Biomechanics

Independent evolution of running in vampire bats

Most tetrapods have retained terrestrial locomotion since it evolved in the Palaeozoic era[1,2], but bats have become so specialized for flight that they have almost lost the ability to manoeuvre on land at all[3,4]. Vampire bats, which sneak up on their prey along the ground, are an important exception. Here we show that common vampire bats can also run by using a unique bounding gait, in which the forelimbs instead of the hindlimbs are recruited for force production as the wings are much more powerful than the legs. This ability to run seems to have evolved independently within the bat lineage.

Bats (Chiroptera) are the only mammals that fly, so their bodies differ from those of terrestrial mammals. As a result, most grounded bats can only shuffle awkwardly from a sprawled position[4]. However, the common vampire bat (*Desmodus rotundus*) walks forwards, sideways and backwards[5], and initiates flight with a single vertical jump from standing[6]. Captive *D. rotundus* have also been found to 'hop' at speeds exceeding 2.0 metres per second[5].

To determine whether this hopping behaviour constitutes a stereotyped running gait by *D. rotundus*, we tested five adult males on a treadmill inside a Plexiglas cage. The animals used a walking gait at low treadmill speeds (0.12 to 0.56 m s^{-1}) and a stereotyped running gait at high speeds (0.28 to 1.14 m s^{-1}). The walking gait was similar to the typical lateral-sequence walking gait of other tetrapods[7]; however, the run was different from any gait previously described (Fig. 1; for methods and video, see supplementary information). We classify this novel gait as a run because it includes a notable aerial phase.

A tetrapod typically increases its speed while walking by increasing its stride frequency. At some transition speed, animals switch to a running gait that permits a further increase in speed, but at stride frequencies that are lower than would be predicted for high-speed walking[8,9]. Our kinematic data from *D. rotundus* fit this general stride-frequency–velocity relationship. In Fig. 2, the slopes of the stride-frequency–velocity regressions, which are best fits to the walking and running data, respectively, and are shown truncated at the intersection, are significantly different (*t*-test, $P < 0.0001$, $n = 61$). These regression lines indicate that common vampire bats, like other running tetrapods, keep their stride frequencies low by walking at low speeds and running at high speeds (Fig. 2).

The walking vampire bats used stride frequencies that were comparable to those of similarly sized terrestrial mammals (mice) over the same range of speeds (Fig. 2; blue line). When running, however, the bats used lower stride frequencies than mice[8]: this could be explained by the vampire bats' long forearms, which allow longer and fewer strides to be taken during running than can be achieved by mice.

The absence of a running gait in all other bat species so far surveyed indicates that running may have been lost early in the evolution of bats, evolving afresh in the vampires at a later time. We have shown that the hopping behaviour reported for *D. rotundus* in captivity[5] is a running gait. But despite detailed knowledge of their roosting and foraging behaviour[10,11], the selective benefit of running for these bats in the wild is not known. Presumably, vampire bats are most likely to run when manoeuvring around prey animals while feeding, and they may have used the gait more before the introduction of domestic livestock to the Americas in the sixteenth century[11].

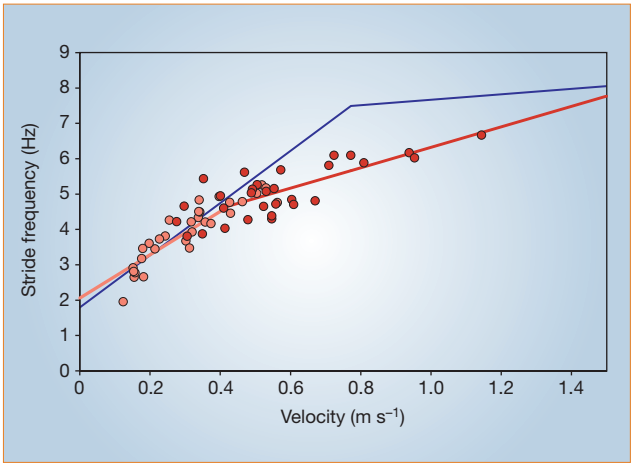

Figure 2 Stride frequency plotted against velocity for vampire bats (*Desmodus rotundus*; $n = 5$) moving on a treadmill. Pink circles, walking; red circles, running. Pink and red lines, best fits for walks and runs, respectively, truncated at their point of intersection; blue lines, best fits for walks and runs, respectively, of similarly sized (29 g) mice (data from ref. 8), shown here for comparison.

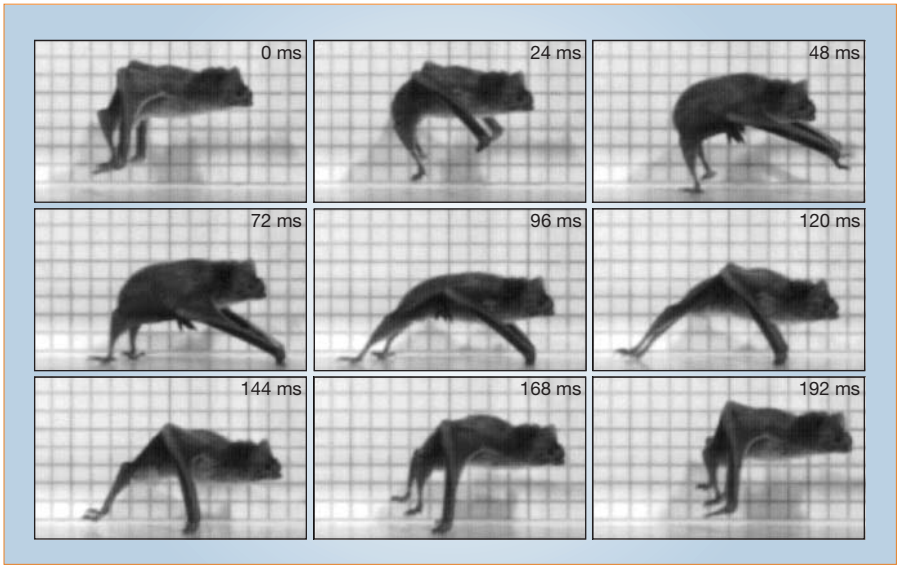

Figure 1 A vampire bat, *Desmodus rotundus*, using a running gait at 0.61 m s^{-1} with a stride frequency of 4.71 Hz. Images are shown at 24-ms intervals; the background is a 1.0-cm^2 grid. For video, see supplementary information.

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Supplementary information accompanies the paper on *Nature*'s website.
Competing financial interests: declared none.

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