundus* and (C) *M. tuberculata*. Blue circles represent the means of left and right forelimbs in each trial, and red squares the means of hindlimbs. Each plot includes a horizontal line at duty factor=0.5, the kinematic separation point between walks (duty factor >0.5) and runs (duty factor <0.5) (Hildebrand, 1976).

The lateral sequence walk of *M. tuberculata* did not include an aerial phase. Duty factors of forelimbs and hindlimbs were not significantly different (paired- $t=-0.05$, d.f.=9, $P=0.96$), and were generally greater than 0.5 ($t=3.30$, d.f.=9, $P=0.005$ and $t=1.79$, d.f.=9, $P=0.053$, respectively). Duty factors of the hindlimbs decreased with increasing speed ($t=-6.58$, $P=0.0002$, $r^2=0.84$) but those of the forelimbs did not change with speed ($t=-0.19$, $P=0.86$, $r^2=0.004$; Fig. 2C).

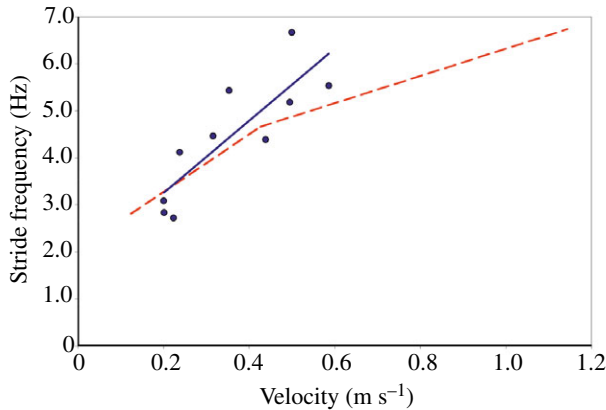


Fig. 3. The gait of *M. tuberculata* (blue) demonstrates a linear increase in stride frequency with speed, just as the gaits of many other tetrapods do (Heglund and Taylor, 1988). The broken red lines represent the linear best fit regressions for walking (left) and bounding (right) gaits of *D. rotundus*, truncated at their point of intersection (see Riskin and Hermanson, 2005).

We do not believe that *M. tuberculata* perform the bounding run, since they traveled without bounding at Froude numbers (and velocities) for which *D. rotundus* used the bounding gait exclusively. The greatest speed of *M. tuberculata* on the treadmill ($Fr=2.1$, $v=0.59$ m s⁻¹) exceeds the top walking speed of *D. rotundus* ($Fr=1.2$, $v=0.56$ m s⁻¹), and lies well within the range of speeds at which *D. rotundus* used a bounding gait ($Fr=0.3$ – 4.9 , $v=0.28$ – 1.14 m s⁻¹).

Force plate trials: New Zealand short-tailed bats

We analysed 24 trials from five individuals, in which animals moved at speeds of 0.13 to 0.95 m s⁻¹ across the force plates. Bats on the stationary force plates demonstrated similar variability in vertical body movement relative to footfall pattern from trial to trial as they did on the moving treadmill, and this was evident in plots of E_K and E_P over the course of each trial (Fig. 4).

Across trials, the magnitude of changes in E_K (1.54 ± 0.86 mJ) was not significantly different from the magnitude of changes in E_P (1.47 ± 0.91 mJ; paired- $t=0.39$, $P=0.69$). As speed increased, changes in E_{TOT} (2.35 ± 1.36 mJ) increased overall ($t=2.25$, $P=0.03$, $r^2=0.19$), but not every component of E_{TOT} did. Bats increased E_{KF} ($t=2.31$, $P=0.03$, $r^2=0.20$) and E_{KV} ($t=2.89$, $P=0.009$, $r^2=0.28$) with speed, but not E_{KL} ($t=-1.27$, $P=0.22$) or E_P ($t=1.25$, $P=0.23$; Fig. 5). Percent congruity ($57.8 \pm 16.4\%$) did not change with speed ($t=-0.16$, $P=0.88$), nor did %recovery ($26.0 \pm 18.1\%$; $t=0.23$, $P=0.82$; Fig. 6).

Discussion

The kinematic walking gaits of both species

We do not find evidence that the ability to fly in these bats prevents them from walking like other tetrapods do. Despite bodies that are highly specialized for flight, both *D. rotundus* and *M. tuberculata* perform lateral sequence walking gaits that

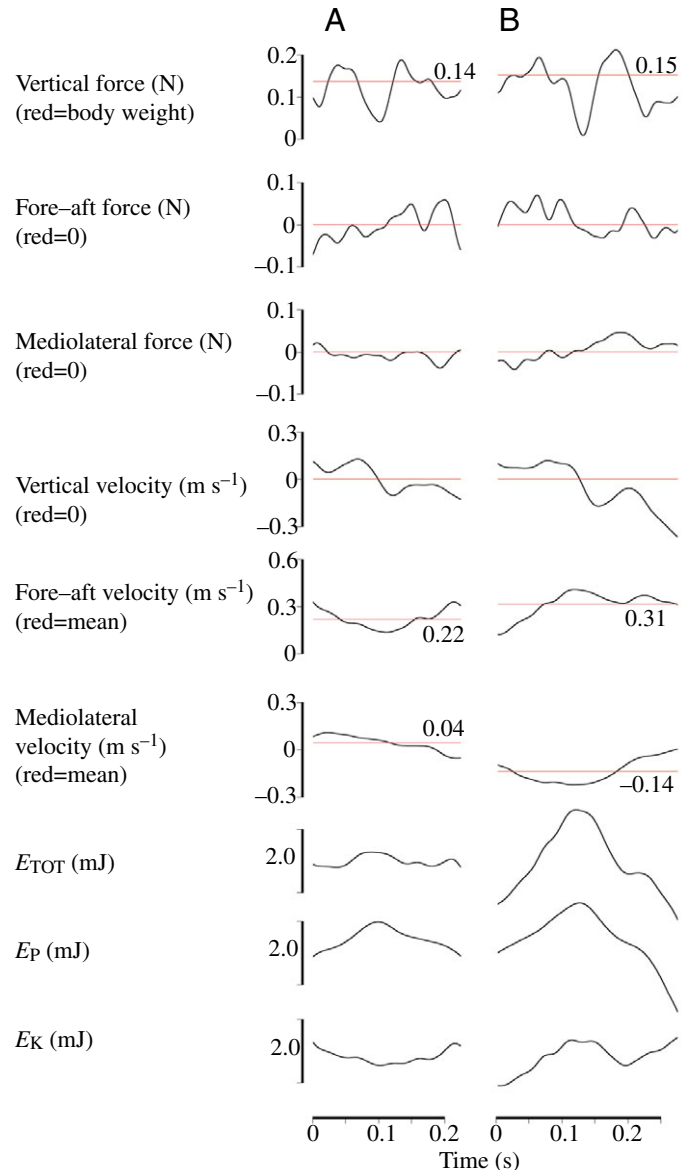


Fig. 4. Energetics of two separate stride cycles, left hind footfall to left hind footfall, of *M. tuberculata* performing (A) a kinetic walk-like stride cycle (body mass=14.0 g, speed=0.27 m s⁻¹, %congruity=19.3%, %recovery=59.5%), and (B) a kinetic run-like stride cycle (body mass=15.5 g, speed=0.28 m s⁻¹, %congruity=60.0%, %recovery=24.0%). Though speed is similar in these two trials, the energetics of the former feature greater pendulum-like changes in E_K and E_P than the latter. Despite such variability in COM energetics from trial to trial, *M. tuberculata* did not transition from a kinetic walk to a kinetic run with increasing speed.

are very similar to each other, and to the symmetrical lateral sequence walks known from a broad range of tetrapods, including amphibians, turtles, crocodilians, and the majority of quadrupedal mammals (Hildebrand, 1985; Figs 7, 8). The walking gaits of bats meet two kinematic definitions of walking that are based on the walks of other animals; there is no aerial phase, and the duty factors of forelimbs and hindlimbs are greater than 0.5.

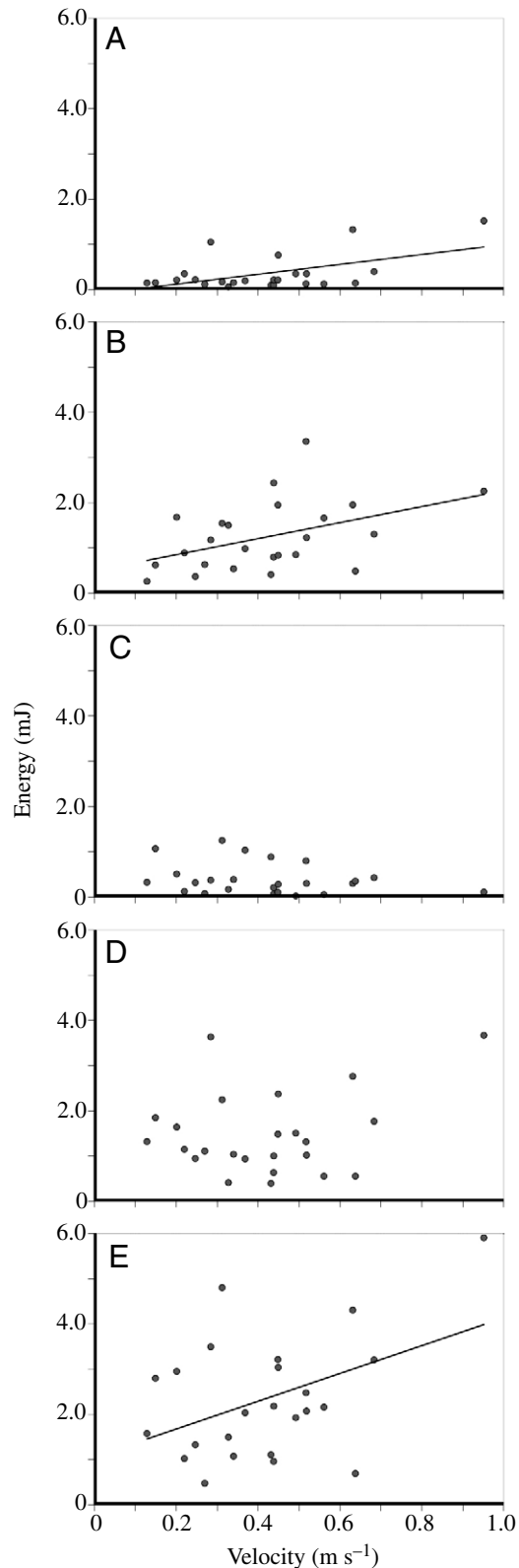


Fig. 5. Magnitudes of oscillations in (A) E_{KV} , (B) E_{KF} , (C) E_{KL} , (D) E_P and (E) E_{TOT} of *M. tuberculata* walking across the force plates at a range of speeds. Bats increased the magnitudes of fore-aft and vertical E_K oscillations with speed, but not of lateral E_K nor of E_P .

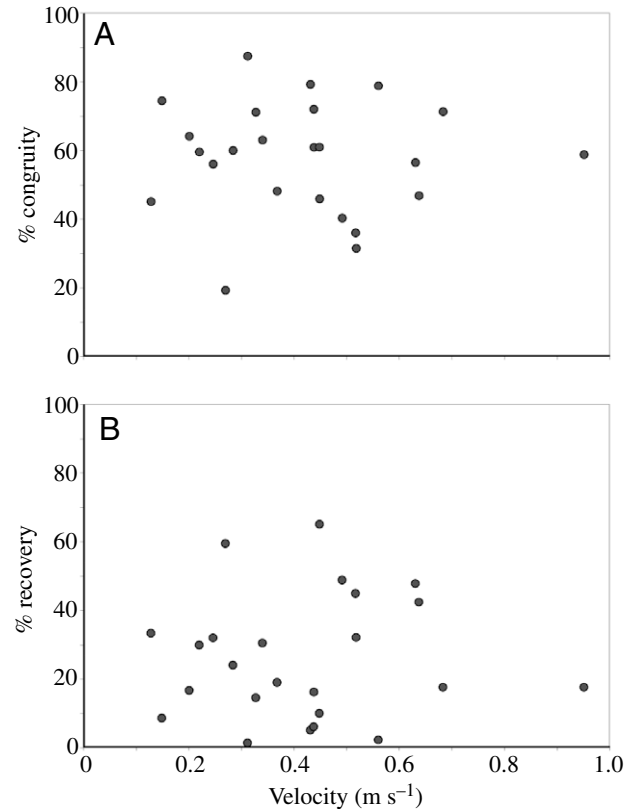


Fig. 6. (A) %congruity and (B) %recovery of *M. tuberculata* crossing the force plates at a range of speeds. The considerable variability of values for both these descriptive statistics supports our observation that the patterns of vertical body movement were extremely variable from trial to trial, both on force plates and on the treadmill. A transition from an energetic walk to an energetic run with increased speed would be reflected by an increasing %congruity and decreasing %recovery, but neither regression has a slope significantly different from zero.

The kinematic walks of *D. rotundus* and *M. tuberculata* are not completely alike, and change differently as speed increases. While both species increase stride frequency with increasing speed, *D. rotundus* keep duty factor somewhat constant in the forelimbs and hindlimbs across speeds. Although *M. tuberculata* follow this pattern with the forelimbs, the duty factor of their hindlimbs decreases with speed. The functional basis of this difference is not clear, but it is interesting that bounding *D. rotundus* decrease duty factor in both forelimbs and hindlimbs as speed increases. In this regard, the lateral-sequence walk of *M. tuberculata* is an intermediate between the walk and bound of *D. rotundus*.

The bounding common vampire bat gait

To our knowledge, the bounding vampire bat gait is kinematically distinct from any other tetrapod gait known. Definitions of walking and running based on duty factor are not appropriate descriptors for this gait, since by those definitions the forelimbs of bounding *D. rotundus* walked (duty

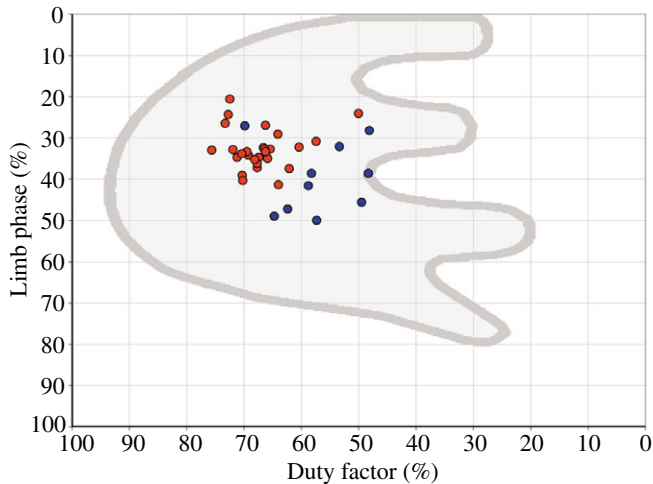


Fig. 7. A Hildebrand gait plot for the walking gait of *D. rotundus* (red) and the single gait of *M. tuberculata* (blue). Duty factor is the percent of the stride cycle for which the feet were in contact with the ground, averaged for all four limbs in a stride cycle. Limb phase is the percent of the stride cycle that elapsed between left hindlimb footfall, and left forelimb footfall. The shaded area encloses 1178 symmetrical gait plots from 156 genera of tetrapods (see Hildebrand, 1985).

factor >0.5) while the hindlimbs simultaneously ran (duty factor <0.5). However, since there is an aerial phase, the gait clearly meets one kinematic definition of a run (Riskin and Hermanson, 2005).

We call the vampire run a bound, because it is superficially similar to the bounding gaits of several terrestrial mammals, including squirrels, jumping mice and tree shrews (Hildebrand, 1985; Jenkins, 1974). Both types of bounds are asymmetrical, because the footfalls of the forefoot and hindfoot on the same side of the body are unevenly spaced in time (Hildebrand, 1966; Hildebrand, 1977; Hildebrand, 1980). However, compared with the bounding gaits of terrestrial mammals, the roles of the forelimbs and hindlimbs are reversed in vampire bats. In the bounding gait of vampire bats, the duty factor of the forelimbs is greater than that of the hindlimbs and the aerial phase is initiated by push-off with the forelimbs. In bounding terrestrial mammals the reverse is true (Fig. 8A,B).

The evolution of vampire bat running

We have suggested previously that the bounding vampire bat gait is an independently evolved run (Riskin and Hermanson, 2005). This is supported by the fact that a running gait has not been reported for any bat species other than *D. rotundus*. Even the closely related and quadrupedally agile white-winged vampire bat (*Diaemus youngi*) does not bound, even when placed on the same treadmill as that used in this experiment (D.K.R., G.G.C. and J.W.H., personal observations).

We propose that as the mammals that gave rise to bats became adapted to flight, they completely lost the ability to run, and that as *D. rotundus* adapted to their unique blood-feeding niche, they 're-invented' running. Because bats have far more musculature in the forelimbs than in the hindlimbs

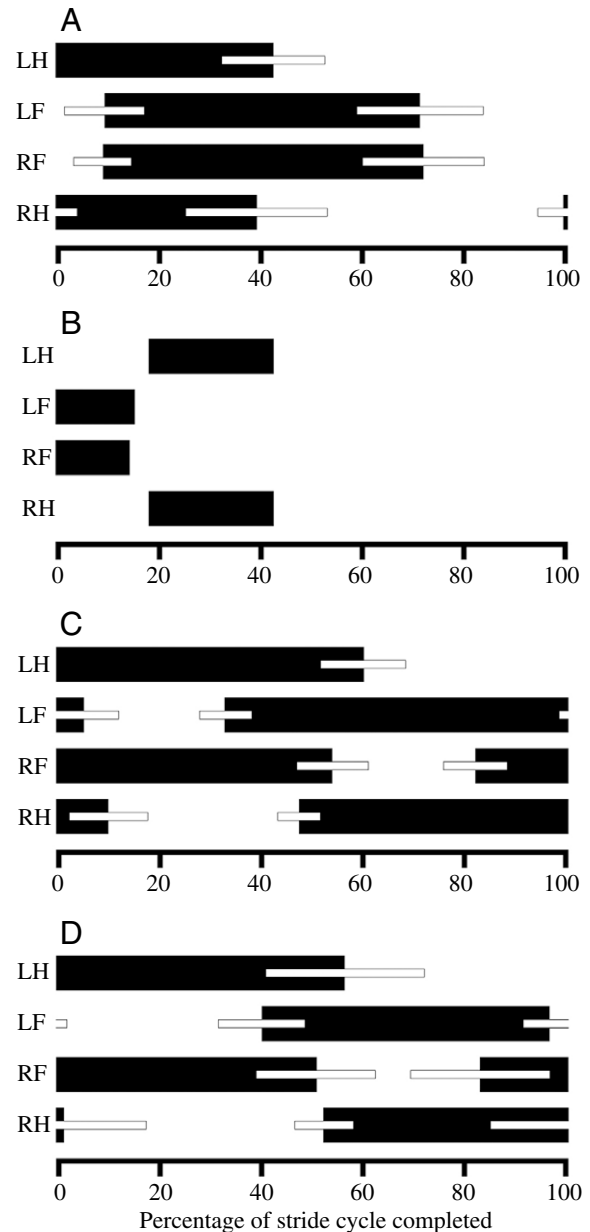


Fig. 8. Footfall patterns, beginning and ending with left hind footfall, on the treadmill for (A) bounding *D. rotundus*, (B) a bounding quadrupedal rodent (see Hildebrand, 1985), (C) walking *D. rotundus*, and (D) *M. tuberculata* using their single gait. Solid bars indicate the time that a foot is in contact with the ground. Open bars represent one standard deviation above and below the mean. F, fore; H, hind; L, left; R, right. Note that the bounding gait of *D. rotundus* is superficially similar to the bounding rodent gait, but with the footfall patterns of the forelimbs and hindlimbs reversed.

(Strickler, 1978), the population of bats ancestral to *D. rotundus*, when selected for high-speed terrestrial locomotion, would have a morphology more suitable to the evolution of a wing-powered run than a hindlimb-driven one. That vampire bats independently converged on the bounding gaits of other vertebrates supports the hypothesis that quadrupedal animals

are forced to choose from a limited range of possible gaits to achieve stability on the ground (Cartmill et al., 2002; Hildebrand, 1985; Jenkins, 1974).

The kinematically defined walking gaits of *D. rotundus* and *M. tuberculata*, on the other hand, are probably synapomorphic with those of other terrestrial vertebrates. While the complete inability (or refusal) to crawl has been reported for some hipposiderid, mormoopid, phyllostomid, rhinolophid and natalid bat species (Dietz, 1973; Lawrence, 1969; Riskin et al., 2005; Schutt and Simmons, 2006; Vaughan, 1959), the distant relationships of non-crawling bats to *D. rotundus* and *M. tuberculata* suggest that the ability to walk was retained throughout the evolution of the bats in this study (Jones et al., 2002; Teeling et al., 2003). Indeed, even among some species that do not crawl as adults, the ability to crawl is retained in juveniles (Dietz, 1973).

It is unlikely that the running gait of vampire bats evolved as a way of permitting them to travel long distances, since flight allows animals to travel greater distances per unit energy than the terrestrial gaits do (Alexander, 2005). Also, Hildebrand noted that the bounding gait of other mammals is energetically inefficient, and is generally used only over short distances (Hildebrand, 1985). Bats in our study used the bounding gait for less than 60 s at a time, and demonstrated fatigue after only a few trials, so the gait appears useful for increasing overall speed in short bursts, rather than for metabolic efficiency over long distances. We therefore infer that in nature the gait has significance to short-term behaviours. Specifically, we suggest that the running gait helps *D. rotundus* follow prey animals that flee or move in the middle of a feeding event.

The feeding behaviour of *D. rotundus* prior to the introduction of livestock to their range in the 16th century is unknown. Captive *D. rotundus* are known to take blood from a broad range of vertebrates, including porcupines, armadillos, small rodents and even snakes (Greenhall, 1988), so it is plausible that some of the wild animals upon which these bats feed might attempt to evade them by running away. Carranza and Campo once observed *D. rotundus* feeding on a capybara (Rodentia: *Hydrochoerus* sp.) that fled upon being disturbed by researchers (Carranza and Campo, 1982). As the capybara ran toward the water, the vampire bat chased after it on the ground without taking flight. Since vampire bats often take some time to locate and prepare a bite area before feeding begins (Greenhall, 1988), locomotory strategies to follow prey that move during a feeding event would have an obvious energetic benefit.

COM energetics of locomotion in the New Zealand short-tailed bat

As *M. tuberculata* increased speed, the amount of energy used to accelerate the COM in both the vertical and fore-aft directions increased, while the range of heights through which the COM traveled did not. This suggests that as speed increases, the way in which energy is cycled among potential and kinetic forms changes. However, we did not observe an increase in %congruity nor a decrease in %recovery with

increasing speed. *M. tuberculata* therefore use a kinetically variable gait that does not transition from a kinetic walk to a kinetic run with increased speed.

The magnitudes of changes in E_K and E_P were similar, suggesting that energy could be exchanged between them in a pendulum-like manner. However, based on its values of %recovery, the single kinematic gait of *M. tuberculata* is more kinetically run-like than walk-like. Known values of %recovery in quadrupeds range from as high as 80% in penguins (Griffin and Kram, 2000) to as low as 30–40% in walking frogs, lizards and giant tortoises (Ahn et al., 2004; Cavagna et al., 1977; Farley and Ko, 1997; Zani et al., 2005), and even less than 5% in opossums (Parchman et al., 2003). The values of %recovery in this study (ca. 26%) certainly fall in the lower end of this spectrum. The inverted-pendulum mechanism of energy conservation therefore does not appear to be of particular importance to *M. tuberculata* at any speed.

Trade-offs in the locomotion of bats

In this study we found no evidence of trade-offs for flight in the terrestrial locomotion of *D. rotundus* or *M. tuberculata*. Their walking gaits fell well within the range of kinematic gaits known for terrestrial quadrupeds, and though the running gait of *D. rotundus* is unique, there is no evidence that it is any less efficient than the gaits of terrestrial mammals. In fact, Heglund and Taylor found a correlation between stride frequency and metabolic cost during the locomotion of terrestrial mammals (Heglund and Taylor, 1988), so the decreased stride frequency of bounding vampire bats compared with similarly sized mice (Riskin and Hermanson, 2005) suggests that vampire bats might even consume less energy while running than other mammals do.

In *D. rotundus* and *M. tuberculata*, evolution from the ancestral condition of diminished crawling ability to their current states of terrestrial agility resulted in kinematic gaits similar to those of other tetrapods. An obvious future research question is to determine whether terrestrial agility has imposed a cost on the ability to fly in these species, since various anatomical features suggest that a trade-off exists. Bats that are terrestrially agile have greater muscle mass in the pectoral girdle than bats that do not (Strickler, 1978), and *D. rotundus* are known to possess slow-twitch muscle fibres in the pectoralis muscle that are absent in bats that do not crawl well (Hermanson et al., 1993). A cost to terrestrial agility might be associated with the upkeep of muscle fibres, or with some other aspect of morphology, such as hindlimb orientation (Schutt, Jr and Simmons, 2006; Simmons, 1994; Vaughan, 1959).

Alternatively, it is possible that no trade-off between aerial and non-aerial agility exists in bats at all, and that bats are simply absent from terrestrial niches for other reasons, such as competition with other mammals (Daniel, 1979). Indeed, *M. tuberculata* evolved in the absence of terrestrial mammal competitors, and vampire bats occupy a niche that is not occupied by any other mammal. Furthermore, the wing shapes of neither species suggest a reduced ability to fly compared

with other bats (Jones et al., 2003; Norberg and Rayner, 1987; Webb et al., 1998). The presence or absence of a trade-off would best be tested by measurements of oxygen consumption during flight in bats that move on the ground well and bats that do not. If *D. rotundus* and *M. tuberculata* suffer trade-offs between these forms of locomotion, we predict a greater rate of oxygen consumption during flight for those species than for bats that avoid the ground most of their lives. With the knowledge from this study that bats move on the ground like other mammals do, such investigations of flight energetics will help us understand how an animal meets the demands of more than one form of locomotion.

List of symbols and abbreviations

COM	centre of mass
E_K	kinetic energy
E_{KF}	fore-aft kinetic energy
E_{KL}	mediolateral kinetic energy
E_{KV}	vertical kinetic energy
E_P	gravitational potential energy
E_{TOT}	Total energy
Fr	Froude number
g	gravitational constant
h	height
l	hip height
m	mass
v	velocity
v_F	forward velocity

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