The fast and forceful kicking strike of the secretary bird

Article

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The fast and forceful kicking strikes of the snake-hunting secretary bird (*Sagittarius serpentarius*)

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The study of animal locomotion has uncovered mechanical design and control principles that can be applied to bio-inspired robotics, prosthetics and human rehabilitation medicine, while also providing insight into musculoskeletal form and function [1-4]. In particular, study of extremes in animal behavior and morphology can reveal mechanical constraints and trade-offs that have influenced evolution of limb form and function [1-2]. Secretary birds (*Sagittarius serpentarius*) (Figure 1A) are large terrestrial birds of prey endemic to sub-Saharan Africa, which feed on snakes, lizards and small mammals [5]. The prey of secretary birds are frequently kicked and stamped on the head until killed or incapacitated, and this hunting technique is particularly important when dispatching larger lizards and venomous snakes [5]. The consequences of a missed strike when hunting venomous snakes can be deadly [5], thus the kicking strikes of secretary birds require fast yet accurate neural control. Delivery of fast, forceful and accurate foot strikes that are sufficient to stun and kill prey requires precision targeting, demanding a high level of coordination between the visual and neuromuscular systems.

We measured kicking strikes from Madeleine, a 24-year old male secretary bird held in the collection at the Hawk Conservancy Trust (Figure 1A), and trained to aggressively strike a rubber snake for public exhibition displays (Movie S1). Strike force impulse and contact duration (Figure 1B) were measured using a portable force plate and synchronized high-speed video, both recording at 500 Hz. Peak forces were determined by fitting a half-sine to the directly measured impulse and duration (Figure 1C; see Supplementary Methods for further detail). Although from a limited sample of a single individual, these data provide the first direct measures of kicking strike biomechanics of the secretary bird.

We find that the peak force demands of secretary bird kicking strikes are remarkably high (Figure 1C), averaging 5.1 ± 0.9 body weights (195 ± 34 N, mean ± s.d.). These forces exceed those typically experienced during moderate to high-speed locomotion (typically 2-3 bodyweights in Galliformes and Ratites) [4], and are comparable to peak forces in maximal leaping, which reach 5.3 bodyweights in helmeted guineafowl (*Numidia meleagris*), for example [6]. Peak forces during landing strikes of barn owls (*Tyto alba*) have been estimated to reach as much as 14.5 body weights [7]. However, these forces are applied as the entire body is rapidly decelerated from downward flight, involving a high momentum of the body centre of mass, powered by gravity. In contrast, in a kicking strike, the secretary bird rapidly accelerates the limb from a static standing position; therefore the momentum subsequently lost in the decelerating strike impact must be powered directly by the limb muscles.

We further discovered that the kick-strikes involve exceptionally fast impacts, lasting only 15 ± 4.4 ms duration in contact (Figure 1B). Such rapid impact time precludes the involvement of proprioceptive feedback control within the contact period, especially considering the likely transmission delays caused by exceptional leg length. We suggest, therefore, that secretary bird hunting behavior must rely on visual targeting and feed-forward motor control within strike events, with opportunity to correct for missed strikes only in subsequent kicks. If so, kicking strikes of the secretary bird involves an unusually constrained control system, which could have interesting implications for the evolution of visual processing in these animals. Observation of head orientation during kick-strikes suggests an important role of visual targeting of foot placement preceding each kick event (Movie S1). The visual field of secretary birds are not known, but are likely to demonstrate a large frontal binocular field with large vertical height – akin to other active-hunting birds of prey – to allow precision striking of the foot [8].

Secretary birds have exceptionally long legs (Figure 1A) – more than twice that of an athletic ground bird of equivalent body mass [4] – which is widely assumed to represent selection for rapid foot-strikes during kick-hunting [9]. The secretary bird's long legs can be attributed to unusually long tibiotarsus and tarsometarsus bones [9]. This morphology facilitates rapid foot velocities for hunting strikes, but also has important potential consequences for gait, due to the associated increase limb rotational inertia [9]. To further explore whether the unusually long-legged morphology of the secretary bird imposes constraints on running dynamics, we fit a spring-loaded-inverted-pendulum model to Madeleine's measured body mass, leg length and experimentally recorded running gait parameters (Figure 1D). We measured velocity, stride period, duty factor and leg angle swept during stance for three running strides at a velocity of $1.82 \pm 0.09 ms^{-1}$ (relative velocity 0.70 ± 0.04, see Supplemental Methods). The model-predicted peak forces and effective limb stiffness suggest that the bipedal running dynamics of these birds is unexceptional (Figure 1D), comparable to those measured in ground birds [4]. Additional data over a broad speed range would be needed to fully address whether the secretary bird's long legs influence the stride-length and stride-frequency relationships with speed, which could impact the metabolic energy cost of locomotion.

Many osteological similarities are shared between secretary birds and members of the extinct Phorusrhacidae ("terror birds") [10], which are thought to have also relied on the use of a kick hunting technique. The forces that are transferred from secretary birds to their prey during such hunting kicks, and the potential consequences for overground locomotion, will be of particular interest to scientists looking to reconstruct the feeding mechanisms of terror birds [10]. The findings here challenge the widely held notion that whole-body locomotor behaviors always place the greatest biomechanical demands on the legs, which can influence the assumptions used when reconstructing musculoskeletal biomechanics of extinct species.

ETHICS

Experimental protocols were approved by the Clinical Research and Ethical Review Board at the Royal Veterinary College and by the Hawk Conservancy Trust.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Videos, Supplemental Experimental Procedures, Supplemental References and one Figure, and can be found with this article online at xxxxx.

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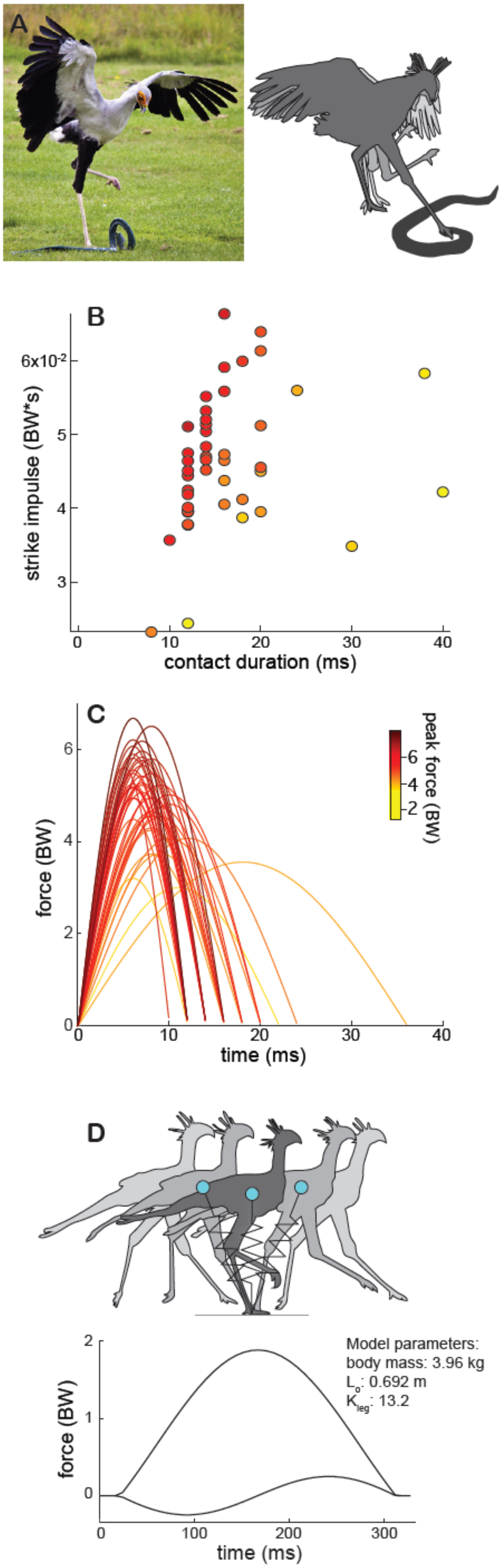
FIGURE LEGEND

(**A**) Madeleine, a 24-year old secretary bird (3.96 kg, 69.2 cm hip height) kept at The Hawk Conservancy Trust (Hants) for 23 years and trained to aggressively strike a rubber snake for public exhibition displays (Movie S1) (Photo credit: Jason Shallcross). (**B**) Strike force impulse and contact duration were measured from 45 individual kicks in 14 trials measured over 2 recording days. (**C**) Peak forces, estimated by fitting a half-sine to data in (B), averaged 5.1±0.9 bodyweights (195 ± 34 N, mean±s.d.) (see Figure S1 and Supplementary Methods). (**D**) We modelled running dynamics and ground reaction forces using a spring-loaded inverted pendulum model, using the birds body mass, leg length and representative measurements of running gait (see Supplementary Methods). Leg stiffness and initial conditions (velocity, body height and leg contact angle) of the model were optimized to match the measured running velocity, stride period and duty factor. The model-predicted peak forces and leg stiffness during running are unexceptional and comparable to those observed in ground birds [4].


A
B
6x10-2
5
4
3
strike impulse (BW*s)
0
10
20
30
40
contact duration (ms)
C
6
4
2
0
force (BW)
time (ms)
peak force (BW)
D
2
1
0
force (BW)
0
100
200
300
time (ms)
Model parameters:
body mass: 3.96 kg
Lo: 0.692 m
Kleg: 13.2