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). Madeleine's mass was 3.96 kg, with a standing hip height of 69.2 cm. Unlike most raptors, secretary birds do not exhibit sexual dimorphism, and this body mass is near the average of secretary birds measured in the field in South Africa (Supplemental information).

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). We used an optimisation algorithm to generate a simulated running gait matching the measured gait kinematics. The model simulation yielded an estimate of effective leg stiffness, peak forces and force impulses typical of overground locomotion for the secretary bird (Figure 1D, see Supplemental information). 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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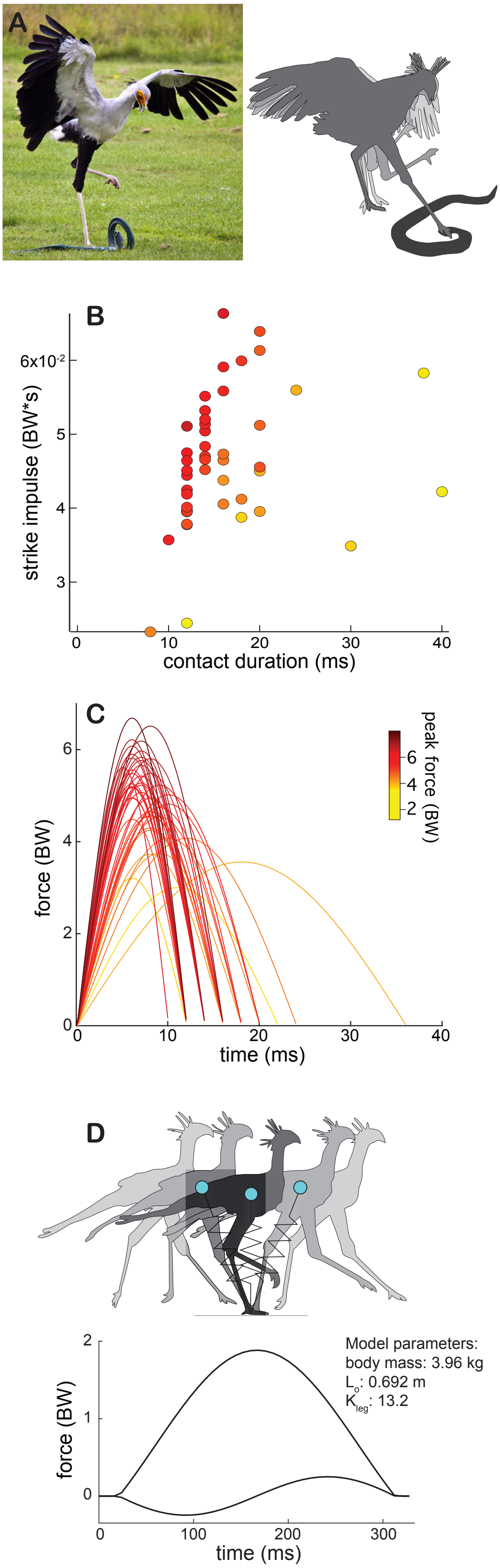
FIGURE LEGEND

(**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
peak force (BW)
6
4
2
force (BW)
0
time (ms)
D
Model parameters:
body mass: 3.96 kg
Lo: 0.692 m
Kleg: 13.2
force (BW)
100
200
300
time (ms)

Supplementary Information: The fast and forceful kicking strikes of snake-hunting Secretary Birds (*Sagittarius serpentarius*)

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Supplemental Materials and Methods

We recorded kicking strikes from Madeleine, a 24-year old male secretary bird (3.9 kg, 69.2 cm hip height) held in the collection at The Hawk Conservancy for 23 years. The average mass of 26 unsexed secretary birds measured in the field in South Africa was 4.02 kg. The range from this study was 2.8 – 5 kg [1]. Unlike most raptors, secretary birds do not exhibit sexual dimorphism. Madeleine's body mass falls comfortably within the published mass ranges. Madeleine had previously been trained to aggressively strike a fake rubber snake for public exhibition displays (SI Video 1). Our experimental procedure was constrained by the need to minimise disruption to Madeleine's daily performance schedule while collecting behaviour representative of the bird's typical kicking strike biomechanics. While Madeleine was in the performance arena, we camouflaged a portable force plate (Kistler, 9286 model, 600 x 400 mm, 500 Hz sampling frequency) under a fitted rectangle of artificial turf within the bird's home enclosure. The force plate was synchronised with a high-speed camera (AOS S-PRI) positioned outside the enclosure, also recording at 500 Hz. This set-up allowed data collection with minimal disruption to the bird's daily routine and trained behaviour. Upon returning to the pen following a public performance, Madeleine was encouraged to strike the rubber snake positioned on top of the force plate. The force plate and cameras were triggered once the bird initiated a series of kick attacks. We analysed 45 individual kicking strikes from 14 trials, recorded on two separate days (November 2014, June 2015).

The exceptionally short duration of ground contact of kicking strikes led to considerable ‘ringing’ vibrations in the force plate signals, simultaneously with applied foot strike impulse, therefore limiting the reliability of peak force measures taken directly from the force plate recordings (Figure S1 A). However, integration of total ground reaction force over short time durations to calculate the impulse of the strike yields a reliable signal that is less sensitive to this issue, because the ringing results in zero net impulse when integrated over time (Figure S1 B). As shown in Figure S1 B, the strike impulse occurs over a short time period, associated with a rapid increase in slope of the integrated force curve. Between strikes, the integrated force trace settles to a steady plateau, showing that integration error due to baseline drift of the force plates is small over the time period of several kicking strikes. In this case, the magnitude of the measured strike impulse is relatively insensitive to the precise period of integration used.

We therefore calculated the strike impulse magnitude by integrating the ground reaction force over the duration of the foot strike. The ‘x’ markers in Figure S1 B indicate the time period over which the force was integrated for a single strike, and the resulting impulse magnitude is shown in red. The time period of strike was determined using two methods, 1) directly from the force impulse traces (Figure S1 B) and 2) from the synchronized high-speed video. From the force impulse traces (Figure S1 B), we measured the strike duration as the time period between the sharp increase in slope of the force impulse trace (1st ‘x’), to the first time the impulse trace crosses the value of the next plateau (2^{nd} ‘x’). From the high-speed video, we determined the strike duration based on period of visible foot contact against the force plate. In comparing these two methods, the absolute difference between them averaged ± 2.8ms. This is within the expected error of the synchronized camera and force sampling rate of 500 Hz, because events can occur between samples, and therefore cannot be resolved to better than the sampling frequency. Consequently, the expected error for strike duration is ± 4 ms, corresponding to ± 2 ms each (1 sample period) for foot contact onset and offset, respectively.

Although directly measured peak forces were not reliable due to force plate ringing, they can be estimated from the measured impulse magnitude and strike duration, assuming that the force trajectory approximated a half-sine wave, starting and ending at zero force. We fitted a cosine wave to each measured impulse (Figure S1 C, n = 45 strikes), and took the derivative of the fitted impulse to estimate the force trajectory of the strike assuming it follows a half-sine wave (Figure 1C, main text). Peak force was taken as the peak magnitude of the fitted force trace. We also calculated mean force of kicking strikes by dividing the impulse magnitude by the strike duration, which is equivalent to fitting a constant slope to the impulse curve. This allowed our methods to be confirmed against recordings of walking and standing, which yielded mean force values of 1BW, as expected.

Due to limited time and space available for force plate data collection, we did not attempt to collect ground reaction force recordings of overground running. Such measurements would have required a large number of trials to collect strides in which the bird successfully ran directly over the hidden force plate. Nonetheless, we were able to obtain representative measures of overground running velocity and gait timing parameters from a video recording of Madeleine in the larger performance arena. Running gait parameters were obtained from a YouTube™ video [2] of Madeleine moving in the larger lawn-based public performance arena. Video data were digitised using a custom-made Matlab programme (R2015a, Mathworks), during segments of the video in which Madeleine was viewed from the side moving in a straight line.

Digitised data were scaled based on the known morphological characteristics of Madeleine's legs. These data were not sufficient for detailed kinematic analysis of limb and joint motions, but were adequate to provide basic gait measurements including average forward velocity, body height, stride period, stance period, duty factor (the ratio of stance period to stride period), the leg angle swept during stance and the leg angular velocity during stance. A spring-loaded-inverted pendulum model [3,4] was generated to match Madeleine's measured body mass, leg length and running gait measures. Three strides were measured from the video, selected because they exhibited aerial running (duty factor < 0.5) and occurred in a relatively straight line in a side view. These strides were found to have an average forward velocity of $1.82 \pm 0.09 ms^{-1}$, which corresponds to a relative velocity (square root Froude) of 0.70 ± 0.04. In simulation, we varied the model leg stiffness, leg contact angle and the initial conditions (body height and forward velocity at apex) using the function 'fminsearch' in Matlab to generate an optimised simulation fit to the measured gait. The objective function used in the optimisation penalised deviations between measured and simulated average forward velocity, stride period and duty factor. This optimisation resulted in a simulated running stride cycle that matched the observed measurements of Madeleine's gait, yielding an estimate of the effective leg stiffness, peak forces and force impulses typical of overground locomotion (Figure 1 D).

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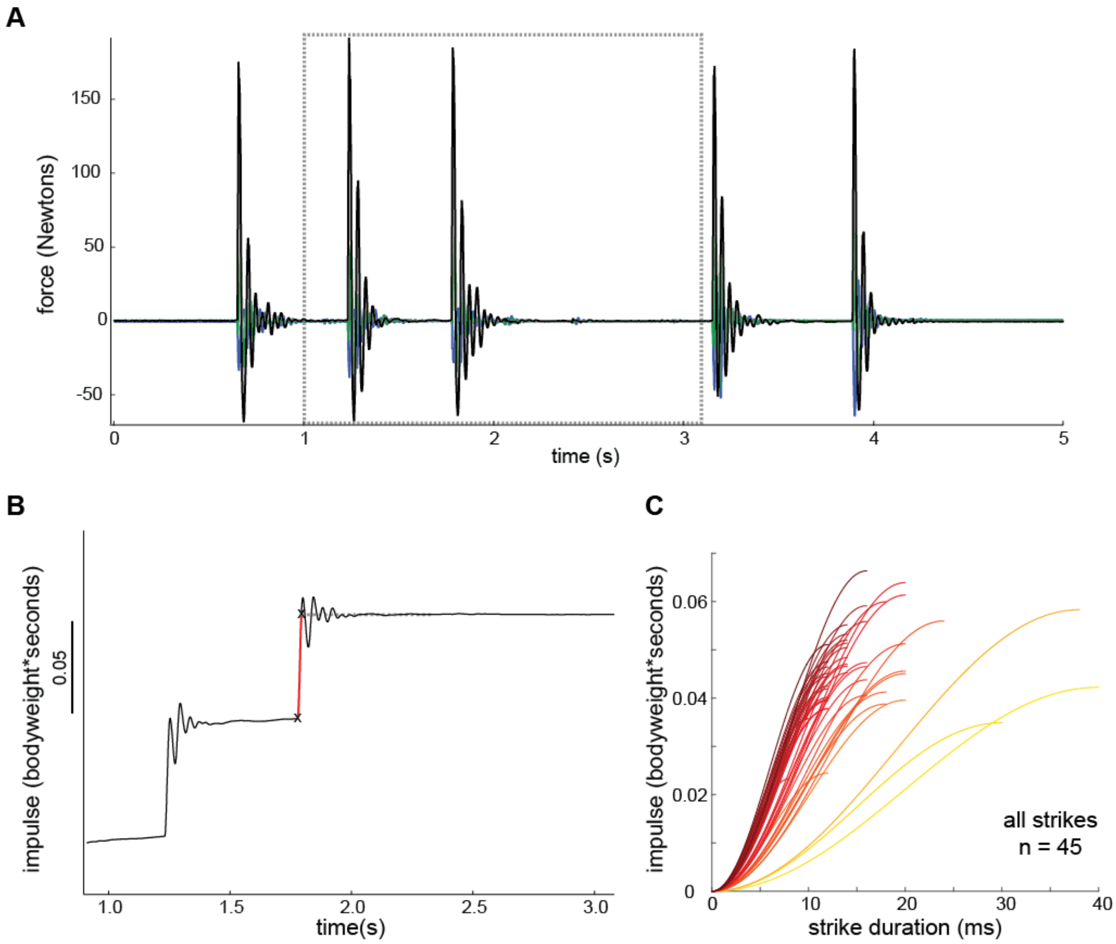

SUPPLEMENTARY FIGURE LEGEND

Supplementary Figure 1

A) Example force plate measures of kicking strikes of secretary bird, shown from a single representative trial. **B)** Integrated total force impulse (black trace) over a subset of the force data shown above (dashed grey box in A), illustrating the impulse magnitude measured for an individual kicking strike (red trace) taken as the force integral over the time period indicated by ‘x’. The onset of foot strike, indicated by the 1st ‘x’, was determined from the sharp increase in slope of the impulse trace, and the end of foot strike, the 2nd ‘x’, was taken as the first time the impulse trace crossed the subsequent plateau value indicated by the horizontal dashed line. Strike durations determined from the impulse trace were found to be agree to within 2.8 ms of durations determined by visible foot contact in the high speed video (see text) **C)** A cosine function was fitted to all measured foot strike impulses (n = 45), matching the measured impulse magnitude (y-axis) and strike duration (x-axis). We took the time-derivative of the fitted impulse in C to estimate the force trajectory and peak force of each strike, assuming it followed a half-sine wave (Figure 1 C, main text).

SUPPLEMENTARY MOVIE 1

High-speed camera (AOS S-PRI, 500 Hz) footage of male secretary bird kicking rubber snake.

AUTHOR CONTRIBUTIONS

Conceptualization, S.J.P. and M.A.D.; Methodology, S.J.P, C.P.M., E.L.S. and M.A.D.; Formal Analysis, M.A.D.; Resources, C.P.M and M.A.D.; Writing - Original Draft, S.J.P. and M.A.D.; Writing - Review and Editing, S.J.P, C.P.M., E.L.S. and M.A.D.