Birds on the run: what makes ostriches so fast?

Image courtesy of John Carnemolla / iStockphoto

What makes ostriches such fast runners? **Nina Schaller** has spent nearly a decade investigating.

When admiring a soaring seagull or a diving penguin, we rarely consider that these feathered animals have something very rare in common with us: whereas most other animals move on four, six or more legs, birds and humans are the only true bipeds. Evolution has solved the challenge of moving on two legs in two ways: humans are plantigrade (we place our entire foot on the ground when we walk or run), whereas birds are digitigrade (they walk on their toes, or *digits*).

Some avian species can run more quickly not only than humans run, but even faster than their flying counterparts fly. The fastest long-distance runner is the African ostrich (*Struthio camelus*). At a steady 60 km/h with top speeds exceeding 70 km/h, it could cover the 42 km Olympic marathon in 40 minutes rather than the two hours needed by a human. This remarkable combination of speed and endurance allows the ostrich to cover great distances to find fresh grazing pasture or to outdistance hungry hyenas.

Scientists have long explored the challenges of terrestrial locomotion, particularly the running abilities of dogs and racehorses. However, studies on avian locomotor modes have typically explored flight dynamics while paying less attention to *cursorial* species (those that are specialised for running).

After finishing my degree in biology in 2002, I volunteered at Frankfurt Zoo in Germany, where I became fascinated by the ostrich's racing ability and decided to investigate it. The hypothesis of my PhD research was that the ostrich locomotor system transmits power to the ground with a high degree of efficiency, maximising energetic output (speed and endurance) while minimising energy demands (muscular and metabolic work).

To test my idea, I decided to study both form and function of the ostrich locomotor system. Using dissection, I explored ostrich anatomy, searching for specialised limb structures that might reduce the metabolic cost of locomotion. Simultaneously, I studied the biomechanics of live ostriches: how physical forces acted on their

10-week-old ostrich chicks in their new home

Image courtesy of Jürgen Gass

anatomy when they moved.

To enable close observation of natural motion sequences, I hand-raised three ostriches in a large outdoor enclosure and, over four years, habituated them both to me and their experimental racetrack. Mutual trust was crucial: a kick from an ostrich can kill a lion.

Maximising speed: long, light legs

In a running animal, higher speeds are achieved by increasing both the length and frequency of steps. Longer legs can swing further, and if the leg's muscle mass is located proximally (close to the body), the leg can then swing faster, in the same way that moving the adjustable weight of a metronome closer to the pivot increases the tempo.

To investigate this principle, I compared leg segment lengths (Figure 1) and muscle mass distribution of fast-running, ground-dwelling bird species. Of all cursorial birds, the ostrich possesses the longest legs relative to its size and has the longest step length when running: 5 m. In addition, to a greater degree than other bird species, it has the majority of its leg musculature located very high on the thigh bone and hip, whereas the lower swinging elements of its leg are comparatively light, moved by long, mass-reducing tendons (Figure 2). This arrangement optimises the os-

REVIEW

- ✓ **Biology**
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The surprising yet obvious statement that 'birds and humans are the only true bipeds' introduces the account of the research that Nina Schaller has been doing for nearly a decade. She offers us a picture of the multidisciplinary approach to a complex phenomenon – the outstanding speed and endurance of the ostrich – investigating the biomechanics and efficiency of the bird's performance by means of anatomy (dissection) and physiology (functional study). The listed resources, in addition, provide a wealth of information and teaching materials on ostrich and human locomotion.

The article would be an interesting and useful means to address topics in biology (biomechanics – bones, muscles, tendons and ligaments; evolution – homology and analogy) and physics (efficiency, forces, speed, springs and motion) at both upper- and lower-secondary school. For example, it could be used to address the biomechanics of walking and running in different species, the evolution of bipedal locomotion in birds and humans, and the functional aspects of lower limb prostheses (for instance those used by the sprint runner Oscar Pistorius). It could also provide valuable background reading before a visit to a natural history museum or zoo, or to a robotics lab.

Suitable comprehension questions include:

1) The hypothesis of Nina Schaller's research was that the ostrich's locomotor system:
   a) maximises energetic output and energy demand
   b) minimises energetic output and maximises energy demand
   c) maximises energetic output and minimises energy demand
   d) minimises energetic output and energy demand.
2) Ostrich legs have
   a) musculature located high on the thigh bone and short tendons
   b) musculature located high on the thigh bone and long tendons
   c) musculature located low on the thigh bone and short tendons
   d) musculature located low on the thigh bone and long tendons.

Giulia Realdon, Italy

Figure 1: Linear leg segment lengths; n indicates number of specimens examined

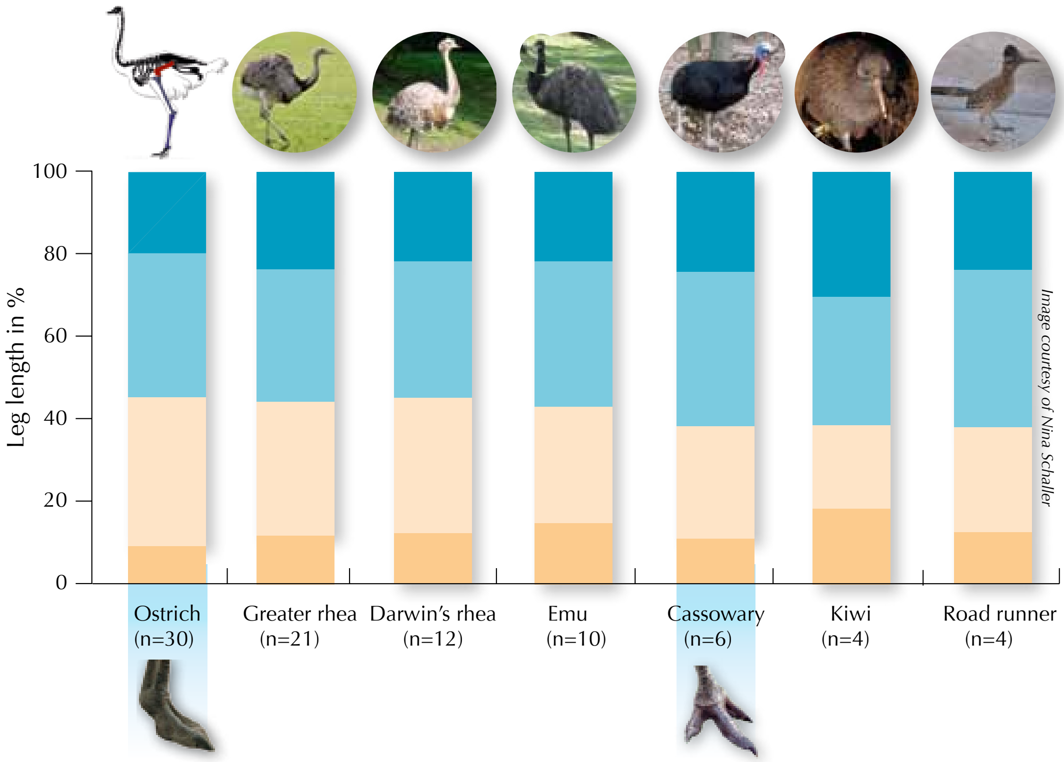

Image courtesy of Nina Schaller

Greater rhea, Rhea americana
Image courtesy of Quartl; image source: Wikimedia Commons

Darwin's rhea, Pterocnemia pennata
Image courtesy of Jennifer Bergk; image source: Wikimedia Commons

Emu, Dromaius novaehollandiae
Image courtesy of Quartl; image source: Wikimedia Commons

Cassowary, Casuarius casuarius
Image courtesy of Dezidor; image source: Wikimedia Commons

Kiwi, Apteryx mantelli
Image courtesy of the Maungatautari Ecological Island Trust; image source: Wikimedia Commons

The greater roadrunner, Geococcyx californianus
Image courtesy of Back1a5h; image source: Wikimedia Commons

Nina and an ostrich displayed at the Royal Ontario Museum, Toronto, Canada

trich leg for high-velocity locomotion, giving it both a long step length and a high step frequency.

Maximising endurance: stable joints

A wide range of joint motion allows humans to climb trees or ballet dance, but this flexibility has a cost. When we run, muscle power is used for propulsion but also to prevent sideways joint movement, thereby increasing our energy requirements over a given distance. I suspected that ostriches had a more efficient approach.

Unlike energy-consuming muscles and their tendons, ligaments can act as a 'joint corset', limiting sideways motion without consuming energy. To demonstrate that this mechanism was present, I filmed my running ostriches from various angles to record the range of motion of their legs. I then repeated these measurements with an intact dead ostrich, and finally with a dissected ostrich leg that had had all muscles and tendons removed, leaving only the skeleton and joint ligaments. The range of sideways motion in live and dead ostrich specimens was nearly identical. In contrast, a similar comparison in humans would reveal a huge difference in sideways motion range, especially at the hip joint, which is stabilised by muscle action. My measurements showed that ligaments are the main elements that guide an ostrich leg through the stride, allowing muscle power to be devoted almost exclusively to forward propulsion.

When manipulating the dissected ostrich legs, I made a further new discovery. When trying to flex the ankle joint, I had to overcome some resistance – an unexpected finding in a lifeless limb devoid of muscles. When I released the joint, it snapped back to an extended position, suggesting that ligaments were passively keeping the bird's leg extended. To test this theory, I exerted pressure from above on the standing, dissected leg until the ankle joint collapsed into a flexed position (Figure 3). It required 14 kg

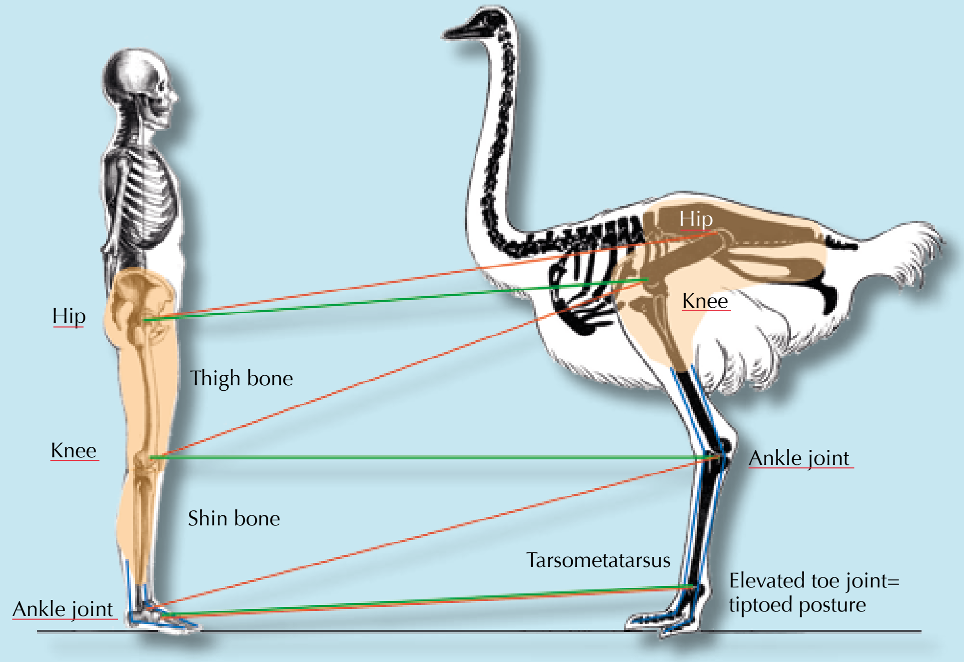

Image courtesy of Nina Schaller

Figure 2: Comparative anatomy of human and ostrich legs: in birds, the bone between ankle and toes, the tarsometatarsus, is much longer than in humans, and serves as a functional equivalent to our upright shin bone. The bird's ankle joint is at our knee level, which explains why a bird appears to flex its 'knee' backwards. Its actual knee joint, hidden under plumage, is permanently flexed and connects to the hip joint through a short, horizontal thigh bone. Red lines connect anatomically equivalent joints; green lines connect functionally equivalent joints.

In the ostrich, muscle mass is concentrated at the top of the leg, while long tendons prevail in the lower regions. Shaded areas show major muscle mass distribution, blue lines indicate location of major tendons

of downward force — 28 kg of weight that an ostrich standing on two legs would not be required to actively support when walking or running. This experiment showed that saving metabolic energy by using ligaments as a passive leg-stabilising mechanism is an excellent locomotor endurance strategy.

Making ground contact

We have seen that light limbs are a precondition for fast, efficient locomotion and that one way in which the ostrich achieves this is by concentrating the leg muscle mass close to the hip joint. A further strategy for reducing lower-leg mass involves specialised toe morphology and positioning. This can also be observed in other cursorial animals; modern horses, for example, have evolved from five-toed ancestors to gallop on the toenail of their middle toe – the hoof. The ostrich has undergone a similar evolution: whereas most birds have four toes and the majority of large flightless birds possess only three, the ostrich is unique among birds in walking on only two toes (Figure 1). Furthermore, it is the only bird to walk on the tips of its toes.

I wondered how this, the largest and heaviest living bird, manages to balance and grip at high-speed on tiptoe. Since there is no established method for investigating toe function in live birds, I used a pressure plate, commonly used by orthopaedists to analyse pressure distribution in

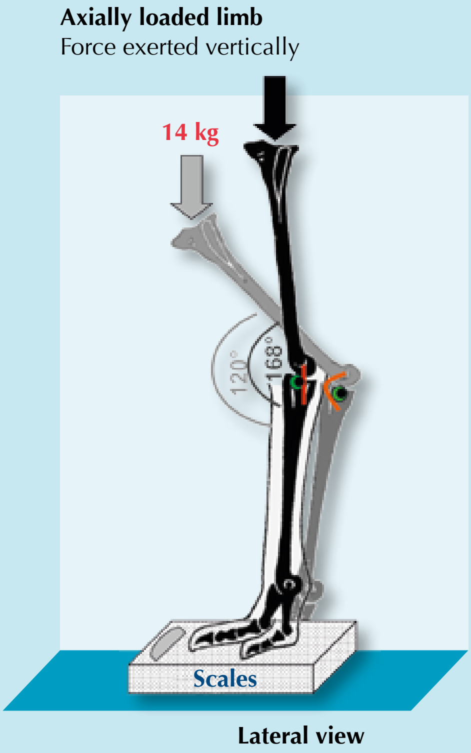

Image courtesy of Nina Schaller

Figure 3: Experiment showing the ability of the ankle joint ligaments to passively support weight from above (only the left side of the left leg is shown). The ankle joint has contoured bone protrusions (in green) on either side. When the joint is fully extended (168°), the ligaments on either side (in red) are tensed because they pass over this protrusion, thereby stabilising the joint. When the ostrich lifts its toes off the ground, the ankle joint is flexed below 140° and the ligaments (in orange) are free to slide around the protrusions: the stabilising mechanism is relaxed

Image courtesy of Nina Schaller

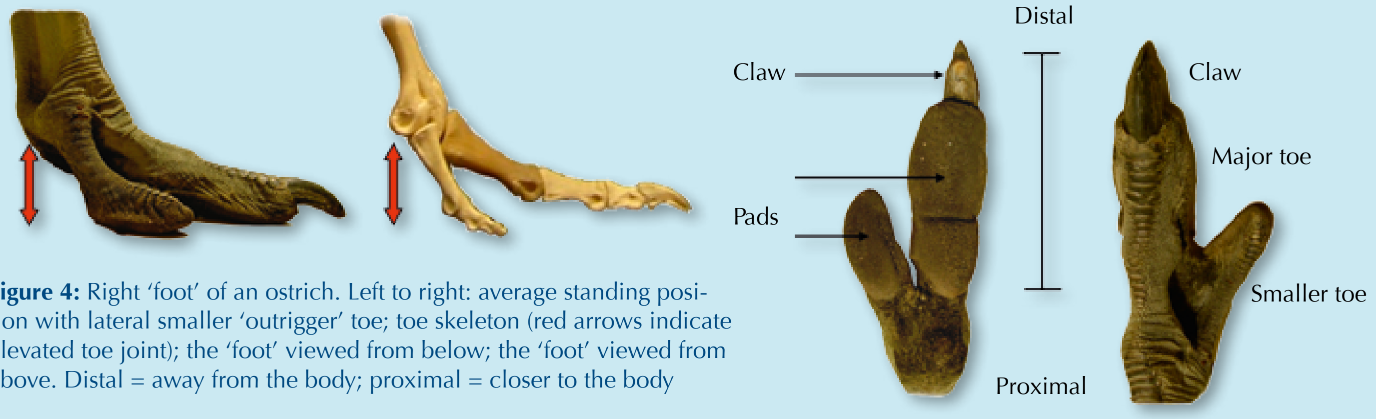

Figure 4: Right 'foot' of an ostrich. Left to right: average standing position with lateral smaller 'outrigger' toe; toe skeleton (red arrows indicate elevated toe joint); the 'foot' viewed from below; the 'foot' viewed from above. Distal = away from the body; proximal = closer to the body

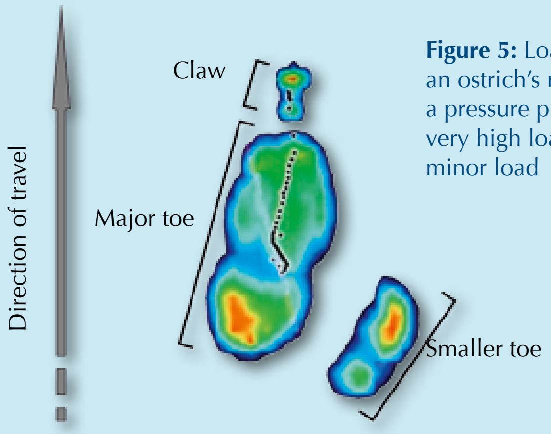

Figure 5: Load-distribution profile of an ostrich's right 'foot' recorded with a pressure plate. Areas in red indicate very high load; dark blue indicates minor load

Image courtesy of Nina Schaller

human feet. I trained my ostriches to walk and run over the plate, capturing high-resolution real-time data of ostrich 'foot' pressure during ground contact. This showed that the big toe supports the majority of the body mass while the smaller toe prevents the ostrich from losing its balance by acting as an outrigger, especially during slow walking.

At high speeds, the toes' soft soles dampen impact stresses, while the spring-loaded tiptoed posture acts as an additional shock absorber (red arrows in Figure 4). The claw barely contacts the ground during walking, but exerts pressures of up to 40 kg/cm^2 when the bird runs. The claw penetrates the ground like a hammered spike to ensure reliable grip at 70 km/h – maximum speed with minimal energy, ideal for endurance running on the level ground of the African savannah (Figure 5).

Image courtesy of Gisela Löffler for Bild der Wissenschaft

Nina and one of her full-grown co-workers, Tiffy

Practical applications

My research has gone a long way to improve our understanding of how the ostrich runs so fast for so long. Now that we understand these biomechanical strategies, perfected over 60 million years of evolution, we may be able to adapt them in modern technologies such as bipedal robotics, suspension systems, and joint-stabilisation engineering. Already, some of my findings have inspired developers of 'intelligent' human prostheses to adapt features of ostrich legs and toes, which may allow amputees a wider range of function and manoeuvrability.

Resources

The 'Confessions of an ostrich' give the ostrich's point of view, and include links to other resources. See: http://tolweb.org/treehouses/?treehouse_id=3303

This introductory lesson on ostriches consists of an essay and a quiz for the students. It is suitable for lower secondary-school level. See: www.lessonsnips.com/lesson/ostriches

A similar activity for primary-school students can be found here: www.enchantedlearning.com/subjects/birds/printouts/Ostrichquiz.shtml

The National Geographic Kids website has a multimedia 'Creature Features' page on ostriches. See: http://kids.nationalgeographic.com/kids/animals/creaturefeature/ostrich

For an introduction to the biomechanics of walking, see: www.pt.ntu.edu.tw/hmchai/BM03/BMClinic/Walk.htm

The Society for Integrative and Comparative Biology's activities on bone and joint biomechanics were developed for university students, but can easily be adapted for older secondary-school students. To build models of joints, see: www.sicb.org/dl/biomechanicsdetails.php3?id=19

For a slide show overview of human locomotion and its biomechanics, with links to sport, see: http://tinyurl.com/c2yrxca

To download the slide show, you will need a Google email account.

If you enjoyed reading this article, you might like to browse the full collection of cutting-edge science articles published in *Science in School*. See: www.scienceinschool.org/cuttingedge

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After finishing her biology studies at the University of Heidelberg, Germany, Nina Schaller volunteered at the Frankfurt Zoo where an exceptionally friendly ostrich sparked her interest in this unique terrestrial vertebrate. For the past nine years, she has studied the unparalleled running performance of the largest living bird. She hand-raised ostriches and collaborated with universities and research institutions in Antwerp, Belgium; Vienna, Austria; Frankfurt and Munich, Germany; and Toronto, Canada. Nina's interdisciplinary approach led to the discovery of energy-conservation strategies that explain how the ostrich manages life in the fast lane.

To learn how to use this code, see page 65.