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Terrestrial locomotion of the Svalbard rock ptarmigan: comparing field and laboratory treadmill studies

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Research into the terrestrial locomotion of birds is often based upon laboratory treadmill experiments. However, it is unclear how transposable these results are for birds moving in the wild. Here, using video recordings, we compared the kinematics of locomotion (stride frequency, stride length, stance phase, swing phase, duty factor) and speed range of Svalbard rock ptarmigan (*Lagopus muta hyperborea*) under field and laboratory treadmill conditions. Our findings indicate that the kinematics of walking and aerial running are conserved when moving on the treadmill and in the field. Differences, however, were found when grounded running under the two conditions, linked to substrate. Substrate effects were confirmed by analysing trials only moving over very hard snow. In line with laboratory treadmill energetic predictions, wild ptarmigan have a preferred speed during walking and to a lesser extent when aerial running but not when moving with a grounded running gait. The birds were also capable of a higher top speed in the field than that observed during treadmill studies. Our findings demonstrate that laboratory treadmill research provides meaningful information relevant to wild birds while highlighting the importance of understanding the substrate the animals are moving over.

Animals may be defined by the way they move around and are often capable of multiple forms of locomotion¹. For example, although most birds can fly, many species during key times of the year, and for such vital processes such as feeding and mating, are dependent on terrestrial locomotion. Research into avian terrestrial locomotion has tended to focus on locomotor energetics and kinematics from treadmill-based studies (see for example^{2–13}). While the treadmill provides a uniform, very hard, rubbery and grippy surface, real world substrates can be anything from grass, mud, loose or firm rocks, snow or ice and combinations thereof. There is comparatively little data from wild free-ranging animals; meaning that information such as speed ranges and gait classifications have yet to be collected under natural conditions⁷. While treadmill studies have facilitated great insight into animal locomotion, they are conducted under idealised conditions^{14,15}. These basic tenants of experimental research allow specific parameters of interest to be manipulated without additional factor(s) confounding results. However, it also means the relevance of these results for an animal moving through a constantly changing landscape needs to be established.

Aside from temperature, wind and light, perhaps the principle difference between laboratory treadmill and field conditions is substrate, which is known to affect locomotion. For example, previous work has shown that moving on a treadmill, as opposed to a natural substrate, can affect the ground reaction forces, causing a reduction in the extension and flexion moments of the foot joint in humans¹⁶. For humans and rats moving on a treadmill there is also an increase in stride frequency concomitant with a decrease in stride length, compared to moving over natural substrates^{16,17}. Substrate differences can also require adjustments in the neuromuscular control of locomotion in order to maintain stability^{18–22}. Interestingly, locomotion over snowy ground has often been chosen to examine the effect of substrate on locomotion. Moving over snow also affects the locomotor behaviour of animals, in terms of the pathway taken over the ground and the speed at which an animal moves^{23–27}.

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Despite the influence of different conditions, a key assumption in all studies into the evolutionary significance of locomotor adaptations is that laboratory treadmill studies reflect what the animals do under natural conditions²⁸.

Research into the congruence between field and laboratory treadmill locomotion data has largely focussed on the effects of substrate on energy expenditure during locomotion in humans, and has found conflicting results. Some studies note differences in kinematics^{16,29–35} and energetics³⁶ while others have found no difference in either of these³⁷. For mammals other than humans, the relatively few studies have focused on Artiodactyls, and have demonstrated that elk and mule deer moving in soft deep snow experience an increase in energy expenditure^{38,39}. In birds there are even fewer studies. Recent work looking at gait transitions in paddock-housed ostriches indicated that the preferred walking speed of these birds was around that predicted to minimise energy expenditure¹⁴. Preliminary attempts to analyse substrate effects on Svalbard ptarmigan locomotion⁴⁰ focused only on grass rather than the natural snowy substrate the birds move over in the wild and did not distinguish between the sexes. Aside from these studies, comparative real-world data from birds moving over natural substrates are lacking. Without this research it is difficult to understand how factors that affect locomotion relate to fitness and therefore place any experimental laboratory treadmill data into an evolutionary context⁷. These data are important because without them it is impossible to determine, for example, what the potential impact might be of environmental change.

Here we examined the locomotor kinematics and self-selecting speed of free-ranging wild, male Svalbard rock ptarmigan (*Lagopus muta hyperborea*) on Spitzbergen, Svalbard. The birds were moving over natural snowy substrates and were compared to existing laboratory treadmill data on the energetics and kinematics of their locomotion^{7,41}. We aim to determine if we can reliably extrapolate from laboratory treadmill data to the field, using the Svalbard ptarmigan as a model species.

Materials and Methods

Study species and data collection. We recorded videos of terrestrial locomotion from wild, free-ranging male *L. muta hyperborea* ($n = 91$) in the Adventdalen valley and adjacent side valleys on Spitzbergen, Svalbard ($78^{\circ}13'18''\text{N}$, $15^{\circ}38'30''\text{E}$), from 22nd April to 4th May 2017 and the 21th April to 7th May 2018. Svalbard ptarmigan were selected for these studies as they are one of the few avian species where a comprehensive laboratory treadmill dataset exists on the kinematics and energetics of their locomotion⁷. During terrestrial locomotion Svalbard ptarmigan move faster by either changing the number of strides they take in a given time or by increasing the length of each stride, or both. These birds are ideal for locomotor studies as they can make use of up to three terrestrial gaits: walking (where one foot is in contact with the ground at all times), aerial running (where both feet are off the ground) and grounded running (a transitional gait with intermediate characteristics of walking and aerial running). During spring the ground is snow covered, the midnight sun was already present and birds were at their summer weight⁴². Only males, identified from their calls and secondary sexual characteristics (red supraorbital combs and eye-stripe) were used to facilitate comparison with existing laboratory treadmill data^{7,41}. Where possible each bird was filmed moving at low and high speed and a total of 165 videos were analysed. Snowmobiles were used to cover the ground between sites. Once a bird was identified it was filmed from a fixed distance moving across level ground at either 25 frames per second (fps) using a SONY[®] Handycam HDR-XR250 (SONY[®] Corporation, Japan) during the 2017 season, or at 100 fps using a SONY[®] Cyber-shot RX10-III camera (SONY[®] Corporation, Japan) during the 2018 season. While filming the camera was maintained in a fixed position at the same height and parallel to the moving bird. After the bird had been filmed a 1 metre scale bar was then placed along the track way of the animal to calculate speed (U). Stride frequency (f_{stride}) and stride length (l_{stride}) were calculated for each bird as the average of 3–5 complete strides during which the birds was neither accelerating or decelerating. f_{stride} was obtained by dividing the number of strides by the duration of the video clip and l_{stride} was calculated as U divided by f_{stride} . Data from the 100fps videos were used to measure stance (t_{stance}) and swing (t_{swing}) duration, and duty factor (DF), apart from l_{stride} and f_{stride} . To reduce pseudo replication of data, bird locations were GPS marked and those locations were used only once. Data collection techniques used in the field were refined from preliminary attempts at comparing treadmill locomotion of captive Svalbard rock ptarmigan to birds moving within an outdoor race over grass⁴⁰.

Previous laboratory treadmill-based studies by our group identified that the Svalbard rock ptarmigan use three different terrestrial gaits identified by the phase relationship between E_{hk} (horizontal kinetic energy vector) and $E_{\text{p}} + E_{\text{vk}}$ (the sum of the potential and vertical kinetic energy vectors) of the centre of mass (CoM)⁷. During walking E_{hk} and $E_{\text{p}} + E_{\text{vk}}$ fluctuate out of phase, whilst during grounded and aerial running E_{hk} and $E_{\text{p}} + E_{\text{vk}}$ are in phase⁴³. To confirm gaits across the speed range for wild ptarmigans, we tracked the movement of the CoM of birds to determine E_{hk} and $E_{\text{p}} + E_{\text{vk}}$ from the 100 fps recordings. The location of the CoM was identified relative to known morphological points; by using the points to build a polygon and then using it to estimate the centre of mass. Points used were either the proximal end of the neck or the eyeball of the bird, the proximal end of the tail, and the sternum. Mean body mass estimates were taken from literature values^{41,44}. To further test the influence of substrate on our results we re-ran the analysis having excluded all trials other than those moving over very hard snow. This was done to allow a close to like-for-like substrate comparison between the animals moving in the wild and on a treadmill in the laboratory, with its uniform firm surface. Video analyses were conducted using Tracker[®] v. 5.0.5 (Open Source Physics). Substrate classification over which the birds were moving (electronic Supplementary Material, ESM, Table S1) was conducted during locomotor trials was based the hardness of deposited snow⁴⁵.

Experimental procedures and methods were carried out under ethical approval from the University of Manchester Ethics Committee in accordance with the Animal (Scientific Procedures) Act 1986, covered by Home Office project licence (40/3549).

Gait	Parameter	model		Slope		Intercept	
		Field	Laboratory treadmill	z	p-value	z	p-value
Walk	l_{stride}	$0.142 + 0.204 U$ ($t = 9.287, r^2 = 0.65,$ $n = 48, p < 0.001$)	$0.102 + 0.246 U$ ($t = 5.319, r^2 = 0.96,$ $n = 3, p < 0.001$)	-0.837	0.401	1.362	0.174
	f_{stride}	$1.022 + 2.051 U$ ($t = 10.08, r^2 = 0.69,$ $n = 48, p < 0.001$)	$1.043 + 2.130 U$ ($t = 36.28, r^2 = 0.99,$ $n = 3, p < 0.001$)	-0.372	0.711	-0.149	0.881
	t_{stance}	$-0.679 - 0.720 \log_{10} U$ ($t = -10.97, r^2 = 0.83,$ $n = 26, p < 0.001$)	$-0.646 - 0.623 \log_{10} U$ ($t = -7.368, r^2 = 0.98,$ $n = 3, p = 0.086$)	-1.178	0.238	-1.217	0.222
	t_{swing}	$-0.879 - 0.184 \log_{10} U$ ($t = -2.30, r^2 = 0.18,$ $n = 26, p = 0.031$)	$-0.838 - 0.012 \log_{10} U$ ($t = -0.20, r^2 = 0.03,$ $n = 3, p = 0.88$)	-1.688	0.091	-1.172	0.242
	DF	$0.814 - 0.230 U$ ($t = -6.21, r^2 = 0.62,$ $n = 25, p < 0.001$)	$0.858 - 0.281 U$ ($t = -6.72, r^2 = 0.98,$ $n = 3, p = 0.094$)	0.930	0.352	-1.390	0.165
Grounded running	l_{stride}	$0.260 + 0.088 U$ ($t = 3.74, r^2 = 0.21,$ $n = 56, p < 0.001$)	$0.194 + 0.158 U$ ($t = 7.934, r^2 = 0.95,$ $n = 5, p < 0.01$)	-2.275	< 0.05	—	—
	f_{stride}	$0.979 + 1.925 U$ ($t = 9.55, r^2 = 0.63,$ $n = 56, p < 0.001$)	$1.621 + 1.258 U$ ($t = 5.728, r^2 = 0.92,$ $n = 5, p < 0.05$)	2.238	< 0.05	—	—
	t_{stance}	$-0.707 - 1.021 \log_{10} U$ ($t = -9.91, r^2 = 0.78,$ $n = 30, p < 0.001$)	$-0.656 - 0.955 \log_{10} U$ ($t = -44.49, r^2 = 0.99,$ $n = 5, p < 0.001$)	-0.845	0.593	—	—
	t_{swing}	$-0.833 - 0.392 \log_{10} U$ ($t = -3.53, r^2 = 0.31,$ $n = 30, p < 0.01$)	$-0.796 + 0.00 \log_{10} U$ ($t = 0, r^2 = 0.51,$ $n = 5, p = 0.167$)	-3.529	< 0.001	—	—
	DF	$0.689 - 0.122 U$ ($t = -4.47, r^2 = 0.42,$ $n = 30, p < 0.001$)	$0.734 - 0.164 U$ ($t = -18.18, r^2 = 0.99,$ $n = 5, p < 0.001$)	1.479	0.139	—	—
Aerial Running	l_{stride}	$0.144 + 0.162 U$ ($t = 11.54, r^2 = 0.69,$ $n = 61, p < 0.001$)	$0.247 + 0.131 U$ ($t = 2.484, r^2 = 0.75,$ $n = 4, p = 0.131$)	0.552	0.582	—	—
	f_{stride}	$2.947 + 0.665 U$ ($t = 5.27, r^2 = 0.32,$ $n = 61, p < 0.001$)	$1.788 + 1.078 U$ ($t = 3.12, r^2 = 0.82,$ $n = 4, p = 0.089$)	-1.122	0.263	—	—
	t_{stance}	$-0.83 - 0.469 \log_{10} U$ ($t = -3.41, r^2 = 0.28,$ $n = 32, p < 0.01$)	$-0.698 - 0.723 \log_{10} U$ ($t = -3.32, r^2 = 0.85,$ $n = 4, p = 0.08$)	0.983	0.327	—	—
	t_{swing}	$-0.855 - 0.136 \log_{10} U$ ($t = -1.20, r^2 = 0.04,$ $n = 32, p = 0.24$)	$-0.722 - 0.311 \log_{10} U$ ($t = -1.71, r^2 = 0.59,$ $n = 4, p = 0.23$)	-0.636	0.522	—	—
	DF	$0.54 - 0.042 U$ ($t = -2.084, r^2 = 0.13,$ $n = 32, p = 0.045$)	$0.621 - 0.095 U$ ($t = -1.992, r^2 = 0.67,$ $n = 4, p = 0.185$)	1.02	0.308	—	—

Table 1. Results of the linear regressions of each kinematics parameter against U for each gait and the z-test comparisons of the slope and intercept coefficients. The lines of best fit are also given. Only the intercepts for the walking gaits were compared, because comparison for grounded running and aerial running would require extrapolating the lines of best fit too far beyond the data range rendering their estimates unreliable. Statistical significance is set as $p < 0.05$.

Statistical analyses. To check for potential differences in l_{stride} and f_{stride} between years we performed ANCOVAs for each of the parameters using U as a co-variate. Walking, grounded and aerial running are distinct gaits and were therefore analysed separately in all analyses. All kinematic parameters within each gait were analysed using linear regression. t_{stance} and t_{swing} data (and U for these two parameters) for locomotion in the wild and on a laboratory treadmill were linearized using a \log_{10} transformation prior to analyses. To facilitate comparison between our results for wild and laboratory treadmill datasets, we reanalysed the laboratory treadmill data from our group using linear regression within each gait. Shapiro-Wilks tests were then performed on the residuals of each linear model to ensure the data were normally distributed. Once the linear models were derived two-tailed Z-tests were performed, in order to identify any differences in the slopes of each kinematic parameter between the data from wild ptarmigans and that of the existing laboratory treadmill dataset. Z-tests were used, as they are robust to violations of the assumption of equal variances for two samples. Only the intercepts for the walking gaits were compared, because doing the same for grounded running and aerial running would be extrapolating the lines of best fit too far beyond the data range rendering their estimates unreliable. All statistical analyses were conducted in R v.3.4.3⁴⁶ and results are summarized in Tables 1 and S2.

Ethics. This project was conducted under ethical approval from the University of Manchester Animal Ethics Committee and a permit from the Governor of Svalbard Research in Svalbard (RiS Project No 10790).

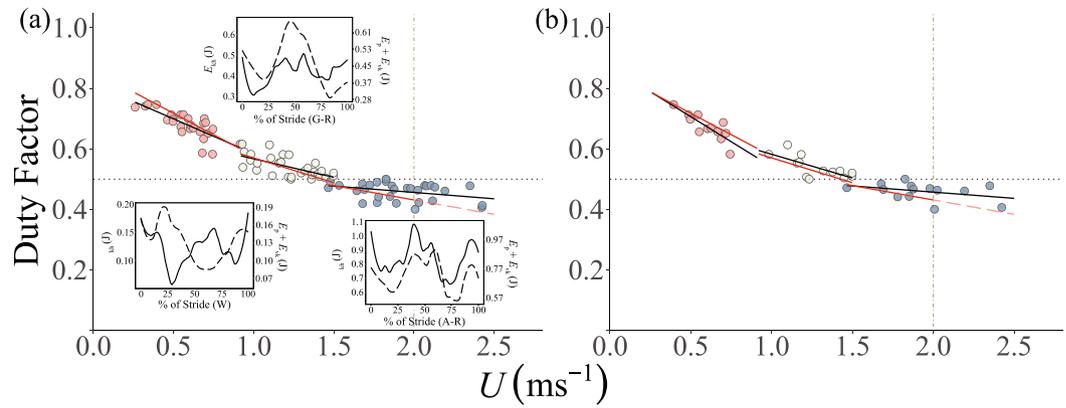


Figure 1. Duty Factor (DF) plotted against speed (U) for walking (red), grounded running (white) and aerial running (blue) gaits. **(a)** Includes data points for trials over all snow conditions and **(b)** includes data points for ptarmigan exclusively moving over a very hard snow surface only. Inlay figures in **(a)** represent the horizontal kinetic energy $E_{kh}(I)$, and potential plus vertical, $E_p + E_{vk}(I)$ energy plots of fluctuations of in the Centre of Mass (CoM) for each gait from one bird; walking (W), grounded running (G-R), aerial running (A-R). On the inlay figures the solid black line within each box are represent the kinetic energy, whereas the dashed black line represents the potential gravitational energy fluctuations. In the main figure the lines of best fit describing the linear regression for wild ptarmigans freely moving in the field are shown in black. The solid red lines represent the lines of best fit for the laboratory treadmill data. The vertical dashed line denotes the maximum sustainable speed from the treadmill data⁷. To the right of the vertical line at 2.0 ms^{-1} , the red line becomes dashed to denote projected speed beyond that sustainable in the laboratory. The horizontal dotted line represents the threshold duty factor of 0.5.

Results

Gait analysis. No significant differences were found for l_{stride} and f_{stride} when comparing data across 2017 and 2018 (Table S3), allowing these datasets to be combined. Walking, grounded and aerial running gaits were confirmed from field data. When the fluctuations of E_{hk} and $E_{vh} + E_p$ were out of phase the birds were walking and suggested a pendular mechanism of energy recovery⁴³, that extended from 0.26 ms^{-1} to 0.91 ms^{-1} (Fig. 1a). Grounded and aerial running gaits were identified from 0.92 ms^{-1} to 2.76 ms^{-1} , where the fluctuations between E_{hk} and $E_{vh} + E_p$ were synchronized and energy recoveries occur by means other than kinetic energy to gravitational energy transfer⁴³. DF was then used to separate grounded running ($DF > 0.5$) and aerial running ($DF \leq 0.5$). The shift between these two gaits occurred at slightly lower speeds than previously suggested⁷ and overlapped between 1.46 ms^{-1} – lowest aerial running speed – and 1.50 ms^{-1} – highest grounded running speed (Fig. 1a).

Walking gait kinematics. l_{stride} and f_{stride} increased linearly with U (Fig. 2a,c, Table 1) for both the field and laboratory treadmill derived measurements. $\log_{10} t_{\text{stance}}$ and $\log_{10} t_{\text{swing}}$ decreased linearly with $\log_{10} U$ and DF with U for the field data (Figs 1a, 2e,g and Table 1). Similar trends are seen in the laboratory treadmill data, although the decrease in t_{swing} , t_{stance} and DF with U was not supported statistically (Figs 1a, 2e,g and Table 1). None of the relationships between the kinematics parameters and U differed (neither intercepts nor slopes) between the field and laboratory treadmill data (Table 1). Birds used walking gaits in 48 trials, from which 25 (52%) were over very hard snow.

Grounded running gait kinematics. l_{stride} and f_{stride} increased linearly with U for both field and laboratory treadmill measurements (Fig. 2a,c, Table 1). The incremental increase in l_{stride} with U , however, was greater in the laboratory treadmill data than in the field data (Table 1). In contrast, the incremental increase in f_{stride} , was less in the laboratory treadmill data than in the field data. $\log_{10} t_{\text{stance}}$ decreased linearly with $\log_{10} U$ and at a similar rate in both data sets (Fig. 2e, Table 1). $\log_{10} t_{\text{swing}}$ decreased linearly with $\log_{10} U$ in the field data, but was not affected by U in the laboratory treadmill data (Fig. 2g, Table 1). The linear decrease in DF with increasing U was similar in both field and laboratory treadmill data (Fig. 1a, Table 1). A grounded running gait was used in 56 trials, from which 23 (41%) were over very hard snow

Aerial running gait kinematics. l_{stride} and f_{stride} increased with U in the field and laboratory treadmill data although these trends were not statistically significant in the latter (Fig. 1a). $\log_{10} t_{\text{stance}}$ decreased linearly with $\log_{10} U$ in the field and a similar trend ($p = 0.08$) was seen in the laboratory treadmill data sets (Fig. 2e). $\log_{10} t_{\text{swing}}$ did not change with $\log_{10} U$ in either field or laboratory treadmill data sets (Fig. 2g). DF decreased linearly with U . For all the kinematic parameters, the relationship with U did not differ between field and laboratory treadmill data (Fig. 1a, Table 1). Aerial running was used in 61 trials, of which 24 (39%) were over very hard snow. There were no aerial running trials over soft or medium snow.

Like for like comparison of kinematics over very hard snow. When only data for birds moving over very hard snow were analysed no differences were detected in the laboratory treadmill and field data kinematics for each specific gait (Figs 1b, 2b,d,f,h and Table S2).

Self-selected speeds. Counts (binned into arbitrary 0.07 ms^{-1} increments) were used to determine the frequency with which each speed was selected and a density bandwidth plot (right axis) was added in order to visualize the speed distribution for ptarmigan within each gait (Fig. S1). The density bandwidth was automatically estimated using the ggplot2 package for R. Ptarmigan in the field used a range of U from 0.26 – 2.76 ms^{-1} . Probability density estimations (Fig. S1), however, suggest that walking at around 0.7 ms^{-1} and to a lesser extent aerial running around 1.7 – 1.85 ms^{-1} was preferred. Generally, the birds infrequently moved at very slow (0.1 – 0.4 ms^{-1}) and very high ($>2.1 \text{ ms}^{-1}$) speeds. There was no obvious preferred speed within the grounded running gait (Fig. S1).

Discussion

It is imperative to our understanding of animal locomotion that we can be confident that locomotion data collected from laboratory treadmill studies is representative of natural movement in the field⁴⁰. These results provide new insight into the congruence between field and laboratory treadmill data. Our findings show that the kinematics of locomotion in the Svalbard ptarmigan when walking and aerial running are conserved across laboratory treadmill and field datasets where the birds were moving over snow. These findings intuitively make sense as both walking and aerial running have clear evolutionary relevance. Birds use a walking gait when foraging for immobile food objects and general exploration⁷, while aerial running functions in predator escape and facilitates the economic movement over large distances^{7,10,47,48}. The birds in the current study utilised walking gaits over a range of substrates from soft, powdered snow to mixed and harder snow as they were commuting between feeding sites, most often tending to use the relatively faster walking speeds which are the most energetically efficient⁷. Optimal foraging theory suggests that foraging decisions (like how and where to move) are made to maximise fitness-related currencies based on combinations of the energy and time to be expended^{49,50}. In other words natural selection should favour animals that forage the most efficiently⁵¹.

Svalbard ptarmigan feed by pecking at the ground, scratching away the snow with their feet to uncover vegetation as they move around, primarily selecting feeding sites that are loosely covered in snow. Selecting a relatively fast walking gait when foraging is the most efficient means for the Svalbard ptarmigan to commute between sites while still being able to identify and access food sites, as found in other species of birds⁵². Moving slowly can also negate the negative effects of moving through a substrate that might otherwise result in an increase in the energetic cost of movement⁵³. Conversely, we found the birds used aerial running gaits exclusively on firmer snow suggesting that the bouncing mechanism, linked to elastic energy recovery during the stance phase when running^{54,55}, only functions when moving over firm ground. Other animals, for example many mesopredators, in snowy conditions also demonstrate a preference for moving over shallow compressed snow either to minimize energy expenditure^{23–27} or simply to travel faster²⁶. A softer substrate would absorb some or (all) of the kinetic and potential energy during the stance phase reducing the elastic energy available for the next stride⁵⁵. Other links between the type of substrate and locomotor gait have previously been noted with slow speed walking linked to softer snow and higher speed running on hard snow in humans⁵⁶. The selection of gaits depending on substrate correlates with increases in energy expenditure which relate to the depth of footprints or trackways^{23–27,38,56–58}.

Interestingly, differences in kinematics were found when the birds were moving with a grounded running gait in the field compared to the laboratory treadmill data, when all snow types were considered. Ptarmigan moving with a grounded running gait in the wild took faster, smaller steps for the same speed range as laboratory treadmill studies. Grounded running is an intriguing gait as it links duty factors over 0.5 with running-like energy fluctuations in the centre of mass⁵⁹. Grounded running is associated with more compliant limbs and improves visual stability through better control of head movements⁴⁷ and reduces the mechanical work of the bouncing non-locomotor body tissues²¹. It has also been suggested that grounded running keeps the centre of mass low and facilitates the execution of fast turns that results from keeping one foot in contact with the ground at all times^{5,21}. The birds in the current study were moving over a variable hardness snowy/icy substrate where stability will be paramount, particularly when the birds want to increase their speed, but are prevented from moving into an aerial running gait by the substrate being too compliant. By taking more frequent and shorter steps whilst keeping their centre of mass lower by selecting a grounded running gait, the birds would be able to effectively improve stability over slippery snow or ice⁶⁰, while also increasing speed above walking range. Maintaining the centre of mass closer to the vertical plane of the contact foot improves the chance of correcting a slide on ice, something that is not an issue on the uniform rubberised substrate of a treadmill. The notion that substrate is important when considering locomotor kinematics was supported when only data for the birds grounded running over very hard snow were analysed. Very hard snow is the substrate that is as close as possible to enable a like-for-like comparison with the laboratory treadmill experiments. Examining data when the birds were moving only over very hard snow eliminated the kinematics differences found during the grounded running gait, whilst maintaining the finding of no differences between laboratory treadmill and field kinematics for walking and aerial running.

Svalbard rock ptarmigan were the first avian species for which a demonstrable decrease in the energetic cost of locomotion was found upon the switch to a high-speed aerial running gait⁷. Maximum running speed is important to the overall fitness of an animal, although it is not always the case that simply moving away the fastest is the best way to avoid predation²⁸. The current study also expands the range of speed these birds can aerial run at, from the previously reported 2 ms^{-1} in the laboratory treadmill study to 2.76 ms^{-1} for birds moving in the wild, a 1.4 -fold increase. Similar results have been reported for other species, for example ostriches have a 1.5 -fold greater speed in the wild than on the treadmill^{14,61}. These findings aren't limited to birds, as the maximum running speed in humans and other mammals ranged from 1.7 to 2.6 -fold higher when freely moving^{62,63}. The

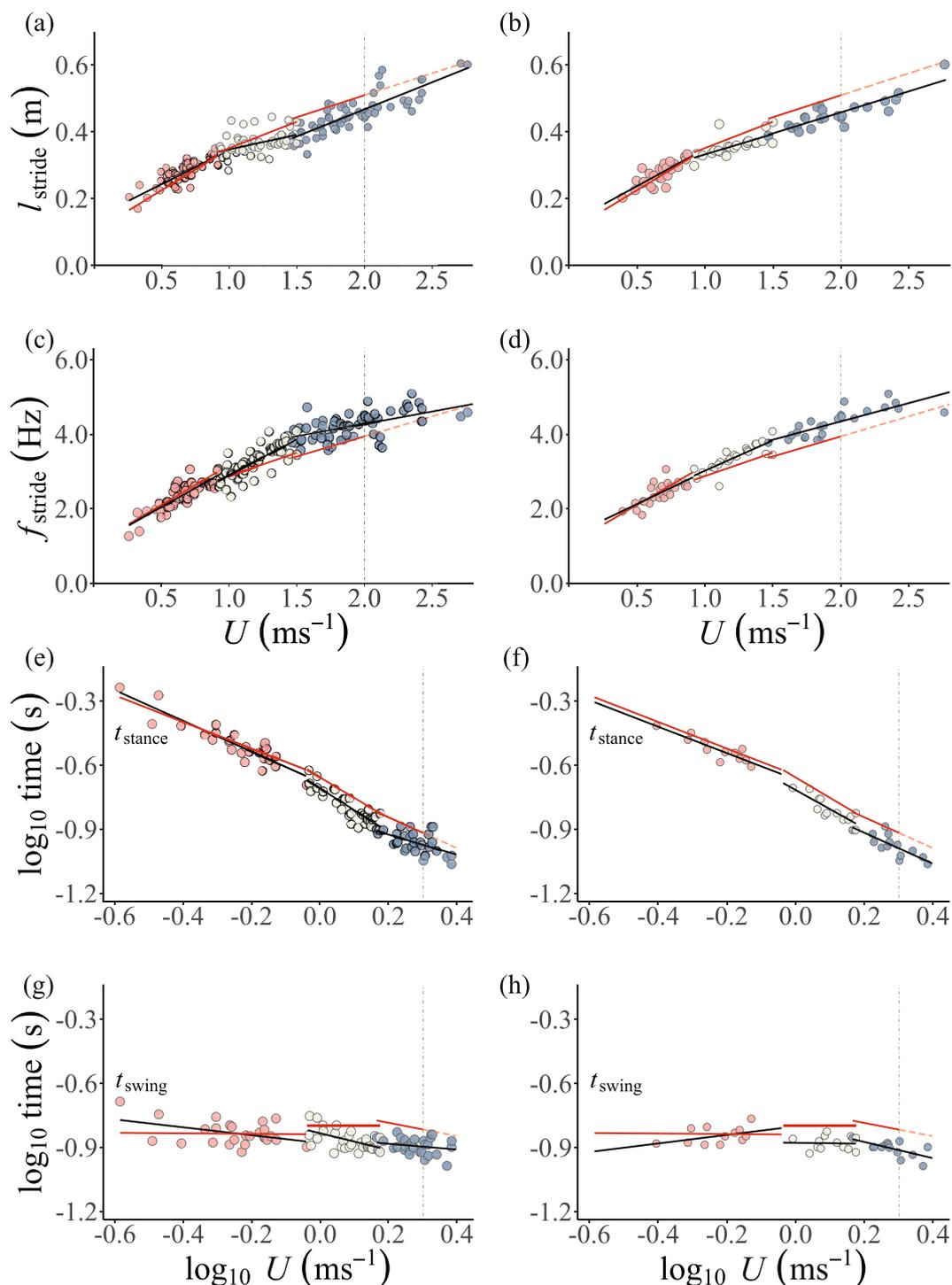


Figure 2. Kinematic parameters plotted against U for each gait - (a,b) l_{stride} against U ; (c,d) f_{stride} against U ; (e,f) $\log_{10} t_{\text{stance}}$ against $\log_{10} U$; and (g,h) $\log_{10} t_{\text{swing}}$ against $\log_{10} U$. The left panels (a,c,e,g) represent data points for the trials over all snow conditions. The right panels represent data points for ptarmigan exclusively moving over very hard surfaces to facilitate like-for-like substrate comparisons between field and laboratory treadmill datasets. Walking, ground running and aerial running gaits are denoted by the red, white and blue circles, respectively. The lines of best fit describing the linear regression for wild ptarmigans are shown in black. The red lines represent the lines of best fit for the laboratory treadmill data. The vertical dashed line denotes the maximum sustainable speed recorded in the laboratory treadmill experiments⁷. To the right of the vertical line at 2.0 ms^{-1} , the red line becomes dashed to denote projected speed beyond that sustainable in the laboratory.

treadmill underestimates top speed because these studies are principally investigating the metabolic cost of locomotion as speed increases, meaning speeds must be maintained for long enough (often 5–10 minutes) to allow stabilisation of respiratory gas measurements.

Very slow speeds (which are the most energetically expensive way to move⁷) and very high speeds (which are not aerobically sustainable for a long period of time⁷) are rarely selected by the Svalbard rock ptarmigan in the wild. The distribution of speeds in the current study indicates that the ptarmigan are making decisions linked to minimising the metabolic cost of locomotion when self-selecting speeds underpinned by the substrate they are moving over. A similar pattern has been found in other cursorial birds, where they select a narrow band of energetically optimal speeds^{14,64}, a trend also found in horses⁶⁵. The maximum attainable top speeds are likely selected as an escape strategy to move as far away as quickly as possible over a short distance rather than for sustained locomotion. Our results suggest that when conducting treadmill experiments examining animal locomotion it would be beneficial to film up to the maximum obtainable speed even if this cannot be sustained as the kinematics could then be compared to wild animals.

Conclusion

The kinematics of locomotion are conserved across walking and aerial running gaits when Svalbard rock ptarmigan are moving under laboratory treadmill or field conditions. Walking is unaffected as moving slow negates the influence of substrate on gait while aerial running is unaffected as the birds can only use this gait over firmer ground mimicking treadmill locomotion. However, on uneven slippery ground when they want to go faster the birds must use a grounded running gait and an icy snowy substrate requires faster, shorter steps when doing this (as found for a range of animals⁶⁶) compared to moving on a treadmill in order to maintain stability. This treadmill versus field difference disappears, however, when only field data from very hard snow conditions is considered (i.e., when differences in substrate are, as far as possible, removed). Currently the feedback mechanism the animal relies on for identifying a given substrate to move on is unknown. Two options appear possible, either that the birds rely on real time information feedback from moving over the substrate (such as substrate hardness or slipperiness) that influences gait choice and subsequent speed, or that they are able to assess substrate properties in some way, perhaps through visual inspection. However, this remains to be determined. Investigations into diurnal and seasonal time activity budgets of gait selection for the birds, likely through bio-logging (see for example e.g.^{14,67,68}) would provide information of great interest towards better understanding the evolutionary significance of gait selection and the influence of substrates in the wild and contribute toward building an accurate picture of the energy budgets of wild animals and how this relates to laboratory treadmill based studies.

Data Availability

All data supporting this article are provided either in the text or as part of the ESM files available through Figshare.

References

1. Tickle, P. G., Ennos, A. R., Lennox, L. E., Perry, S. F. & Codd, J. R. Functional significance of the uncinate processes in birds. *J. Exp. Biol.* **210**, 3955, <https://doi.org/10.1242/jeb.008953> (2007).
2. Taylor, C. R., Heglund, N. C. & Maloij, G. M. Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 1 (1982).
3. Heglund, N. C. & Taylor, C. R. Speed, stride frequency and energy cost per stride: how do they change with body size and gait? *J. Exp. Biol.* **138**, 301–318 (1988).
4. Kram, R. & Taylor, C. R. Energetics of running: a new perspective. *Nature* **346**, 265–267, <https://doi.org/10.1038/346265a0> (1990).
5. Gatesy, S. M. & Biewener, A. A. Bipedal locomotion: effects of speed, size and limb posture in birds and humans. *J. Zool.* **224**, 127–147, <https://doi.org/10.1111/j.1469-7998.1991.tb04794.x> (1991).
6. Ellerby, D. J., Henry, H. T., Carr, J. A., Buchanan, C. I. & Marsh, R. L. Blood flow in Guinea fowl *Numida meleagris* as an indicator of energy expenditure by individual muscles during walking and running. *J. Physiol.* **564**, 631–648, <https://doi.org/10.1113/jphysiol.2005.082974> (2005).
7. Nudds, R. L. *et al.* Evidence for energy savings from aerial running in the Svalbard rock ptarmigan (*Lagopus muta hyperborea*). *Proc. R. Soc. B* **278**, 2654–2661, <https://doi.org/10.1098/rspb.2010.2742> (2011).
8. Reilly, S. M. Locomotion in the quail (*Coturnix japonica*): the kinematics of walking and increasing speed. *J. Morphol.* **243**, 173–185, [10.1002/\(SICI\)1097-4687\(200002\)243:2<173::AID-JMOR6>3.0.CO;2-E](https://doi.org/10.1002/(SICI)1097-4687(200002)243:2<173::AID-JMOR6>3.0.CO;2-E) (2000).
9. Nyakatura, J. A., Andrada, E., Grimm, N., Weise, H. & Fischer, M. S. Kinematics and Center of Mass Mechanics During Terrestrial Locomotion in Northern Lapwings (*Vanellus vanellus*, Charadriiformes). *J. Exp. Zool. A. Ecol. Genet. Physiol.* **317**, 580–594, <https://doi.org/10.1002/jez.1750> (2012).
10. Rubenson, J., Heliam, D. B., Lloyd, D. G. & Fournier, P. A. Gait selection in the ostrich: mechanical and metabolic characteristics of walking and running with and without an aerial phase. *Proc. R. Soc. Lond. Ser. B: Biol. Sci.* **271**, 1091–1099, <https://doi.org/10.1098/rspb.2004.2702> (2004).
11. Provini, P., Goupil, P., Hugel, V. & Abourachid, A. Walking, Paddling, Waddling: 3D Kinematics Anatidae Locomotion (*Callonetta leucophrys*). *J. Exp. Zool. A. Ecol. Genet. Physiol.* **317**, 275–282, <https://doi.org/10.1002/jez.1721> (2012).
12. Stoessel, A. & Fischer, M. S. Comparative intralimb coordination in avian bipedal locomotion. *J. Exp. Biol.* **215**, 4055, <https://doi.org/10.1242/jeb.070458> (2012).
13. Fischer, M. S., Schilling, N., Schmidt, M., Haarhaus, D. & Witte, H. Basic limb kinematics of small therian mammals. *J. Exp. Biol.* **205**, 1315 (2002).
14. Daley, M. A., Channon, A. J., Nolan, G. S. & Hall, J. Preferred gait and walk–run transition speeds in ostriches measured using GPS-IMU sensors. *J. Exp. Biol.* **219**, 3301–3308, <https://doi.org/10.1242/jeb.142588> (2016).
15. Höfling, E., Abourachid, A. & Renous, S. Locomotion behavior of the Lettered Aracari (*Pteroglossus incriptus*) (RAMPHASTIDAE). *Ornitol. Neotrop.* **17**, 363–371 (2006).
16. Riley, P. O. *et al.* A kinematics and kinetic comparison of overground and treadmill running. *Med. Sci. Sports Exerc.* **40**, 1093–1100, <https://doi.org/10.1249/mss.0b013e3181677530> (2008).
17. Herbin, M., Hackert, R., Gasc, J.-P. & Renous, S. Gait parameters of treadmill versus overground locomotion in mouse. *Behav. Brain Res.* **181**, 173–179, <https://doi.org/10.1016/j.bbr.2007.04.001> (2007).
18. Daley, M. A. & Biewener, A. A. Running over rough terrain reveals limb control for intrinsic stability. *Proc. Natl. Acad. Sci. USA* **103**, 15681, <https://doi.org/10.1073/pnas.0601473103> (2006).
19. Daley, M. A., Usherwood, J. R., Felix, G. & Biewener, A. A. Running over rough terrain: guinea fowl maintain dynamic stability despite a large unexpected change in substrate height. *J. Exp. Biol.* **209**, 171, <https://doi.org/10.1242/jeb.01986> (2006).

20. Daley, M. A. & Biewener, A. A. Leg muscles that mediate stability: mechanics and control of two distal extensor muscles during obstacle negotiation in the guinea fowl. *Philos. Trans. R. Soc. Lond., Ser. B: Biol. Sci.* **366**, 1580–1591, <https://doi.org/10.1098/rstb.2010.0338> (2011).
21. Daley, M. A. & Usherwood, J. R. Two explanations for the compliant running paradox: reduced work of bouncing viscera and increased stability in uneven terrain. *Biol. Lett.* **6**, 418–421, <https://doi.org/10.1098/rsbl.2010.0175> (2010).
22. Voloshina, A. S., Kuo, A. D., Daley, M. A. & Ferris, D. P. Biomechanics and energetics of walking on uneven terrain. *J. Exp. Biol.* **216**, 3963, <https://doi.org/10.1242/jeb.081711> (2013).
23. Dowd, J. L. B., Gese, E. M. & Aubry, L. M. Winter space use of coyotes in high-elevation environments: behavioral adaptations to deep-snow landscapes. *J. Ethol.* **32**, 29–41, <https://doi.org/10.1007/s10164-013-0390-0> (2014).
24. Droghini, A. & Boutin, S. Snow conditions influence grey wolf (*Canis lupus*) travel paths: the effect of human-created linear features. *Can. J. Zool.* **96**, 39–47, <https://doi.org/10.1139/cjz-2017-0041> (2018).
25. Droghini, A. & Boutin, S. The calm during the storm: Snowfall events decrease the movement rates of grey wolves (*Canis lupus*). *PLoS One* **13**, e0205742, <https://doi.org/10.1371/journal.pone.0205742> (2018).
26. Whiteman, J. P. & Buskirk, S. W. Footload influences wildlife use of compacted trails in the snow. *Wildl. Biol.* **19**, 156–164, <https://doi.org/10.2981/12-112> (2013).
27. Murray, D. L. & Boutin, S. The influence of snow on lynx and coyote movements: does morphology affect behavior? *Oecologia* **88**, 463–469, <https://doi.org/10.1007/bf00317707> (1991).
28. Irschick, D. J., Herrel, A., Vanhooydonck, B., Huyghe, K. & Damme, R. V. Locomotor compensation creates a mismatch between laboratory and field estimates of escape speed in lizards: A cautionary tale for performance-to-fitness studies. *Evolution* **59**, 1579–1587, <https://doi.org/10.1111/j.0014-3820.2005.tb01807.x> (2005).
29. Elliott, B. C. & Blanksby, B. A. A cinematographic analysis of overground and treadmill running by males and females. *Med. Sci. Sports* **8**, 84–87 (1976).
30. Nelson, R. C., Dillman, C. J., Lagasse, P. & Bickett, P. Biomechanics of overground versus treadmill running. *Med. Sci. Sports* **4**, 232–240 (1972).
31. Riley, P. O., Paolini, G., Della Croce, U., Paylo, K. W. & Kerrigan, D. C. A kinematic and kinetic comparison of overground and treadmill walking in healthy subjects. *Gait Posture* **26**, 17–24, <https://doi.org/10.1016/j.gaitpost.2006.07.003> (2007).
32. Wank, V., Frick, U. & Schmidbleicher, D. Kinematics and electromyography of lower limb muscles in overground and treadmill running. *Int. J. Sports Med.* **19**, 455–461, <https://doi.org/10.1055/s-2007-971944> (1998).
33. Aaslund, M. K. & Moe-Nilssen, R. Treadmill walking with body weight support: Effect of treadmill, harness and body weight support systems. *Gait Posture* **28**, 303–308, <https://doi.org/10.1016/j.gaitpost.2008.01.011> (2008).
34. Buchner, H. H. F., Savelberg, H. H. C. M., Schamhardt, H. C., Merckens, H. W. & Barneveld, A. Kinematics of treadmill versus overground locomotion in horses. *Vet. Q.* **16**, 87–90, <https://doi.org/10.1080/01652176.1994.9694509> (1994).
35. Marsh, A. P. *et al.* Effect of treadmill and overground walking on function and attitudes in older adults. *Med. Sci. Sports Exerc.* **38**, 1157–1164, <https://doi.org/10.1249/01.mss.0000222844.81638.35> (2006).
36. Daniels, F., Vanderbie, J. H. & Winsman, F. R. Energy cost of treadmill walking compared to road walking. (US Office of the Quartermaster General, Lawrence, Massachusetts, 1953).
37. Bobbert, A. C. Energy expenditure in level and grade walking. *J. Appl. Physiol.* **15**, 1015–1021, <https://doi.org/10.1152/jappl.1960.15.6.1015> (1960).
38. Parker, K. L., Robbins, C. T. & Hanley, T. A. Energy expenditures for locomotion by mule deer and elk. *J. Wildl. Manage.* **48**, 474–488, <https://doi.org/10.2307/3801180> (1984).
39. Fancy, S. G. & White, R. G. Energy expenditures for locomotion by barren-ground caribou. *Can. J. Zool.* **65**, 122–128, <https://doi.org/10.1139/z87-018> (1987).
40. Vik, A. M. *Terrestrial locomotion in the Svalbard ptarmigan (Lagopus muta hyperborea): How does treadmill running compare with running overground?* Master in Biology thesis, University of Tromsø (2013).
41. Lees, J., Nudds, R., Stokkan, K.-A., Folkow, L. & Codd, J. Reduced metabolic cost of locomotion in Svalbard rock ptarmigan (*Lagopus muta hyperborea*) during winter. *PLoS One* **5**, e15490, <https://doi.org/10.1371/journal.pone.0015490> (2010).
42. Mortensen, A., Unander, S., Kolstad, M. & Blix, A. S. Seasonal changes in body composition and crop content of Spitzbergen ptarmigan *Lagopus mutus hyperboreus*. *Ornis Scand.* **14**, 144–148, <https://doi.org/10.2307/3676018> (1983).
43. Cavagna, G. A., Heglund, N. C. & Taylor, C. R. Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **233**, R243–R261, <https://doi.org/10.1152/ajpregu.1977.233.5.R243> (1977).
44. Lees, J. J., Nudds, R. L., Folkow, L. P., Stokkan, K. A. & Codd, J. R. Understanding sex differences in the cost of terrestrial locomotion. *Proc Biol Sci* **279**, 826–832, <https://doi.org/10.1098/rspb.2011.1334> (2012).
45. Fierz, C. *et al.* The international classification for seasonal snow on the ground. (UNESCO, Paris, 2009).
46. R: A language and environment for statistical computing v. 3.4.3 (R Foundation for Statistical Computing, Vienna, Austria, 2017).
47. Hancock, J. A., Stevens, N. J. & Biknevicius, A. R. Whole-body mechanics and kinematics of terrestrial locomotion in the Elegant-crested Tinamou *Eudromia elegans*. *Ibis* **149**, 605–614, <https://doi.org/10.1111/j.1474-919X.2007.00688.x> (2007).
48. Heglund, N. C., Cavagna, G. A. & Taylor, C. R. Energetics and mechanics of terrestrial locomotion III. Energy changes of the centre of mass as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 41–56 (1982).
49. Bautista, L. M., Tinbergen, J. & Kacelnik, A. To walk or to fly? How birds choose among foraging modes. *Proc. Natl. Acad. Sci. USA* **98**, 1089–1094, <https://doi.org/10.1073/pnas.98.3.1089> (2001).
50. Stephens, D. W., Lynch, J. F., Sorensen, A. E. & Gordon, C. Preference and profitability: Theory and experiment. *Am. Nat.* **127**, 533–553 (1986).
51. Lemon, W. C. Fitness consequences of foraging behaviour in the zebra finch. *Nature* **352**, 153–155, <https://doi.org/10.1038/352153a0> (1991).
52. Prop, J. & Loonen, M. J. J. E. Goose flocks and food exploitation: the importance of being first. *Proceedings of the XIX International Ornithological Congress, Ottawa*, 1878–1887 (1989).
53. Halsey, L. G., Tyler, C. J. & Kuliukas, A. V. The energy costs of wading in water. *Biology Open* **3**, 571–574, <https://doi.org/10.1242/bio.20147831> (2014).
54. Cavagna, G. A. & Legramandi, M. A. The bounce of the body in hopping, running and trotting: different machines with the same motor. *Proc. R. Soc. B.* **276**, 4279–4285, <https://doi.org/10.1098/rspb.2009.1317> (2009).
55. Lejeune, T. M., Willems, P. A. & Heglund, N. C. Mechanics and energetics of human locomotion on sand. *J. Exp. Biol.* **201**, 2071–2080 (1998).
56. Heinonex, A. O., Karvones, M. J. & Ruosteenoja, R. The energy expenditure of walking on snow at various depths. *Ergonomics* **2**, 389–394, <https://doi.org/10.1080/00140135908930455> (1959).
57. Pandolf, K. B., Haisman, M. F. & Goldman, R. F. Metabolic energy expenditure and terrain coefficients for walking on snow. *Ergonomics* **19**, 683–690, <https://doi.org/10.1080/00140137608931583> (1976).
58. Pinnington, H. C., Lloyd, D. G., Besier, T. F. & Dawson, B. Kinematic and electromyography analysis of submaximal differences running on a firm surface compared with soft, dry sand. *Eur. J. Appl. Physiol.* **94**, 242–253, <https://doi.org/10.1007/s00421-005-1323-6> (2005).

59. Andrada, E., Rode, C. & Blickhan, R. Grounded running in quails: Simulations indicate benefits of observed fixed aperture angle between legs before touch-down. *J. Theor. Biol.* **335**, 97–107, <https://doi.org/10.1016/j.jtbi.2013.06.031> (2013).
60. Cappellini, G., Ivanenko, Y. P., Dominici, N., Poppele, R. E. & Lacquaniti, F. Motor Patterns During Walking on a Slippery Walkway. *J. Neurophysiol.* **103**, 746–760, <https://doi.org/10.1152/jn.00499.2009> (2009).
61. Fedak, M. A. & Seeherman, H. J. Reappraisal of energetics of locomotion shows identical cost in bipeds and quadrupeds including ostrich and horse. *Nature* **282**, 713–716, <https://doi.org/10.1038/282713a0> (1979).
62. Garland, T. The relation between maximal running speed and body mass in terrestrial mammals. *J. Zool.* **199**, 157–170, <https://doi.org/10.1111/j.1469-7998.1983.tb02087.x> (1983).
63. Weyand, P. G. & Bundle, M. W. Energetics of high-speed running: integrating classical theory and contemporary observations. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **288**, R956–R965, <https://doi.org/10.1152/ajpregu.00628.2004> (2005).
64. Watson, R. R. *et al.* Gait-specific energetics contributes to economical walking and running in emus and ostriches. *Proc. R. Soc. B.* **278**, 2040–2046, <https://doi.org/10.1098/rspb.2010.2022> (2011).
65. Hoyt, D. F. & Taylor, R. C. Gait and the energetics of locomotion in horses. *Nature* **292**, 239–240 (1981).
66. Granatosky Michael, C. *et al.* Inter-stride variability triggers gait transitions in mammals and birds. *Proc. R. Soc. B.* **285**, 20181766, <https://doi.org/10.1098/rspb.2018.1766> (2018).
67. Wilson, A. M. *et al.* Locomotion dynamics of hunting in wild cheetahs. *Nature* **498**, 185–189, <https://doi.org/10.1038/nature12295> (2013).
68. Gómez Laich, A., Wilson, R. P., Gleiss, A. C., Shepard, E. L. C. & Quintana, F. Use of overall dynamic body acceleration for estimating energy expenditure in cormorants. *J. Exp. Mar. Biol. Ecol.* **399**, 151–155, <https://doi.org/10.1016/j.jembe.2011.01.008> (2011).

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Author Contributions

J.C. designed the study with assistance from A.M.-G., R.N., L.F. and J.M. J.C., A.M.-G., R.N. J.M. and L.F. all assisted in collection of field and laboratory data, writing and approval of the final manuscript. A.M.-G. and R.N. analysed the data.

Additional Information

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