CONSTRAINTS ON THE BIOMECHANICS OF LOCOMOTION IN THE SVALBARD ROCK PTARMIGAN (*LAGOPUS MUTA HYPERBOREA*): FIELD AND LABORATORY-BASED APPROACHES

A thesis submitted to the University of Manchester for the degree of Doctor of
Philosophy in the Faculty of Biology, Medicine and Health

2020

Andrés C. Mármol-Guijarro

School of Biological Sciences

Contents

Figures

Abstract of a thesis by Andrés C. Mármol-Guijarro submitted to the University of Manchester for the degree of PhD in the Faculty of Biology, Medicine and Health and entitled 'Constraints on the biomechanics of locomotion in the Svalbard rock ptarmigan (*Lagopus muta hyperborea*): field and laboratory-based approaches'

October 2020

Terrestrial locomotion is crucial for many animals as a way for to travel to find food, avoid predators, and to find mates and therefore is of great relevance to a species overall fitness. Terrestrial locomotion has been extensively studied in birds of varied body sizes on a treadmill where conditions are idealised, providing great insight into animal locomotion. However, conditions in the real-world are variable and often can depart from these idealised laboratory conditions. The main objective of my PhD is to elucidate the biomechanics of locomotion of wild Svalbard rock ptarmigan moving within their natural environment and how this is constrained. Where possible this will be compared with ptarmigan locomotion from treadmill-based laboratory studies.

The Svalbard rock ptarmigan is the only bird that permanently inhabits the Arctic Archipelago of Svalbard year-round. It faces extreme environmental conditions, with temperatures fluctuating below freezing during winter, above 5 degrees in summer and annual cycles of 24hr of total darkness and daylight. Although they can fly, they are predominantly ground-dwelling birds that commute over snowy irregular ground to graze for food. These birds therefore are an excellent model species for investigating locomotor biomechanics in the wild as they experience natural fluctuations that will influence the way they move. A comprehensive dataset exists on the Svalbard rock ptarmigan locomotor biomechanics and energetics while moving on treadmills under laboratory conditions. These existing data make the ptarmigan an ideal model to gain insight into how these animals move in the natural environment compared to during the more idealised laboratory conditions and allow us to examine the effects of sex and substrate in a free-ranging wild animal.

In this thesis I compared the biomechanics of locomotion in the wild and on a treadmill in males and female ptarmigan using video recordings of their locomotor kinematics. I provided evidence that the biomechanics of locomotion in males comparable when moving on the treadmill and in the field for walking and aerial running gaits. The kinematics of grounded running gait, however, are modified to negotiate the snowy substrate. Such modifications, however, are not detected in wild females as grounded running remained similar on treadmills and in the field. I argue that the conserved grounded running biomechanics in females may indicate a postural sexual dimorphism towards a more crouched leg enhancing stability. I also examined the accuracy of using trackways to gain insight into animal movement; using 3D photogrammetry and thin blade force gauge to measure footprint depth and snow supportiveness, I demonstrated that both parameters do affect self-selected speed on ptarmigan males when foot sinking depth do not exceed the intertarsal joint. It remains unclear how the ptarmigan are capable to detect suitable snow patches for locomotion. although they might be detecting visual cues for that purpose. Finally, I assessed the accuracy in predicting speed using trackway stride lengths on a species-specific model and two Froude number-based models. The results suggest that predicted speeds are problematic when if only stride lengths are available and no other additional information of the trackmaker is known.

Altogether, the findings of my thesis highlight the importance that laboratory studies have in providing meaningful transposable information to the locomotion of wild animals, indicating intraspecific variation in the mechanisms for stability in a changeable substrate through kinematic plasticity and leg posture.

Declaration

No portion of the work referred to in this thesis has been submitted in support of an application for another degree or qualification of this or any other university or other institute of learning.

Signed: Date:

Copyright statement

i. The author of this thesis (including any appendices and/or schedules to this thesis) owns certain copyright or related rights in it (the "Copyright") and s/he has given The University of Manchester certain right to use such Copyright, including administrative purposes.

ii. Copies of this thesis, either in full or in extracts and whether in hard or electronic copy, may be made **only** in accordance with the Copyright, Designs and Patents Act 1988 (as amended) and regulations issued under it or, where appropriate, in accordance with licensing agreements which the University has from time to time. This page must form part of any of such copies.

iii. The ownership of certain Copyright, patents, designs, trademarks and other intellectual property (the "intellectual Property") and any reproductions of copyright works in the thesis, for example graphs and tables ("Reproductions"), which may be described in this thesis, may not be owned by the author and may be owned by third parties. Such Intellectual Property and Reproductions cannot and must not be made available for use without the prior written permission of the owner(s) of the relevant Intellectual Property and/or Reproductions.

iv. Further information on the conditions under which disclosure, publication and commercialisation of this thesis, the Copyright and any Intellectual Property and/or Reproductions described in it may take place is available in the University IP Policy (see http://documents.manchester.ac.uk/DocuInfo.aspx?DocID=24420), in any relevant Thesis restriction declarations deposited in the University Library, The University Library's regulations (see http://www.manchester.ac.uk/library/aboutus/regulations) and in the University's policy on presentation of Theses.

Author Information

Name: Andrés Camilo Mármol Guijarro

Date of birth: 9th July 1988

Nationality: Ecuadorian

Curriculum Vitae

1994-2006	Pensionado Universitario, Quito, Ecuador.
2008-2014	BSc. Biological Sciences, Pontifical Catholic University of Ecuador. Quito Ecuador.
2016-2020	PhD, Faculty of Biology, Medicine and Health, University of Manchester, UK. Supervisor: Dr. Jonathan R. Codd.

Publications

(1) Narváez, A. E., **Marmol-Guijarro, A. C.**, and Argoti, A. (2019). Blow fly infestation on Anolis parvauritus: Notes of the effects of myasis on lizard's behaviour. Herpetology Notes 12: 847-852.

(2) Quirola, D. R., **Marmol-Guijarro, A. C.**, Torres-Carvajal, O., Narváez, A. E., Ayala-Varela, F., and Moore, I. T. (2017). Use of a rostral appendage during social interactions in the Ecuadorian Anolis proboscis. Journal of Natural History 51(27-28): 1625-1638.

(3) **Marmol-Guijarro, A. C.**, Nudds, R., Marrin, J. C., Folkow, L. P. and Codd, J. R. (2019).

Terrestrial locomotion of the Svalbard rock ptarmigan: comparing field and laboratory treadmill studies. Scientific Reports 9(1): 11451.

(4) **Marmol-Guijarro, A. C.**, Nudds, R., Folkow, L., and Codd, J. R. (2020). Examining the accuracy for trackway predicting gait selection and speed of locomotion. Frontiers in Zoology 17:17

(5) **Marmol-Guijarro, A. C.,** Nudds, R., Folkow, L., Lees, J. and Codd, J. R. Does posture explain the kinematic differences in a grounded running gait between male and female Svalbard rock ptarmigan moving on snow? Polar Biology in review

(6) **Marmol-Guijarro, A. C.,** Nudds, R., Folkow, L., Sellers, W., Falkingham, P., Borstad, C. and Codd, J. R. Potential evidence for route choice through snow in the Svalbard rcok ptarmigan. PNAS under review.

Conference Presentations

(1) Marmol-Guijarro, A. C. and Torres-Carvajal, O. Are anoles from Yasuní better climbers than Caribbean anoles? An evolutionary approach. Poster presentation at the III World Summit on Evolution, Galápagos, 2013

(2) Marmol-Guijarro, A. C. and Torres-Carvajal, O. Clinging ability in Ecuadorian anoles: A case study of mainland vs. Island evolution. Poster presentation at the Society of Integrative and Comparative Biology, West Palm Beach, FL, 2015

(3) Marmol-Guijarro, A. C., Nudds, R., Folkow, L. and Codd, J. Comparing the kinematics and speed of locomotion in the Svalbard rock ptarmigan under field and laboratory conditions. Oral presentation at the 12th International Congress of Vertebrate Morphology, Prague, July, 2019.

Acknowledgements

First I would like to thank my supervisor, Jonathan Codd for his massive support over the course of my PhD, in particular during the most exacting and adverse times. My time in Manchester could not have been better thanks to his friendship and his mentorship throughout my studies, which have provided me with a renovated approach to science.

Second, I would like to thank my co-supervisor Robert Nudds for his advise and help over the past years. His contribution to my research, specially on the statistics and experimental desing in all the experiments of my PhD has been invaluable. I am also grateful to Bill Sellers, who kindly assited me with equipment and introduced me to the "3D world".

I am also grateful to former members of the Codd-Nudds lab – Kayleigh, John Lees, Peter Tickle and John Marrin (briefly) – for their previous work that has been the foundation of my PhD. Although we shared just a brief time of laugh and conversation together at BH, it certainly has been memorable.

I would also like to thank to all my friends in Ecuador and Manchester for their constant support and help throughout my whole PhD. In particular to Javo, lets hope the beers and football never end.

To Andrea, who unexpectedly became one of the most important parts of my life in Manchester, and to whom I am very grateful for her selfless support during the most difficult times.

Most importantly I would like to express my deepest gratitude to my parents Miguel, Silvia and my siblings Miguel, and María Jose, who have been a constant source of inspiration, help, support and encouragement thorughout my whole life.

Finally, I would like to thank to Secretaría Nacional de Ciencia, Tecnología e Innovación de Ecuador (SENESCYT) for funding my PhD studies here at the University of Manchester. The only way in which we could brind a better future to our country is by investing in the development of our people.

Organization of this PhD thesis

I have submitted this PhD thesis for examination at the University of Manchester in the Alternative Format. This format allows the inclusion of chapters that are either already published, or in the format of journal articles. In this thesis, research chapters (2-5) are presented in the format particular to the journal where articles are either submitted or are to be submitted. All these chapters have their own reference list, provided at the end of each chapter and pagination is separate for each article. Citations from the main introduction and main discussion chapters (1 and 6) are listed at the end of the thesis. I am the first author of all the papers submitted as part of this thesis. However, all the research was in collaboration with other colleagues, therefore the contribution of the authors in each article is disclosed below.

Chapter 1

General introduction

Chapter 2 (*Published peer-reviewed manuscript*)

Marmol-Guijarro, A. C., Nudds, R., Marrin, J. C., Folkow, L. P. and Codd, J. R. (2019). Terrestrial locomotion of the Svalbard rock ptarmigan: comparing field and laboratory treadmill studies. Scientific Reports 9(1): 11451.

Chapter 3

Marmol-Guijarro, A. C., Nudds, R., Folkow, L., Lees, J. and Codd, J. R. (in review). Does posture explain the kinematic differences in a grounded running gait between male and female Svalbard rock ptarmigan moving on snow?

Chapter 4

Marmol-Guijarro, A. C., Nudds, R., Folkow, L., Sellers, W., Falkingham, P., and Codd, J. R. (in review) Potential evidence for route choice through snow in the Svalbard rock ptarmigan. PNAS.

Chapter 5 (*Published peer-reviewed manuscript*)

Marmol-Guijarro, A. C., Nudds, R., Folkow, L., and Codd, J. R. (2020). Examining the accuracy for trackway predicting gait selection and speed of locomotion. Frontiers in Zoology 17:17

Chapter 6

General discussion

Statement of Contribution to Publications

I conducted all the experiments in the field, at Adventdalen valley and adjacent side valleys in Spitsbergen, Svalbard (78° 13' 18" N, 15° 38' 30" E). Following the completion of data collection, I processed and analysed the data in the Faculty of Biology, Medicine and Health at the University of Manchester (Ch 2-5). The initial study (Chapter 2 in this thesis) was based upon the original idea of my supervisor Dr. Jonathan Codd, as a continuation of previous locomotor and energetic work on captive Svalbard rock ptarmigan. All subsequent studies arose through discussion of the initial findings between co-authors and myself. Dr. Robert Nudds provided assistance with project design, data analysis and interpretation. Professor Lars Folkow, Dr. John Lees, Dr. William Sellers and Dr. Peter Falkingham provided assistance with project design and implementation. MSc. John Marrin a provided field assistance in Adventalen. I wrote all the articles with editing assistance and advice on drafts provided by all co-authors.

Chapter 1

General Introduction

1. Introduction

1.1. Terrestrial locomotion

Intuitively, we recognize individual animal species, in part, by the characteristic ways that they move from one place to another either on ground, in the water or air. For most animals, locomotion is tightly linked to the animal's own fitness manifested in one or more advantageous phenotypic traits in response to specific biological/ecological pressures and that are constrained by the evolutionary history of the species (Alexander 2003a; Reilly et al. 2007). For example, species that migrate very long distances – e.g. to more favourable grounds for feeding and/or breeding – may show adaptations towards greater locomotor efficiency to cover such distances while balancing their overall energetic budget (e.g. Maresh et al. 2015; Sapir et al. 2010). Also, predators may benefit more from a greater acceleration capacity powered by fast twitch muscles, whilst a musculoskeletal system capable of support high lateral accelerations to make sharper turns may be of greater importance for prey to avoid predation. Alternatively, animals with relatively low top speeds may possess a greater oxygen uptake and/or a higher lactate threshold on muscles (Booth et al. 2015). However, an advantageous trait may come at the expense of others (Alexander 2003b). Thus, only by understanding how animals move in their natural environment and how this interacts with laboratory-based studies can we gain insight into the ecological and evolutionary significance of their locomotion.

From the basic principles of animal movement to studies on applied robotics mimicking animal locomotion (e.g. Li et al. 2013; Mazouchova et al. 2013; Schiller et al. 2019), terrestrial legged locomotion has been an active field of study over the last decades. These studies have led to a deeper understanding on how animals move while describing the compromises between energetic efficiency (Hoyt and Taylor 1981; Rubenson et al. 2004; Watson et al. 2011), structural safety of the locomotor system (Andrada et al. 2013b;

Biewener 1989; Daley and Usherwood 2010) and self-selected speed (Daley et al. 2016; Rubenson et al. 2004). These studies have helped to better understand how movement is shaped by the animal's morphology in terms of size and limb architecture, and the consequences of interspecific and intraspecific variation of these traits have upon locomotion (Alexander 2003b). The vast majority of these studies, however, have been conducted under strict experimental conditions either on treadmills or firm ground to allow the specific parameters of interests to be manipulated without the pervasive effects of additional confounding factors. However, the totality of these results remains to be determined; animals in the real-world often move over complex environments where steady locomotion is seldom possible, and conditions depart from ideal and where neuromuscular and biomechanical adjustments are key to maintain the stability of the system. Such changes, even if they are minor, could translate into greater energetic demands.

Birds are one of the most diverse clades of extant vertebrates, being found on all continents of the world. The dispersal across the globe of birds has led to a range of derived morphological traits of the locomotor system that has enable them to move in the air, in the water, or on land. Many birds are capable of all three modes of locomotion and a few are limited to only terrestrial locomotion. However, vital biological processes of many birds, including feeding and/or mating, are still dependent on moving bipedally on the ground. Interestingly, studies seeking to understand the parallels between locomotion on natural substrates of varying properties and on treadmill are scarce for birds (e.g. Daley et al. 2016; Turner et al. 2020; Zhang et al. 2017), and the majority of information comes from humans and other mammals (e.g. Heinonen et al. 1959; Herbin et al. 2007; Lejeune et al. 1998; Pandolf et al. 1976; Parker et al. 1984; Ramaswamy et al. 1966; Riley et al. 2008). Humans are the other vertebrates where obligated bipedalism has evolved independently. Although the same natural laws (i.e. earth gravity) governing locomotion are affecting both humans and birds, the unique avian morphology makes direct comparisons between the biomechanics of these two groups difficult (Alexander 2004; Blum et al. 2011).

The main objective of this thesis is to examine the biomechanics of terrestrial locomotion of the Svalbard rock ptarmigan (*Lagopus muta hyperborea*) in their natural environment and to particularly consider the effects that a natural substrate (snow, found throughout the Arctic) has on the locomotion of this species. The Svalbard rock ptarmigan offers a great opportunity to study this overarching question because extensive research on laboratory treadmill conditions has been conducted in the past few years (e.g. Lees et al. 2013; Lees et al. 2014a; Lees et al. 2014b; Lees et al. 2010; Lees et al. 2012a; Lees et al. 2012b; Nudds et al. 2011), setting a baseline for a comparative analysis between locomotion on treadmill *vs*. locomotion in the wild on snow. In this thesis, I present novel insights into how the ptarmigan traverse ground with snowy substrates, with a link to the morphological and behavioural attributes that may influence their overall fitness.

Although the current knowledge into the adaptations for terrestrial locomotion is vast thanks to the research on animals moving on uniform non-slippery substrates or treadmills, they might not be necessarily congruent with animal performance under natural conditions. For example, while the treadmill belt is designed to provide strong grip, it is also more compliant than firm ground causing a reduction in the ground reaction forces acting on the feet (Riley et al. 2008; Riley et al. 2007). In line with these differences, a number of studies in humans show conflicting results; some of them report substrate effects on the kinematics (Elliott and Blanksby 1976; Riley et al. 2008; Wank et al. 1998), locomotion dynamics (Riley et al. 2008) and energetics (Daniels et al. 1953), while others do not detect any effects on these parameters (Van Ingen Schenau 1980). Snow, as a substrate, may dictate specific behavioural responses to regulate the energetic demands moving on it, including lower self-selected traveling speeds and economic gaits to prevent an energetic imbalance to tip against the animal (Crête and Larivière 2003; Droghini and Boutin 2018a; Pandolf et al. 1976; Parker et al. 1984). In **Chapter 2**, I analyse how comparable the kinematics of locomotion (stride length, stride frequency, stance phase, swing phase and duty factor) and the speed range of wild free ranging ptarmigan are to what has been previously reported for males of this species moving on a treadmill. The results suggest comparable kinematics for two of the three gaits that ptarmigan males are capable of and the differences in the third gait are linked to the substrate. They also suggest ptarmigan select speeds favouring energetic economy. I discuss the ecological implications of studying the kinematics of wild birds *in situ* and provide evidence of the validity of treadmill data to understand locomotion in wild populations.

From differences in plumage colours to differences in body size, birds are known for being sexually dimorphic. Many aspects of their natural history such as intraspecific competition, the mating systems and parental care are thought to be correlated with how dimorphism manifest in species (Dunn et al. 2001; Owens and Hartley 1998). In the Svalbard rock ptarmigan, the males are usually larger than the females, which could be attributed to the intense competition between males to defend their territories during the mating season (Lees et al. 2012a; Steen and Unander 1985; Unander and Steen 1985). Males also have an improved locomotor performance when compared to females, as they are capable of using an aerial running gait and can move faster at lower energetic costs (Lees et al. 2012a). The factors dictating the disparities in the locomotor systems between sexes in the ptarmigan are unclear; however, evidence from intraspecific comparison in leghorns suggest that they might be explained by differences limb posture and muscle architecture (Rose et al. 2016a; Rose et al. 2015a; Rose et al. 2016b). In **Chapter 3,** I present data on the kinematics of wild females moving *in situ* and I compare it to females on treadmills. I also analyse the effects of sexual size dimorphism upon the locomotor kinematics in the Svalbard rock ptarmigan by comparing size corrected data for the wild females and wild males. Contrary to the males, the kinematics of the females remain conserved independent of the gait they use and despite moving on a snowy substrate. I discuss how sexual dimorphism in leg posture and limb muscle architecture may explain the lack of kinematic adjustments observed in the females, which enable them to be more stable when moving on snow.

Snow depth and snow supportiveness (defined as snow resistiveness to penetration of a thin-blade gauge; see methods in **chapter 4**) are among the most important physical properties affecting animal locomotion on snow. Several lines of evidence exist suggesting important energetic increases depending upon how deep the feet penetrates on snow. In fact, a positive correlation exists between energetic costs of locomotion with foot sinking depths in ungulates – including the elk, mule deer (Parker et al. 1984) and caribou (Fancy and White 1987) – canids (Crête and Larivière 2003) and humans (Heinonen et al. 1959; Pandolf et al. 1976; Ramaswamy et al. 1966). When foot sinking depths exceed 25% of the leg length, it may double the energetic costs compared to walking on firm ground at a given speed; increasing asymptotically when footprint depths are beyond 50% of the leg length (Crête and Larivière 2003; Fancy and White 1987; Heinonen et al. 1959; Pandolf et al. 1976; Parker et al. 1984; Ramaswamy et al. 1966). As a result, animals may adopt behavioural strategies including the reduction of travelling self-selected speeds (Crête and Larivière 2003; Fancy and White 1987; Heinonen et al. 1959; Pandolf et al. 1976; Parker et al. 1984; Ramaswamy et al. 1966), the use of naturally or man-made compacted snow patches (Crête and Larivière 2003; Droghini 2016; Droghini and Boutin 2018b; Fancy and White 1987; Murray and Boutin 1991) or a reduction in the overall activity when snow severely impedes locomotion (Droghini and Boutin 2018a). In **Chapter 4**, I present data on snow supportiveness and footprint depths and how these two factors affect the self-selected speed of ptarmigan locomotion. By incorporating these two factors into a linear mixed model, I show negligible effects on ptarmigan self-selected speeds. Interestingly, ptarmigan sinking depths do not exceed the intertarsal joints, which might indicate that they are deliberately choosing optimal routes that minimize the energetic costs (Alexander 2000).

It is vital to gain insights on the constraints that are relevant to animal locomotion in the field. Of particular interest are those regarding the time budgets for specific locomotor gaits and speeds of locomotion which may provide key data on the energetic landscape of the species of interest (Reilly et al. 2007; Shepard et al. 2013). However, conducting this type of research is challenging, depending on how elusive the species in question is or how costly it is do fieldwork and to buy equipment. A cheap more practical alternative to circumvent these issues might be to measure l_{stride} directly from the footprints. In order to estimate speed of locomotion and gait preferences using footprints, in **Chapter 5** I present a ptarmigan specific model to examine the predictive accuracy of this model and two additional models based on the dimensionless "Froude number" proposed by Alexander (1976) and Thulborn (1984). The analysis revealed that estimating speeds and gaits solely from footprints is problematic, even when the ptarmigan model is applied. I discuss the morphological factors obscuring our predictions and propose alternatives that can be incorporated to better understand how animals move in their environment.

1.2. The musculoskeletal system and locomotion

Striated muscles are the motors powering locomotion in all animals. These muscles are capable of producing work by transforming the chemical energy contained in the adenosine triphosphate molecule (ATP) through hydrolysis into mechanical energy mediated by the actin-myosin complex (Huxley 1969). Work is defined as the force exerted over a distance, and in locomotion, these forces are transmitted to ground via bones and tendons. How much force a muscle can generate or how fast a muscle can contract depends on a number of physiological aspects of the muscle itself and the rest of constituent parts of the musculoskeletal system, which ultimately shape the manner in which organisms move through their environment.

1.2.1. Muscle function

Muscle force output is the result of the contraction of a number of cellular units called myofibrils, mainly driven by the actin-myosin protein complex where the thin filament of actin slide past over the think filament myosin. Both filaments are anchored to densely packed regions called Z disks at both extremes of the complex forming sarcomeres, although the myosin is indirectly to it by the elastic titin (Huxley 1963). Several sarcomeres longitudinally aligned forms the myofibrils. Myofibril contraction may vary depending on the energetic pathway used, which depends on the number of mitochondria to power contractions.

Force generation involves cyclic contraction/stretch of the sarcomeres where actin interlock with myosin though the formation of cross-bridges; an ATP-mediated reaction triggered by the release of Calcium ions into the cellular matrix (Huxley 1969). Force, however, depends on the length and the speed at which myofibrils contract. With longer myofibrils a greater number of cross-bridges could be formed, therefore resulting in higher force outputs up to a peak just before actin filaments overlap each other (Gordon et al. 1966).

On the other hand, fast shortening velocities of myofibrils negatively impacts the cross-bridges formation rate of success (Hill 1938). A trade-off exists between muscle efficiency and muscle power depending on the velocity of muscle contraction (Biewener and Patek 2018). For efficient contractions, the muscle must shorten at 30% of the maximum shortening velocity. Conversely, maximum power usually requires almost half the maximum shortening velocity. Animals migrating may prioritize muscle efficiency with lower shortening velocities, whilst fast shortening velocities would be preferred if a predatory response is required.

The shortening velocities may differ between myofibrils, depending on how fast the cross-bridges can be formed. Given that formation requires the mediation of ATP, the energetic pathway to form ATP will qualitatively distinguish between muscle fibre types. Three main groups exist: The slow-oxidative (SO) or type I fibres, the fast-oxidative-glycolytic (FOG) or type IIA fibres and the fast-glycolytic (FG) or type three fibres (Peter et al. 1972). The SO fibres rely on aerobic pathways for ATP at expenses of slower but sustained formation rates of cross-bridges. Conversely, FG obtain ATP faster from glycolytic pathways, enabling fast muscle contractions. However, they can only sustain work for short periods before reaching lactic acidosis. FOG are intermediate between SO and FOG. Again, animal ecology shapes muscle fibre type proportions; animals that rely on rapid burst to catch prey may possess greater proportions of FG fibres (Williams et al. 1997), while others may show greater proportions of SO and FOG fibres for sustained locomotion in order to fatigue preys (Biewener and Patek 2018).

1.2.2. Muscle architecture

At a higher level, muscle anatomy is intimately linked to muscle performance. Muscle can vary in length and in the orientation of attachment of myofibrils. Two major groups can be recognized: (1) muscles with long fibres attached to short tendons (or directly to bones) running parallel to the force they exert and (2) muscles with shorter fibres obliquely attached to long tendons and to the force direction. The latter subdivides into uni-pinnate, bi-pinnate and multi-pinnate muscles. Muscle architecture may have profound implications on muscle performance and the energetic demands for contraction on muscles with the same volume. Generally, parallel muscles provide proportionally faster contractions, while pinnate muscles generate proportionally greater forces. Conversely, pinnate muscles are energetically more efficient than parallel ones given the larger number of cross-bridges to be formed in the latter.

1.2.3. Bones

Transmitting the forces that have been generated by muscles through the bones is required so that the animal is able to move. Bones form through the mineralization of cartilage (Currey 1984). Being composed of collagen and hydroxyapatite (a mineral with calcium), variations in the amount of mineralization is strongly correlated to bone elasticity and its resistance to fracture. Thus, bones with high levels of mineralization have reduced elasticity, which may promote bone fracture with relatively lower stresses, compared to bones with less amount of mineralization (Currey 1984). On the other hand, excessive elasticity may reduce the ability to transfer forces in bones given that deformation would absorb a significant amount of the force applied (Biewener and Patek 2018). During terrestrial locomotion, bones suffer compression stresses generated mainly by the ground reaction forces acting on the hindlimb during each stride when the foot is in contact with the surface. This compression is particularly important for larger animals as the reaction forces are directly proportional to the mass of the animal (Biewener 1991). Larger animals, however, prevent possible fractures by having a more upright postures that allows a reduction in the mass specific force generation of muscles; meaning that maximum stresses do not increase due to a proportional reduction of muscle mass compared to smaller animals (Biewener 1991). Further, sex plays a key role in the structural strength of bones, given that calcium may be sequestered from bones in order to form the eggshell in gravid females laying eggs (Whitehead 2004). This is particularly relevant when comparing the locomotion between sexes of a species (Lees et al. 2012a; Rose et al. 2016a) and is discussed in **chapter 3**.

1.2.4. Tendons

Muscles are attached to bones via tendons and these tendons play a key role in force generation via elastic storage and recoil, thus producing work passively. Tendons also are characterized by their ability to return energy to the system very efficiently, with energy lost that rarely exceed one tenth (on average) of the total amount stored (Daley and Biewener 2003; Matson et al. 2012; Pollock and Shadwick 1994). In animals, the elastic properties of tendons are directly related to the power generation during accelerations (Aerts 1998; Roberts and Scales 2002) and power absorption when deceleration is required (Konow et al. 2012; Roberts and Azizi 2010), which depends upon muscle length, muscle power and force capacities of the muscle tendon unit (MTU). During accelerations, the power generated by the MTU is achieved by an initial slow muscle contraction progressively stretch its associated tendon, thereby storing energy. During this phase, there is no change in the joints angle. Following, energy recoveries occur when tendons shorten quickly back just before the joints rotate, delivering a higher power output (referred to as Power Amplification) (Aerts 1998; Roberts and Scales 2002; Sawicki et al. 2015).

Conversely to decelerate, energy is first absorbed by the MTU by a fast tendon stretch with little or no length change of its associate muscle. This is then followed by tendon shortening to its natural length while the muscle slowly stretches, allowing the muscle to dissipate the energy; however, power is attenuated given the reduced speed of lengthening of the muscle (Konow et al. 2012; Roberts and Azizi 2010), preventing muscle damage caused by an excessively fast contraction (Roberts and Azizi 2010; Thelen et al. 2005). Thus, the ability of tendons to produce passive work is key for activities that require rapid acceleration and power outputs, which are likely important for fast sprints, jumping performance, landing and take-off, and to keep stable locomotion on irregular terrain (Roberts 2016). Also, the level of mineralization of tendons may also affect the elastic modulus of these tissue (Bennett and Stafford 1988; Landis et al. 1995; Silver et al. 2000)(Bennett and Stafford, 1988, Landis et al., 1995, Silver et al., 2000).

1.2.5. Effects of speed on muscle recruitment and energetics

Faster speeds require muscle contraction cycles to occur at faster rates. Usually, animals increase the number of strides per unit time to go faster, meaning that muscles must be recruited faster to meet the power demands of moving fast. Following force-velocity relation described by Hill (1938), it is inferred that at faster strides would require faster cross-bridges cycles and therefore greater demands of ATP (Ellerby et al. 2005; Heglund et al. 1982b). This energetic increase, however, is not independent of size given that in smaller species (> 1kg) the cross-bridge cycles must be even faster compared to larger animals (< 1kg) as they often show higher stride frequencies (Alexander and Jayes 1983; Gatesy and Biewener 1991). The costs of muscle activation through Calcium ions pumped into the muscle cells to trigger contraction are comparable in small and large species; yet muscle activation occurs at faster rates in smaller species in order to swing the limbs faster (Heglund et al. 1982b) (Heglund et al. 1982b).

The total energy increase required by the limb muscles, overall, appear to be somewhat linear; however, the muscle-specific fractional contribution to the energy increases largely depend on the speed and gait used during locomotion and the specific function of the muscle. During level locomotion in the guinea fowl, for example, Ellerby et al. (2005) reported three differentiated groups of muscles that are more active under specific speed and gait conditions. The first group of muscles (Group 1; see Figure 1.1) which account for 25% of the total muscle mass of the limb account for more than a half of the total energy required by the limb from rest to walking speeds around 0.5 ms^{-1}. This proportion, however, decreases to only 14% at speeds beyond 0.5 ms^{-1}. In contrast, the second muscle group (Group II; see Figure 1.1) shows the opposite pattern, where only 15% of the total energetic demands of the limb are accounted for this group from rest to walking at 0.5ms^{-1}, despite being 46% of the limb muscle mass. At higher running speeds, these muscles become more active contributing with 58% of the total energetic demands of the limb. In the third group of muscles (Group III; see Figure 1.1), the proportion of energy required remains relatively constant at more than a quarter of the total amount required by the limb, regardless the speed of locomotion (Ellerby et al. 2005).

Some studies have suggested that the majority of work done by muscles is done against gravity, while positive work to move forward, to counter air friction, or to swing the limb is less relevant (e.g. Kram and Taylor 1990; Roberts et al. 1997). Ellerby et al. (2005) and Marsh et al. (2004), by directly measuring blood flow and aerobic energy expenditure, suggest that in fact, limb swing and joint stability through co-activation of agonistic muscles may also account for significant proportions of the total energy expenditure. Swinging the limb may take up to 25% of the total energy expenditure (Marsh et al. 2004), while knee stability require knee flexors and extensors to be simultaneously active, contributing with 15-30% of the total energy costs of the limb. These costs, however, could be overestimated as muscles may also be involved in other functions (Ellerby et al. 2005).

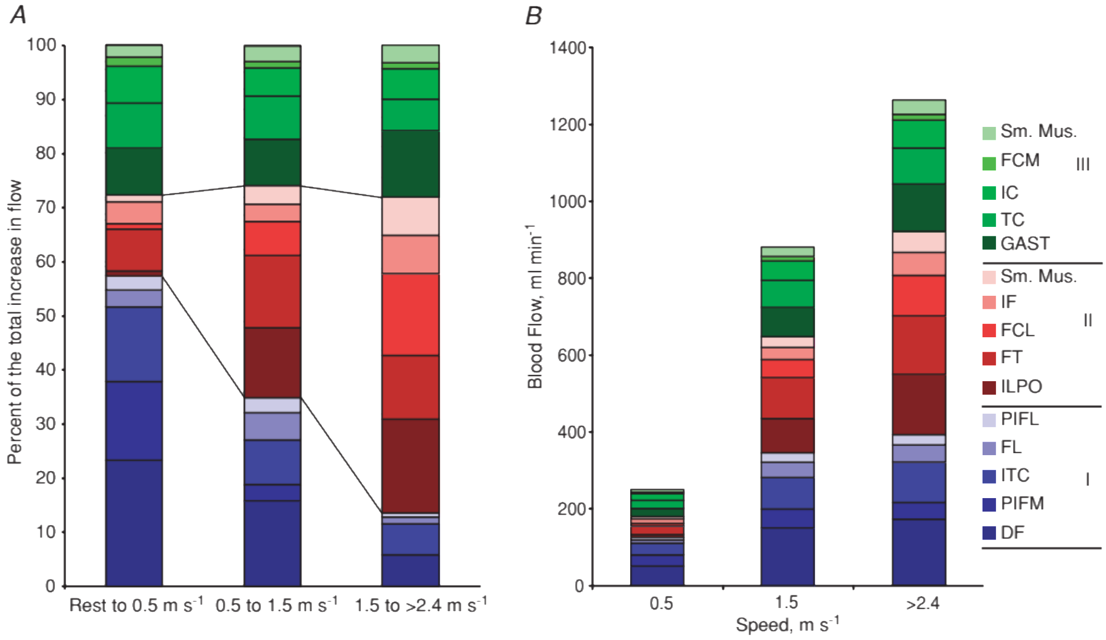

Figure 1. 1. Blood flow distribution to the hind-limb muscles with increasing speed in the Guinea fowl during level locomotion. The three groups of muscles represented in degrades of blue (Group I), red (Group II) and green (Group III) based on statistical differences in the fractional contribution in blood flow of a specific muscle to the blood flow increases of all limb muscles overall. Bars in A represent proportional blood flow increases, while the bars in B represent the absolute increases for each speed category. The muscles included in the figure are the flexor cruris medialis (FMC), the iliotibialis cranialis (IC), the tibialis cranialis (TC), the iliofibularis (IF), the flexor cruris lateralis (FCL), the femerotibialis (FT), the iliotibialis lateralis pars postacetabularis (ILPO), the puboischiofemeralis pars lateralis (PIFL), the fibularis longus (FL), the ilitrochantericus caudalis (ITC), the puboischiofemeralis pars medialis (PIFM) and the digital flexors combined (DF). The small muscles category (Sm. Mus.) in group II includes the iliotrochantericus cranialis (ITCR), the caudofemoralis pars pelvica (CFP), the iliotibialis lateralis pars preacetabularis (ILPR), the caudofemoralis pars caudalis (CFC) and the ambiens (Amb). The Sm. Mus. in group III includes the ischiofemoralis (ISF), obturatorius medialis (OM) and the digital extensors combined (DE). The three heads of the gastrocnemius – gastrocnemius intermedia, gastrocnemius lateralis and gastrocnemius medialis – are included into the GAST category. Taken from (Ellerby et al. 2005).

1.3. Intrinsic stability of locomotion - a spring-mass model

The intricate configuration of the animal limb makes it extremely difficult to set up models that fully mimic the dynamics of such an elaborate structure complex system. For instance, muscles of different architecture can cross more than one articulation. By incorporating these complex systems into simple templates, it is possible to gain insights into the dynamics of legged locomotion. Although two models have been traditionally used to describe and predict the mechanical patters of walking and running (Mochon and McMahon 1980), evidence suggest that both gaits can be studied under one unified model: a simple spring-mass model (Geyer et al. 2006).

By adjusting the length, stiffness and touchdown angle of the limb at the beginning of stance, the simple spring-mass model predicts remarkably well the mechanical energy patterns of a steady run from a number of taxa including mammals (Farley et al. 1993), birds (Birn-Jeffery et al. 2014; Daley and Biewener 2006), lizards (Li et al. 2012) and insects (Jindrich and Full 2002; Reinhardt et al. 2009), where the vertical and horizontal energy components of the centre of mass (COM) oscillate in phase, and muscle work is reduced via elastic store and rebound (Blickhan 1989; Cavagna et al. 1977; McMahon and Cheng 1990) (see below). This model is also capable to mimic the trajectory of the COM during steady walk more precisely than a stiff rod inverted pendulum (Mochon and McMahon 1980), as it accounts for the double support phase. In this case the vertical and the horizontal energy are cyclically exchanged up to a 70% (Cavagna et al. 1977), and the remainder is restored via passive work done by the elastic elements of the limb (Geyer et al. 2006).

The spring-mass model has also been useful to understand how fast animals recover from an external perturbation (i.e. stability) and how strong should the perturbation be to impede locomotion (i.e. robustness) (Daley 2018). Simulations of bipedal locomotion and empirical evidence in humans skipping obstacles have provided evidence that early swing-leg retraction just before foot contact with the ground improves locomotion stability (Seyfarth et al. 2003). Similarly, studies in guinea fowls facing sudden drops and obstacles have shown high variability in leg posture during the perturbed step mediated by swing-leg retraction that modulates how fast the foot contacts the ground, which in turn dictates leg loading (Blum et al. 2014; Daley and Biewener 2006).

Depending on the leg retraction angular velocity at late swing, two conflicting control targets can be identified: (1) fasts limb retractions allow for shorter delays on ground contact, reducing limb loadings by minimizing the changes in the vertical velocity of the COM; whereas (2) slower limb retractions increase the time of fall, resulting in greater vertical velocities and therefore large leg loadings. Although in the first case injury avoidance is favoured, fast limb retraction increases the risk of missing stance phase. Conversely, if limb support is the control target, this may compromise limb safety as limb may operate under stresses near to bone fracture (Birn-Jeffery et al. 2014; Blum et al. 2014; Daley and Biewener 2006; Daley and Usherwood 2010; Daley et al. 2006).

Evidence suggest that birds often target swing-leg trajectories favouring gait economy and injury avoidance by keeping leg loadings at minimum rather than optimizing one-step recoveries at expenses of comparatively higher GRFs and impulses (Birn-Jeffery et al. 2014; Blum et al. 2014; Daley and Biewener 2006; Daley and Usherwood 2010). Low GRFs forces favour economy as they do require less muscle work to counter joint moments (Biewener 1989). Further, depending on the leg posture at ground contact, leg actuates either by storing energy of by doing positive work in order to negotiate with uneven ground while keeping the mechanical energy of the COM dynamically stable (Birn-Jeffery et al. 2014; Blum et al. 2014; Daley and Biewener 2006). The spring-mass model is not only capable to explain and predict the basic mechanics of locomotion on uneven ground, but also appear to be similar when species traverse slippery surfaces (Clark and Higham 2011).

To effectively accomplish dynamic stability of the system, however, the interplay between active feedforward, proprioceptive and feedback responses coupled with intrinsic mechanical controls of the muscles are critical for muscle activation in uneven locomotion (Daley et al. 2007). In the guinea fowl, the best studied avian species, the neuromechanical response begins with an anticipated recruitment (i.e. feedforward response) of muscles at the hip and knee, as well as the distally located digital flexors (Daley and Biewener 2011; Daley et al. 2007; Daley et al. 2009). Once at the perturbation, the instant proprioceptive responses allow to tune the force and work output at touch down, as centrally mediated responses take longer (e.g. 30-40 ms in the Guinea fowl (Daley et al. 2009)). At this point, for example, the lateral gastrocnemius (LG) electromyography (EMG) is no different to the one observed in guinea fowl at level ground, although the LG force output is reduced to a fifth (Daley et al. 2009), indicating a greater influence of the proprioceptive response in this muscle. It is in the subsequent steps to the perturbation when proprioceptive stimulus become relevant for a feedback response for stabilisation. In the case of the guinea fowl lateral gastrocnemius, the EMG in the following step after perturbation duplicates the one during a normal and perturbed stride (Daley et al. 2009).

Given the applicability of the spring-mass model to understand the mechanical patterns of locomotion of avian bipeds, we use this model as a template to interpret the kinematic tuning observed in the Svalbard rock Ptarmigan as it moves through snow in **chapter 2** and **3**. Snow may hide sudden drops or obstacles that may compromise the ptarmigan stability, thus the mechanical responses described theoretically in a spring-mass model as well as empirically in the Guinea fowl could parallel those occurring in the ptarmigan.

1.4. Factors influencing terrestrial locomotion

1.4.1. Gaits

Most animals are capable of moving at a range of speeds. Typically, to change speed animals change their gait altering the associated kinematics of footfall. Alexander (1989) defined gaits as “a pattern of locomotion characteristic of a limited range of speeds, described by quantities of which one or more change discontinuously at transition to other gaits". Moreover, with increasing speed, the fluctuation between the potential and kinetic energy of the centre of mass (CoM) shift from pendular-like energy exchange to a bouncing-like exchange, in order to minimize work performed by muscles (Cavagna et al. 1977). The integration of these two approaches has proven useful in to better understand gait transitions from walking to running, particularly in avian species (Nudds et al. 2011). In the following paragraphs, I would refer only to the gaits reported for striding birds. However, extensive work understanding the energetics and biomechanics of gaits and gait transitions has been done for other organisms, including mammals (e.g. Cavagna et al. 1977), lizards (e.g. Irschick and Jayne 1999) and a number of invertebrates (e.g. Full 1987; Full and Tu 1991).

1.4.1.1. The walking gaits

The walking gait encompass the lower speed ranges used by birds. When birds walk one foot is always in contact with the ground, and no aerial phases are observed. In other words, the duty factor (DF) – the time proportion of foot contact during a whole stride – is always greater than 0.5. Within this gait, the horizontal kinetic energy component (E_{kh}) of the COM fluctuates half a cycle out phase with the sum of the potential and vertical kinetic energy components ($E_{\mathrm{p}} + E_{\mathrm{kv}}$) resembling to an inverted pendulum (Figure 1.2) (Cavagna et al. 1977). $E_{\mathrm{p}} + E_{\mathrm{kv}}$ is greatest during midstance when the COM passes over the supporting limb, while E_{kh} is at its lowest. Energy transfer occurs as the bird shifts the weight to the next supporting limb. Thus, while the COM falls, E_{kh} increases at expenses of a decrease in $E_{\mathrm{p}} + E_{\mathrm{kv}}$. This whole process minimizes the work required by muscles and may account for up to 70% of the energy required to lift and reaccelerate the COM (Cavagna et al. 1977). The additional work is required to compensate for the energy losses due to the inelastic collisions of the limb on the ground

(Biewener and Patek 2018), which is accounted by the spring leg inverted pendulum (SLIP), also known as a spring-mass model (Geyer et al. 2006).

1.4.1.2. Aerial running gaits

The highest range of speeds in striding birds are during aerial running gaits. Contrary to walking, in the running gaits E_{kh} fluctuates in phase with $E_{\mathrm{p}} + E_{\mathrm{kv}}$, meaning that energy transfer between the two energy components of the COM do not occur. Conversely, the elastic elements of the limb play a key role to minimize muscle work by releasing stored energy through tendons recoil (Cavagna et al. 1977). In fact, the elastic elements of the limb in running turkeys can supply almost two thirds of the work required from the lateral gastrocnemius (Roberts et al. 1997). Further, aerial running is associated to DF below 0.5 (Figure 1.2).

1.4.1.3. Grounded running gaits

Grounded running is an intermediate gait between walking and aerial running. Intriguingly, it benefits from the bouncing-like fluctuations in the centre of mass of a running gait, while always keeping foot contact with the ground ($DF > 0.5$) (Figure 1.2) via increased leg compliance (Andrada et al. 2013b). The conundrum around the grounded running, however, relates to the evolutionary significance of this gait (Nudds et al. 2011). It has been suggested that the increased leg compliance on the grounded running gaits coupled with a COM that is closer to the ground provide a greater visual stability through head movement control (Andrada et al. 2013b) while reducing the negative work done by bouncing viscera (Daley and Usherwood 2010). Manoeuvrability is favoured by the increased foot contact of this gaits, allowing for fast turns while running (Daley and Usherwood 2010; Gatesy and Biewener 1991). Grounded running gaits have been reported for a wide number of striding birds, including ostriches *Strutio camellus* (Rubenson et al. 2004), the emu *Dromaius novaehollandiae* (Watson et al. 2011) , the rhea

Rhea americana, turkey *Meleagris gallopavo*, guineafowl *Numida meleagris*, bobwhite *Collinus virginianus*, the painted quail *Excalfactoria chinensis* (Gatesy and Biewener 1991), the quail *Coturnix coturnix* (Andrada et al. 2013b), leghorns *Gallus gallus* (Rose et al. 2015b) and the Svalbard rock ptarmigan itself (Lees et al. 2012a; Nudds et al. 2011), while moving on treadmills. However, the paucity of data on birds using grounded running in the wild raises the question if this gait is only an artefact of the treadmill-based experimental design on studies of locomotion (Nudds et al. 2011). In **chapter 2** and **3** I provide evidence of the natural occurrence of grounded running linked to the greater stability of this gait to move over snow substrates with challenging conditions in the Svalbard rock ptarmigan. I discuss the ecological relevance of this gait for the ptarmigan as it allows these birds to move fast while preventing falls during locomotion on snow of varying physical properties. I also discuss on the different mechanisms for stability during grounded running largely driven by sex.

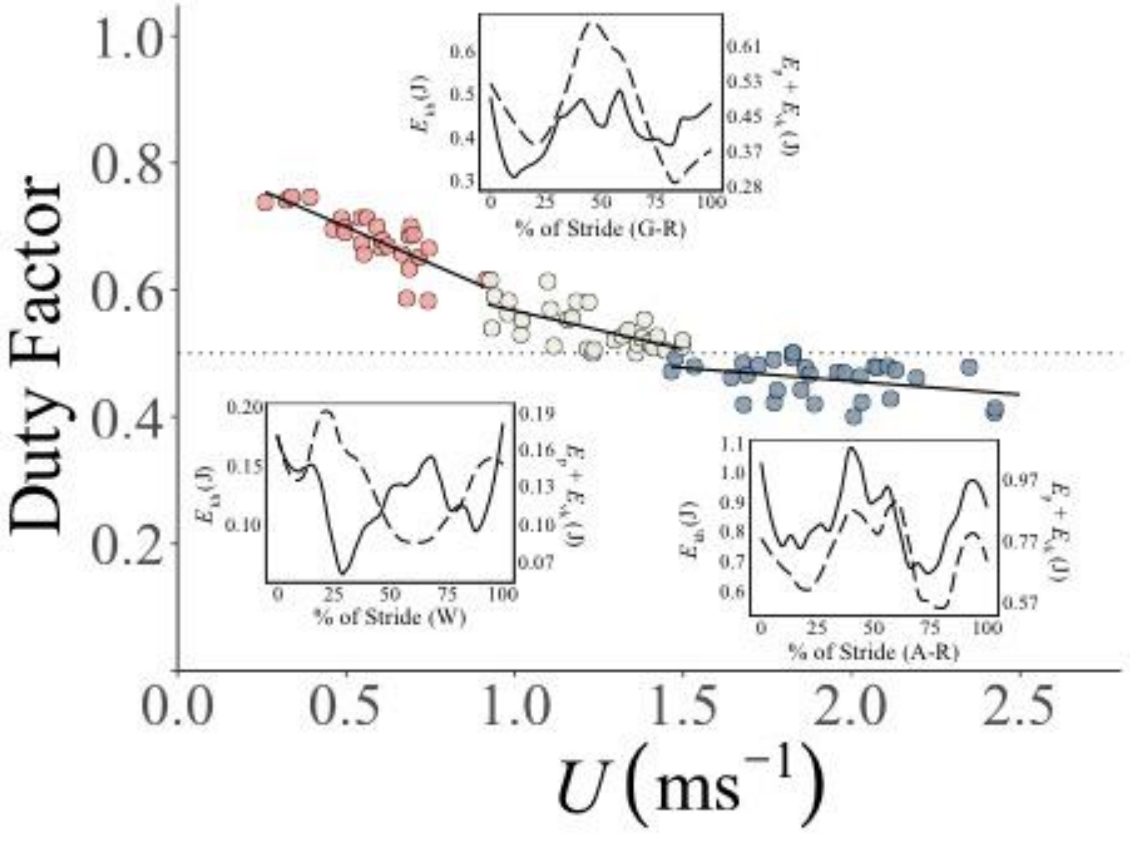

Figure 1. 2. Relation between duty factor (DF) against speed (U) for the three gaits recorded in the Svalbard rock Ptarmigan *in situ*. Red, white and blue filled circles represent birds while using walking (W), grounded running (G-R) and aerial running (A-R) gaits, respectively. The inlay plots are approximate estimates of the energy horizontal (E_{kh}; solid line) and vertical ($E_{\mathrm{p}} + E_{\mathrm{kv}}$; dashed line) components of the centre of mass (COM): the lower-left inlay plot shows the typical fluctuations between E_{kh} and $E_{\mathrm{p}} + E_{\mathrm{kv}}$ during the walking gait, whilst in the upper-mid and the lower-right inlay plots E_{kh} and $E_{\mathrm{p}} + E_{\mathrm{kv}}$ fluctuate in phase with no energy exchange between the two. Aerial phases are only possible only at DF below 0.5 where all aerial running circles are located. Adapted from Marmol-Guijarro et al. (2019).

1.4.1.4. Gait and speed preferences.

With increasing speed there is also an increase in the metabolic demands that are arguably attributed to the time available to support body weight and push it forward in all animals moving terrestrially (Kram and Taylor 1990). Contrary to the cost of locomotion (i.e. mass-specific energy rate of consumption), however, the mass-specific energy per unit distance (Cost of Transport, COT) decreases with increasing speed in the majority of species for which data exist as a result of energy optimization (Figure 1.3), mainly through the decrease of the number of strides per metre travelled (Reilly et al. 2007) and selection of speeds and gaits that minimise the muscle work (Alexander 1989; Dawson and Taylor 1973; Hoyt and Taylor 1981; Langman et al. 1995; Langman et al. 2012; Maloiy et al. 2009; Nudds et al. 2011; Rubenson et al. 2004; Watson et al. 2011). Thus, it has been proposed that natural selection favours self-selected speeds and abrupt gait transitions that optimize the use of energy (i.e. those that are the most energetically efficient); although, exceptions have been as reported for the platypus (Fish et al. 2001), the golden-mantled ground squirrel (Hoyt and Kenagy 1988), the barnacle geese (Nudds et al. 2010) and the common eider (Rose et al. 2014).

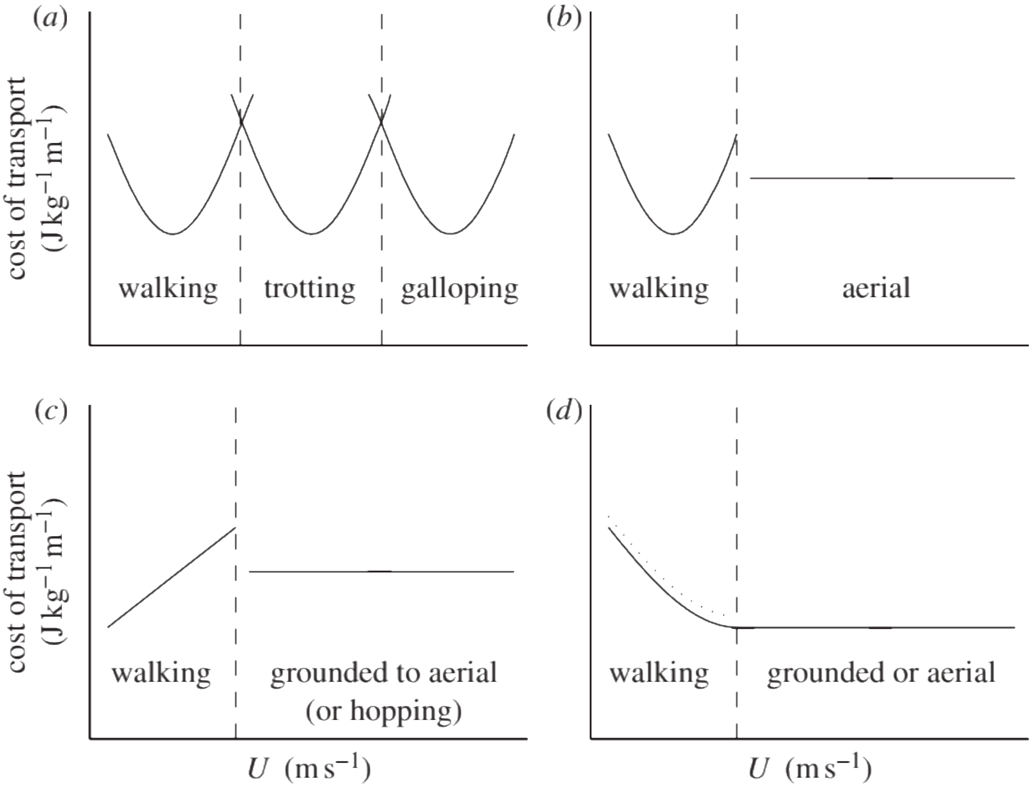

Figure 1. 3. The relation between the Cost of Transport (COT) with increasing U varies across different taxa. At gait transitions, in particularly from walking to running or trotting, step changes in the cost of transport occur in several species including (a) horses, (b) human, camel and donkeys and (c) ostriches and kangaroos, suggesting optimal speeds and gaits with minimums COT. (d) In small mammas including the platypus (solid line), and in the barnacle geese (dotted line) step changes in the COT at gait transitions are absent, where COT decrease smoothly with increasing U. Taken from Nudds et al. (2011).

Alternatively, other studies suggest that speed and gait selection in animals may not be aligned only to energy optimization in locomotion, but it may be strongly influenced by the foraging strategies of the species. Species relying on sit-and-wait predatory strategies use preferentially bouncing gaits associated to fast sprinting bursts only for few moments of the time budget where they are active, whilst the rest of the time they remain still and ready to ambush. Such is the case of the zebra-tailed lizard *Callisaurus draconoides* (Anderson and Karasov 1981; Reilly et al. 2007). On the other hand, species that are actively looking for food sources would predominantly walk, despite this being a relatively less efficient gait (in terms of energy use), and bouncing gaits are only used in very specific behaviours: to escape from predators or intraspecific competitions. This is the case of the western whiptail *Cnemidophorus tigris* (Anderson 1993; Reilly et al. 2007). In the case of active hunters like coyotes, they use bouncing gaits that are more efficient ~88% of the time they are active (Reilly et al. 2007; Switalski 2003). Although these studies are revealing, the scarcity of data linking locomotor energy expenditure with the time budge/activity patterns is still present, in particular for ground dwelling birds. Moreover, the evolutionary significance of gait selection and speed of locomotion across species remains to be studies. Of particular interest is to understand the activity patters of species facing extreme environmental conditions, where food availability is restricted and energy imbalances mat be significant due to excessive locomotor costs/low food availability.

In **chapter 2** I briefly discuss speed and gait selection in the Svalbard rock ptarmigan while moving under the variable environmental conditions found in the Arctic region. In fact, males are known to be exceptional athletes capable of three terrestrial gaits (walking, grounded running and aerial running), incurring in energy drops at the transition from grounded to aerial running gaits.

1.4.2. Body size

1.4.2.1. Effects of body size on locomotion kinematics

By altering the frequency at which limbs are swung (i.e. stride frequency, f_{stride}) in tandem with increases in the length of each stride (l_{stride}), animals are capable of modulating how fast they move. It appears that both parameters increase linearly with increasing speed (Alexander and Jayes 1983; Gatesy and Biewener 1991); however, the ability to run at higher top speeds is size dependent, given that l_{stride} increases more rapidly than f_{stride} with increasing body size, explaining why larger species to go faster (Figure 1.4) (Alexander and Jayes 1983; Biewener and Patek 2018; Gatesy and Biewener 1991). The obvious reason for this pattern has to do with the fact that smaller species have smaller limbs that must be swung faster to increase speed. It is important, however, to consider the pervasive effects of body size on locomotion kinematics, as they may reveal differences in body form between the species under comparison. Meaningful comparisons on the locomotion mechanics and kinematics of different-size species can be obtained under the dynamic similarity hypothesis, a framework proposed by(Alexander and Jayes 1983).

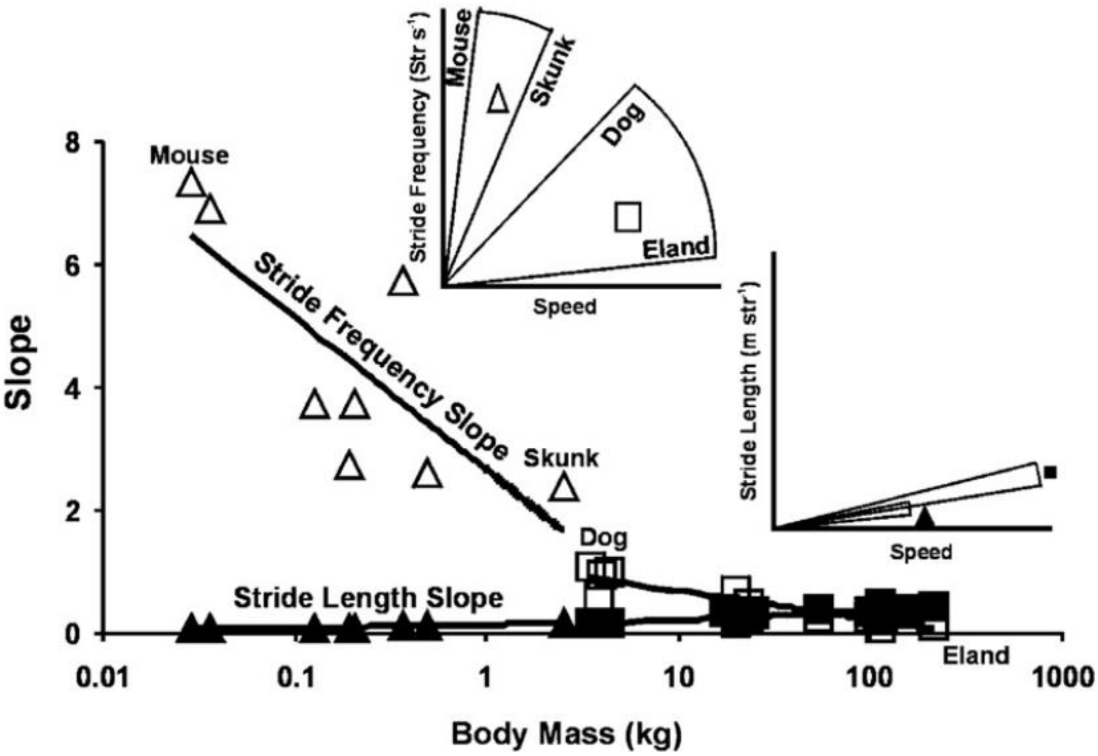

Figure 1. 4. Effect of body size (main graph) and speed (inset graphs) on l_{stride} and f_{stride}. The slope (y-axis) in the main graph represent the rates of increase for each of the kinematic speed with speed, which are greater in smaller species (inlet graph). f_{stride} slopes sharply decrease with increasing body size at a faster rate for animals the size of a mouse up to skunks. From them f_{stride} slopes decrease more discretely. Conversely, the slope of l_{stride}, has a more attenuated uniform increase with increasing body size. Taken from Reilly et al. (2007).

The dynamic similarity hypothesis states that all parameters involved in locomotion such as length, time and force are proportional in animals of different size and change predictably by multiplying them by a fixed factor (Alexander 1976; Alexander and Jayes 1983). Thus, it is possible to compare terrestrial locomotion across species of all sizes by equalising the centripetal and gravitational force ratio by means of the dimensionless Froude number (Fr) (Alexander and Jayes 1983). Fr is defined as:

$$Fr = \frac{U^2}{gh} \tag{1}$$

where U is speed of locomotion, g is gravity (9.8 ms^{-2}) and h refers to the effective limb length defined as the distance between the acetabular joint and the feet at midstance in bipeds. If species are geometrically similar – i.e. all body dimensions are proportional and scalable – it can be assumed that animals move in a dynamically similar fashion at given Fr. The basic kinematic parameters of locomotion – l_{stride}, f_{stride}, stance phase (t_{stance}) and swing phase (t_{swing}) – can also be normalized by relating them to effective limb length and to gravity.

By taking this approach, it has been possible to elicit the effects of limb posture acting upon the kinematics of locomotion when comparing small (< 5kg) non-cursorial species with larger (> 5kg) more cursorial species (Alexander and Jayes 1983; Jenkins 1971). At a given Fr, small non-cursorials show longer relative stride lengths ($\hat{l}_{\mathrm{stride}} = l_{\mathrm{stride}}/h_{\mathrm{hip}}$), while relative stride frequencies ($\hat{f}_{\mathrm{stride}} = f_{\mathrm{stride}}/\sqrt{g/h_{\mathrm{hip}}}$) are higher in the more cursorial ones (Alexander and Jayes 1983; Gatesy and Biewener 1991). The longer $\hat{l}_{\mathrm{stride}}$ in smaller species are explained by the greater excursion angles of the feet plus the smaller $h_{\mathrm{hip}}/l_{\mathrm{leg}}$ ratios in this group, which are both characteristic of a crouched limb (Gatesy and Biewener 1991). Similarly, non-cursorial crouched species use higher duty factors (i.e. the time proportion of limb support over the time for a whole stride, DF) compared to the larger species with upright limbs. This difference in DF implies that force generation in small non-cursorials is more demanding compared to large species due to the inverse relation between development of force exerted to ground and time of limb support (t_{stance}) (Kram and Taylor 1990). Differences in limb posture are major factors affecting affects the limb biomechanics, locomotor energy efficiency, and performance.

1.4.2.2. Effects of body size on posture

Limb posture may be defined by how the limb segments align to each other and with GRF at midstance. It scales with body mass. Increasing body mass led to an increase in the stress acting on the musculoskeletal system. Consequently, muscles must be capable to develop enough forces to counteract the GRF and bones must resist the forces acting upon them without breaking (Biewener 1989). Resisting such forces might seem trivial for relatively small species, but in larger animals the musculoskeletal system would operate close to failure if locomotor stresses also scaled isometrically with body size. Regardless of body size, however, peak locomotor stresses in bones are highly conserved across animals spanning from 0.1 to 300 kg, reaching up to half the stresses needed for bone fracture (Biewener 1989). By aligning the limb joints more vertically to the GRF, large animals increase the effective mechanic advantage (EMA), allowing not only to reduce the stress that bones must resist, but also reducing the amount the force that muscles must exert to counter the external joint moments created by the GRF (Figure 1.5) (Biewener 1989; Biewener 1990; Biewener 2005). High mechanical stresses on extremely large animals, however, may constrain top speeds and manoeuvrability during locomotion, as it is found adult elephants relatively to younger and smaller ones (Hutchinson et al. 2006). Thus, the evolution of an upright posture is well explained by need to alleviate the physiological and mechanical constrains of being bigger. The muscle-force hypothesis, however, does not explain why small species do not benefit from upright limbs, which are usually related to increased stability and manoeuvrability (Biewener 1989; Gatesy and Biewener 1991).

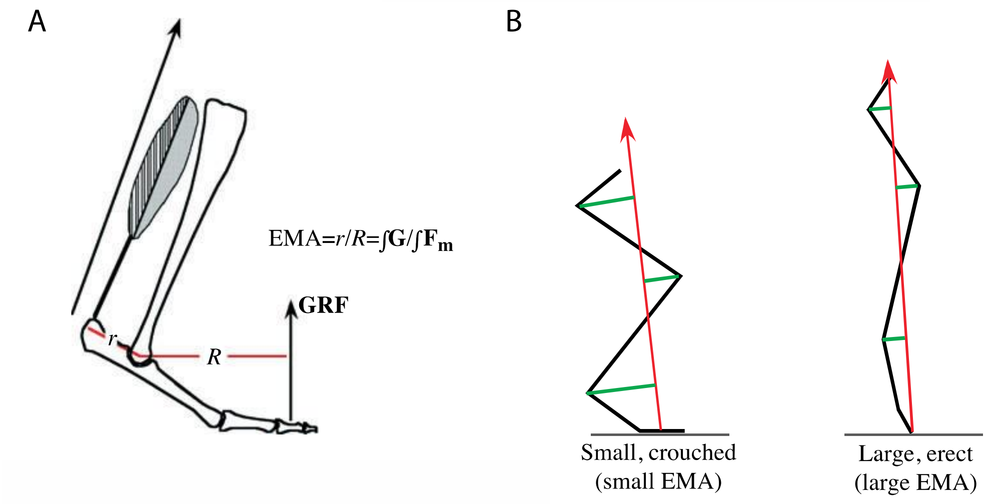

Figure 1. 5. Effective mechanic advantage (EMA) of a limb. The distance from the rotating joint perpendicular to the force applied is known as a moment arm. In (a) EMA is defined as the ratio between joint extensor muscle moment arm r and the moment arm R of the ground reaction force (**GRF**). The two limbs in (b) represent a crouched (left) and an upright (right) limb, respectively. Thus, the EMA of the crouched limb are relatively smaller. Taken from Biewener (2005).

Alternatively, Usherwood (2013) suggested that postural scaling can be explained by the costs of locomotion if those are linked to the recruit demands of activated muscle per kilogram to do work and to provide enough power for push-off, which are associated to t_{stance} (therefore DF). Increased amounts of activated muscle would be recruited either to do work at long t_{stance} to counter the large impulses accelerating and decelerating the COM or to power very brief push-offs. For equal values of Fr, the more upright limb of large species optimises the amount of activated muscle required by orienting the GRF more vertically, resulting in a reduction of the horizontal impulses on the COM and therefore minimizing the work required (Usherwood 2013). Conversely, the higher power demands of being small to swing their limbs more frequently, are alleviated by the proportionally longer leg length compared to the hip height, which require greater limb excursion (Gatesy and Biewener 1991) and longer stance periods (therefore higher DF) as a result of a more crouched posture (Figure 1.6). Thus, it provides evidence for the physiological constraints being circumvented by having a more compliant limb (Usherwood 2013).

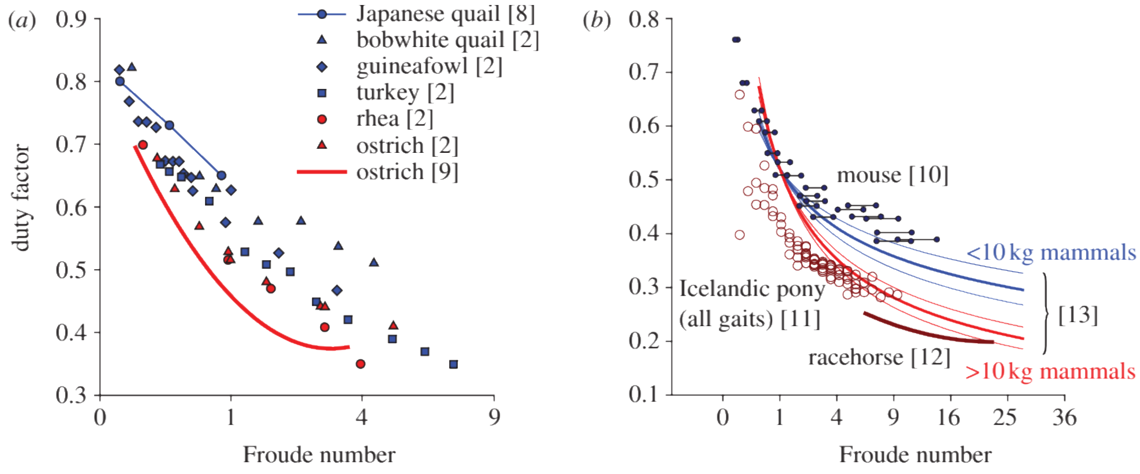

Figure 1. 6. The relationship between DF with increasing Fr across (a) birds and (b) mammals of different body sizes. Bold lines represent the lines of best fit for each of the species included into the analysis. Small species ($>$ 10 kg) are in blue, whilst large species ($<$ 10 kg) are in red. The uncertainty on the Fr of mice is due to the lack of precise measurements on their effective limb length, which is assumed to be 2-3 cm long. Taken from Usherwood (2013).

Usherwood (2013) hypothesis about postural scaling is in line with previous findings on the effects of animal size on the cost of locomotion – i.e. the rate of energy used per kilogram at running – and the time available for force production on each stride. By measuring the costs of locomotion and the average time of foot contact to the ground in 5 species of running mammal differing three orders of magnitude in body size (from 32 g to 141 kg), Kram and Taylor (1990) suggested that the energetic costs decrease with increasing size as a result of longer stance periods for muscles to generate forces supporting the limb. In other words, the (absolute) longer t_{stance} as a result of (absolute) longer legs, allow active muscles to generate forces at a slower rate, which explains why large mammals show lower energetic demands compared to smaller mammals. The ground-contact time is also proportional to the cost of locomotion in birds, explaining 70-90% of the increases in energy costs with speed (Roberts et al. 1998).

Although, the rate of force generation hypothesis predicts the costs of locomotion of running species, it makes assumptions that obliviate basic physiological aspects of muscles restricting its ubiquity only to terrestrial locomotion. For instance, the energetic costs of force development are not only a result of muscle work to develop forces opposing gravity – as assumed by (Kram and Taylor 1990) – but they are also influenced by the costs of different rate changes in muscle length (Alexander 2005) and the cost associated to muscle activation-relaxation (Pontzer 2016) that are likely important for predicting the energetic costs of climbing or flight. For terrestrial locomotion itself, this model neglects the muscle work done to swing the limbs, which may underestimate the overall energetic costs of locomotion; swing phase can account for up to over 25% of the total energy used during a stride in guinea fowl (*Numida meleagris*) (Marsh et al. 2004). A unified model that can predict the energetic costs of locomotion based on the amount of activated muscle required to power locomotion, irrespective of the locomotor mode, remains undeveloped and it is a key area for future study.

1.4.3. Sex

While natural selection drives phenotypical differences among species, intraspecific variation within sexes of the same species is mainly driven by sexual selection. Phenotypic variation between sexes is highly correlated to the specific reproductive strategies of the individual of a species – i.e. if one sex is polygamous or both are monogamous – and to the role that each of the sexes take for parental care (Owens and Hartley 1998). Thus, species with sexually dimorphic individuals are often the result of strong intrasexual selection upon males (most commonly it is on males) that intensely compete for mates and where females are choosy (Bateman 1948), given the disparate resource allocations for gamete formation that are usually lower in males (Trivers 1972).

Extensive research on sexual dimorphism exists; however, the physiological basis underlying these adaptations remains poorly understood (Lailvaux and Husak 2014).

Sexual dimorphism in locomotor performance is also influenced by sexual selection. For example, a study in the territorial lizard (*Crotaphytus collaris*) indicate that increases in fitness (i.e. number of offspring sired) of the males are intimately linked to higher sprinting speed and territoriality (Husak et al. 2006). Interestingly, the females of this species show similar absolute sprinting speeds compared to males, despite being smaller (Peterson and Husak 2006), suggesting an improved locomotor capacity on females compensating a reduction on sprinting speed when females are gravid (Husak 2006). Far fewer examples of sexual dimorphism on locomotor performance in ground dwelling birds exist. However, two previous studies in the leghorns and the Svalbard rock ptarmigan have sought to contribute into that gap of knowledge. In the first case using two varieties of leghorns – the bantam and the standard breeds, it has been reported that males run at higher sustainable speeds that are linked to intrasexual agonistic behaviours, while females move more economically with more upright limbs to compensate for the cost of carrying extra weight during gravity (Rose et al. 2015a). In the Svalbard rock ptarmigan, males (relative to females) have a higher top speed, are capable of three locomotor gaits and greater locomotor efficiency in terms of the metabolic cost of transport, which are thought to be important to engage in combat against other males to defend their breeding territories. The lower speed of the females, on the other hand, is thought to be linked to greater resource partitioning towards reproductive effort such as development of the eggs, which can have a detrimental effect on the hindlimb musculoskeletal system, or by larger visceral mass associated with the reproductive tissues and organs (Lees et al. 2012a). By comparing the kinematics of terrestrial locomotion in both sexes in the wild under natural conditions, in **chapter 2** I increase understanding of the ecological and evolutionary significance of sexual dimorphism and selection to locomotor performance previously reported in the Svalbard rock ptarmigan.

1.4.4. Substrate

The physical properties of a given substrate are correlated with the work muscles must exert to counter the GRF and push-off the body during locomotion. However, the vast majority of studies on animals have been conducted on a treadmill, where substrates are firm and grippy (e.g. Alexander and Jayes 1983; Cavagna et al. 1977; Gatesy and Biewener 1991; Heglund et al. 1982a; Heglund et al. 1982b). The first detailed attempt to examine the effects of increased substrate compliance on the leg dynamics of running humans was conducted by McMahon and Greene (1979). By instructing eight males to run over plywood tracks of different compliance, including an extremely compliant pillow track, they found that greater track compliance resulted in increased foot contact times, reduced top speeds and a reduction in the initial peak ground reaction force compared to firmer tracks. Similarly, a number of studies have examined if the energetics and kinematics of treadmill-based locomotion, where subjects run over a compliant belt, were comparable to studies conducted on firm ground, finding conflicting results. Most studies on human locomotion report that movements of the treadmill itself shorten the stride cadence (Aaslund and Moe-Nilssen 2008; Elliott and Blanksby 1976; Nelson et al. 1972; Riley et al. 2008; Riley et al. 2007), which makes strides shorter and faster but with proportionally longer t_{stance}'s, that directly reduce GRF – therefore muscle work – making treadmill locomotion ~ 10% cheaper than overground locomotion (Daniels et al. 1953). However, these results are not ubiquitous as Wank et al. (1998) reported shorter t_{stance}'s in their study. Furthermore, other studies report negligible differences when comparing treadmill and overground locomotion (Van Ingen Schenau 1980). Discrepancies between treadmill and overground kinematics have been reported in nonhuman mammals including mice (Herbin et al. 2007), cats (Blaszczyk and Loeb 1993) and horses (Buchner et al. 1994). The reasoning as to why the kinematic and dynamic departures between both approaches are found is arguably the result of net energy transfers from the moving belt during stance, which reduces the amount of work required by muscles (Buchner et al. 1994). Also, elastic recoil of the compliant treadmill belt could also contribute in part to the greater energetic efficiency on treadmills (Kerdok et al. 2002).

Most studies on locomotion standarise the friction coefficient between the animal foot and the substrate. Slippery substrates, like ice, are challenging because the frictional forces are usually lower than the shear forces generated in the stance, hindering body weight support and horizontal thrust, and increasing the risk of fall and injury. Specifically, a slip event occurs if the required friction is higher than the available friction (i.e. foot-substrate friction coefficient) (Redfern et al. 2001). To keep stable locomotion, humans may reduce their stride lengths and cadence to reduce the required friction (Cappellini et al. 2010; Cham and Redfern 2002). Keeping the COM above the supporting limbs also decreases the chances of slipping (Cappellini et al. 2010). These kinematic adjustments may be representative for avian bipeds, despite the disparate body geometries in both groups, as shown for the Guinea fowl (*Numida meleagris*) by Clark and Higham (2011).

Real world substrates, however, are seldom solid and the vast number of them are composed of an array of particles of differing sizes, such as sand, mud, gravel and snow. Often, the interaction between the supporting limb and granular media are complex mainly because grains flow if the yield stresses between particles are exceeded (Li et al. 2012; Li et al. 2013), which ultimately leads to energy loss to the substrate (Li et al. 2012). Under such conditions, energy recovery through elastic elements in legged locomotion decrease while mechanical work done to the substrate increase (Lejeune et al. 1998; Li et al. 2012; Zamparo et al. 1992). In humans walking on sand, for example, the additional mechanical work that must be done to compensate for the energy loss to the substrate may increase up to a 150% compared to walking on firm ground (Lejeune et al. 1998). Similarly, in the zebra-tailed lizard, *Callisaurus draconoides*, almost 20% of the mechanical energy of the centre of mass is lost to the sand, which is compensated by extra work of the hindlimb muscles (Li et al. 2012). Studies of granular media in birds have provided meaningful data on the mechanisms by which this group, and probably their theropod ancestors (Falkingham and Gatesy 2014; Gatesy and Falkingham 2017; Turner et al. 2020), deal with granular sedimentary substrates in terms of foot subsurface rotation and pattern changes of plantar pressure over the firm ground and sand (Zhang et al. 2017); although the aim of these studies has focused only into the foot kinematics-substrate contact interaction, rather than gait kinematics itself. Thus, it remains to further compare the basic kinematics of birds and how these are influenced over a greater array of substrates compared to *terra firma.*

Of particular interest for this thesis are the effects that snow has on the kinematics and energetics of locomotion. Snow may behave as a granular media when fresh and dry, but its mechanical properties change with the environment. For example, snow melts due to temperature increases, whereas snow crusts can be formed by snow compaction due to gravity and other external loadings, or the formation of an upper layer of ice after rain over snow (Bruland et al. 2004; Hagenmuller et al. 2014; Nicot 2004). Thus, snow properties in terms of the depth of the snow column and the supportiveness can drastically change in short time periods. These two parameters are arguably the most influential for locomotion, as they have profound effects on the energetics and the biomechanics of moving animals. For example, when foot sinking depths exceed 60% of the effective limb length, the energetic costs increase dramatically. This phenomenon has been demonstrated in human (Heinonen et al. 1959; Ramaswamy et al. 1966), elk (*Cervus elaphus nelsoni*), mule deer (*Odocoileus hemionus*) (Parker et al. 1984), white-tail deer (*Odocoileus* *virginianus*) (Mattfeld 1974) and barren ground caribou (*Rangifer tarandus granti*) (Fancy and White 1987), where energy increases are attributed to the extra work required to lift the supporting limb. In the majority of studies, however, a common finding is that behaviour is key to optimise the related energetic cost of locomotion. Namely, arctiodactyls (Telfer and Kelsall 1984), canids (Crête and Larivière 2003; Droghini 2016) and humans (Heinonen et al. 1959; Ramaswamy et al. 1966) will reduce their travel speed to keep the energetic imbalances caused by snow under acceptable margins. Other species would use specific niches where snow is supportive enough to prevent foot sinking (Murray and Boutin 1991; Pozzanghera et al. 2016). Data on foot sinking depth and snow supportiveness is non-existent for avian species, in spite of a large number of ground dwelling birds inhabiting temperate regions. By studying the effects of these snow parameters upon terrestrial locomotion in the Svalbard rock ptarmigan, we add a valuable data point that may be relevant to other avian species and also reveal new factors key to our understanding of animal locomotion in the wild.

1.5. The Svalbard rock ptarmigan

The Svalbard rock ptarmigan is a ground dwelling species member of the family Phasianidae, subfamily Tetraoninae, endemic to the Norwegian archipelago of Svalbard (77° – 81° N) that permanently inhabits these islands the whole year round (Blix 2005). Given that the ptarmigan does not migrate to more amenable latitudes, it faces extreme variations in environmental conditions with temperatures changing seasonally by up to ~40° C (Mortensen et al. 1983) and fluctuations in light from 24 hours of total daylight to 24 hours of total darkness. One important consequence of these environmental changes is that food sources and access to food intake become highly unpredictable (Blix 2005). These factors are of great relevance for the ptarmigan survival and the survival of other permanent residents in the Arctic including: Svalbard reindeer (*Rangifer tarandus* *platyrhynchus*) (Hansen et al. 2011) and the Arctic fox (*Vulpes lagopus*) (Hansen et al. 2013) (Hansen et al. 2013). Ptarmigan, however, have evolved physiological and behavioural mechanisms to cope with this extreme environment. For instance, the ptarmigan feathers have air-filled sacs between barbules that increase light reflectance giving the characteristic white winter plumage to these birds, serving both for camouflage and for heat isolation during winter (Dyck 1979). Conversely during summer months, these birds possess a more pigmented plumage that becomes whiter with the advent of shorter daylight periods at late August, indicating that moulting depends on photoperiod (Stokkan 1979). Similarly, food intake is linked to photoperiod, being higher at the beginning of Spring, when sunlight returns to the Arctic, until September when it disappears again until the following Spring (Stokkan et al. 1986). Body mass, on the other hand, is low at the beginning of spring and at increases to a maximum in late Autumn (Stokkan et al. 1986). Such increases are mainly in body fat (Stokkan et al. 1986). The increases of body mass in spite of a reduction in food intake may be explained by a reduction in locomotor activity dictated by higher concentrations of plasma melatonin during winter (Reierth et al. 1999). By reducing locomotor activity, ptarmigans are capable of avoiding any further energetic imbalance, in particular when food intake during winter is unpredictable (Hansen et al. 2013; Mortensen and Blix 1985; Stokkan et al. 1986). Yet, unpredictable changes in the seasonal variation in the Svalbard Archipelago as a result of climate change that have increased over the past decades are likely to impact on the Svalbard ptarmigan survival, as they may not be able to adapt fast enough to these rapid changes.

The Arctic is among the most threatened ecosystems by climate change caused by anthropogenic activities. The warming rate observed at this region is well above the global average (Jansen et al. 2020) thereby resulting in the transformation of the Svalbard rock ptarmigan habitat in terms of food availability and competition. For example, although plant biomass is thought to increase with increasing temperatures, the production of bulbils of *P. viviparum*, a primary food item of the Svalbard rock ptarmigan chicks (Steen and Unander 1985), may be reduced to favour flowering production (Fan and Yang 2009), which is likely to affect the proper development of chicks prior to winter (Henden et al. 2017). Similarly, increased food competition for these bulbils due a climate change-driven increase in the population of another transient herbivore during the breeding season, the pink-footed geese *Anser brachyrhyncus*, may constitute a major threat to the Svalbard rock ptarmigan (Henden et al. 2017) as this food item may be depleted earlier before the Svalbard rock ptarmigan start to build up the fat reserves key to winter survival (Grammeltvedt and Steen 1978). Higher predator pressures could be also expected if the timing of snow cover appearance and retreat is altered, creating a mismatch between plumage colour with the background (Henden et al. 2017); ultimately plumage moulting is photoperiod dependent (Höst 1942). All these changes are expected to contribute to greater energetic imbalances affecting the Svalbard rock ptarmigan fitness in the mid- and long-term.

Extreme weather events, on the other hand, are likely to have the strongest effect on the Svalbard Archipelago fauna, including the Svalbard rock ptarmigan, as they can drastically change population numbers from one year to another (e.g. Hansen et al. 2011; Hansen et al. 2013). In particular, relatively warmer days coupled with rain-on-snow events in winter promote stronger defrost-freezing cycles of the snowpack that result in the formation of ice layers that cover plant food items on or beneath the ground (Cohen et al. 2015), on which large herbivores (e.g. Svalbard reindeer (Hansen et al. 2011)), small herbivores (e.g. sibling vole (Yoccoz and Ims 1999) and the Svalbard rock ptarmigan (Hansen et al. 2013)) feed upon. Thus, a decrease in the population of these species can be expected after years with warmer winters and relatively higher number of days with rain on snow events, as many individuals will not survive due the very limited food sources available (Hansen et al. 2013).

1.5.1. Svalbard rock ptarmigan locomotion – laboratory-based studies

Increases in body mass by external loads are correlated to increases in metabolic costs of transport (e.g. Marsh et al. 2006; Taylor et al. 1980; Tickle et al. 2013; Tickle et al. 2010). Following this line of thinking would imply that in winter, when the ptarmigan almost double their body weight via increase in subcutaneous fat reserves (Grammeltvedt and Steen 1978), the metabolic costs of locomotion would increase accordingly. The extra fat that these birds gain prior to the onset of winter is thought to prevent heat losses and provides an extra source of energy that could be used for a short time, while new food sources are found although this can sustain them for only a short time (14 days approx.) (Grammeltvedt and Steen 1978; Mortensen et al. 1983). However, the Svalbard rock ptarmigan possess one of the most striking adaptations among many Arctic species: winter males are capable of transporting the extra body fat at no extra metabolic cost (Lees et al. 2010).

It has been hypothesised that the improved locomotor performance of the Svalbard rock ptarmigan males is a trait under strong sexual selection, given that males often combat vigorously with other males to establish and defend a breeding territory, thus increasing fitness (Lees et al. 2012a; Steen and Unander 1985; Unander and Steen 1985). Fitness in females, in contrast, is more related to number and survival of the hatchlings until adulthood as only female ptarmigan provide parental care to the young (Steen and Unander 1985); thus, sexual selection may act upon other morphological traits that remain unknown. The improved locomotor capacity of the males rapidly develops in subadult prior their first winter, prioritising a developed locomotor system arguably to move more efficiently while foraging in winter, and for future reproductive success for their first mating season (Lees et al. 2012b). Given that females do not have the same locomotor capacities as males, it is assumed that their locomotor capacity remains very similar compared to sub adult females. Yet it is unknown how locomotor perfomance develop on females.

Despite the increasing knowledge on locomotion in the Svalbard rock ptarmigan, several questions have also arisen regarding the applicability of these findings to wild populations of the species. Without validating the ptarmigan locomotion models obtained under the idealised controlled conditions typical of laboratory-treadmill experimental design by ground truthing them with data on ptarmigan freely moving on their natural environment, it is difficult to assess the utility of extrapolating predictions from these models and determine if they are meaningful in a biological, ecological and evolutionary context. Data validation may also be particularly useful if it is viewed as a baseline for comparative analysis to gain insight on the effects that the change of one factor (e.g. substrate compliance) has over the Svalbard ptarmigan locomotion.

This has been particularly recognized by Nudds et al. (2011) as they found it difficult to explain the occurrence of a grounded running gait in the Svalbard ptarmigan running on treadmills. Grounded running is enigmatic as it is a transitional gait that benefits from bouncing-like mechanics of the COM while keeping permanent contact with the ground. While walking might be strongly related to foraging and aerial running may be linked to predation avoidance, it is not clear the evolutionary relevance of grounded running gait. Nudds et al. (2011) question if this gait is actually an artifact of treadmill-based studies or if it is naturally performed in the wild. Indeed, the ecological and evolutionary relevance of grounded running and the mechanisms by which the Svalbard ptarmigan are capable of keeping dynamic stability on highly variable snow, irrespective of sex, are explored in **Chapters 2** and **3.**

Another adaptation that is thought to be relevant for the Svalbard rock ptarmigan when moving over the snowy Arctic tundra are the snowshoe-like feet found in this species. In fact, the name *Lagopus* comes from the Greek “*lagṓ*” which means hare, and “*poús*” which mean feet, in clear reference to the feet densely cover by feather. Thus, snowy substrates have likely played a major role on shaping the ptarmigan feet. By increasing the foot surface via feet densely covered in feathers, it is possible to alleviate the foot loads exerted on ground, which are key to a more efficient locomotion on snow (Höhn 1977; Knapik et al. 1997; Muray and Larivière 2002; Whiteman and Buskirk 2013). Yet, all previous studies have not assessed the effects of snow has on ptarmigan locomotion. Therefore, it remains to be established up to what extend the results of previous treadmill-based studies can be extrapolated to the wild Svalbard rock ptarmigan, in particular by taking into account the effects of snow on locomotion that are explored in **chapter 4**.

1.6. Overview and thesis aims

A pressing question in all treadmill-based studies on animal locomotion is how representative are the results of their studies for wild populations of the same species. The Svalbard rock ptarmigan offers an opportunity to address how comparable are the treadmill-based approaches with animals moving on their natural environments were conditions depart from ideal and substrate becomes highly significant. I consider the evolutionary and ecological implications of the morphological and behavioural adaptations of ptarmigan locomotion through the interactions these birds have with the snowy substrate that they encounter.

The specific aims of this thesis are:

1) To determine how comparable are the kinematics of locomotion of the Svalbard rock ptarmigan males previously reported on treadmills to ptarmigan moving *in*

situ, at a self-selected speed using ground truth data obtained video recordings. I will test the hypothesis that reliable extrapolations can be made from treadmill-based studies to birds moving in their natural environment.

2) To determine how substrate influences the locomotor kinematics of wild female ptarmigan moving *in situ* compared to females on treadmills and wild males moving at comparable gaits, using ground truth data obtained from video recordings. I will test the hypothesis that females should move using faster but shorter strides and reduced stance phases when compared to wild males and to females on treadmills.

3) To assess, using trackways, the effects of footprint sinking depth and snow supportiveness on ptarmigan self-selected speed of locomotion and route choice, using video recordings, 3D photogrammetry and a thin blade force gauge. I will test the hypothesis that speed decrease as footprint depths increases and snow supportiveness decreasing.

4) To develop a species-specific predictive model to examine gait and speed preferences derived from stride length by measuring the latter directly from the trackways of the Svalbard rock ptarmigan. I will test the hypothesis that it is possible to acquire meaningful speed values solely from the trackways, data which can be used to better understand the activity patterns of this species.

Chapter 2

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

This chapter is a reprint of an article published in *Scientific Reports:*

Marmol-Guijarro, A.C., Nudds, R., Marrin, J.C., Folkow, L.P. and Codd, J.R. (2019). Terrestrial locomotion of the Svalbard rock ptarmigan: comparing field and laboratory treadmill studies. *Scientific reports* 9, 11451 (https://doi.org/10.1038/s41598-019-47989-6).

SCIENTIFIC REPORTS
natureresearch

OPEN

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

Received: 25 March 2019
Accepted: 25 July 2019

Andres C. Marmol-Guijarro[1], Robert L. Nudds[1], John C. Marrin[2], Lars P. Folkow[3] & Jonathan R. Codd[1]

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 locomotion[1]. 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 conditions[7]. 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 humans[16]. 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].

[1]Faculty of Biology, Medicine & Health, University of Manchester, Manchester, UK. [2]Faculty of Biological Science, University of Leeds, Leeds, UK. [3]Department of Arctic and Marine Biology, University of Tromsø – the Arctic University of Norway, Tromsø, Norway. Correspondence and requests for materials should be addressed to J.R.C. (email: jonathan.codd@manchester.ac.uk)

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 conditions[28].

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 energetics[36] while others have found no difference in either of these[37]. 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 expenditure[14]. Preliminary attempts to analyse substrate effects on Svalbard ptarmigan locomotion[40] 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 context[7]. 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°13′18″N, 15°38′30″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 locomotion[7]. 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 weight[42]. 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 grass[40].

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 $E_{\mathrm{p}} + E_{\mathrm{vk}}$ (the sum of the potential and vertical kinetic energy vectors) of the centre of mass (CoM)[7]. During walking E_{hk} and $E_{\mathrm{p}} + E_{\mathrm{vk}}$ fluctuate out of phase, whilst during grounded and aerial running E_{hk} and $E_{\mathrm{p}} + E_{\mathrm{vk}}$ are in phase[43]. To confirm gaits across the speed range for wild ptarmigans, we tracked the movement of the CoM of birds to determine E_{hk} and $E_{\mathrm{p}} + E_{\mathrm{vk}}$ 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 snow[45].

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).

		model		Slope		Intercept	
Gait	Parameter	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}	$1.022 + 2.051\ U$ $(t = 10.08, r^2 = 0.69,$ $n = 48, p < 0.001)$	$1.043 + 2.130$ $(t = 36.28, r^2 = 0.99,$ $n = 3, p < 0.001)$	−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 ANCOVA's 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.3.4.3[46] 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).

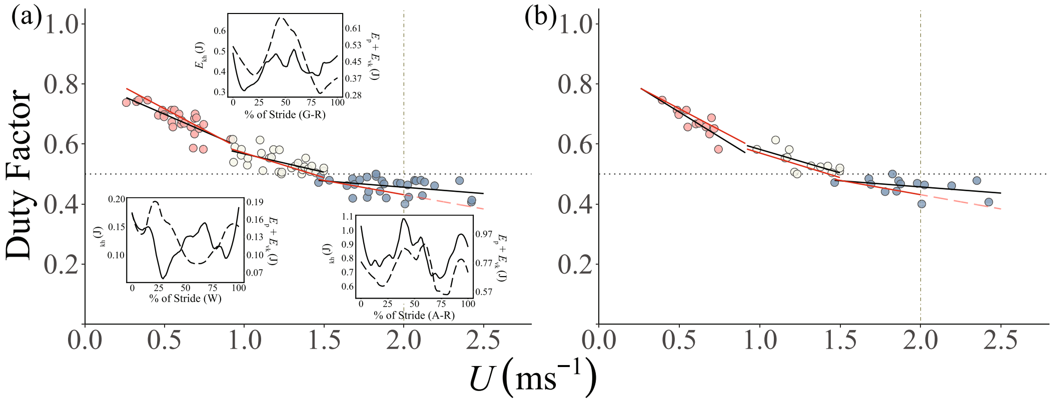

Figure 1. Duty Factor (DF) plotted against speed (U) for walking (red), grounded running (white) and aerial running (blue) gaits. (**a**) Includes data points for trials over all snow conditions and (**b**) includes data points for ptarmigan exclusively moving over a very hard snow surface only. Inlay figures in (**a**) represent the horizontal kinetic energy E_{kh}(J), and potential plus vertical, $E_p + E_{vk}$ (J) 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 data[7]. 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 recovery[43], 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 transfer[43]. DF was then used to separate grounded running (DF > 0.5) and aerial running (DF ≤ 0.5). The shift between these two gaits occurred at slightly lower speeds than previously suggested[7] 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. $\mathrm{Log}_{10}\, t_{\mathrm{stance}}$ and $\log_{10} t_{\mathrm{swing}}$ 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. $\mathrm{Log}_{10}\, t_{\mathrm{stance}}$ decreased linearly with $\log_{10} U$ and at a similar rate in both data sets (Fig. 2e, Table 1). $\log_{10} t_{\mathrm{swing}}$ 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). $\mathrm{Log}_{10}\, t_{\mathrm{stance}}$ 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). $\mathrm{Log}_{10}\, t_{\mathrm{swing}}$ 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 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 field[40]. 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 exploration[7], 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 efficient[7]. 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 efficiently[51].

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 birds[52]. 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 movement[53]. 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 faster[26]. 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 stride[55]. 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 humans[56]. 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 mass[59]. Grounded running is associated with more compliant limbs and improves visual stability through better control of head movements[47] and reduces the mechanical work of the bouncing non-locomotor body tissues[21]. 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 ice[60], 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 gait[7]. 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 predation[28]. 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

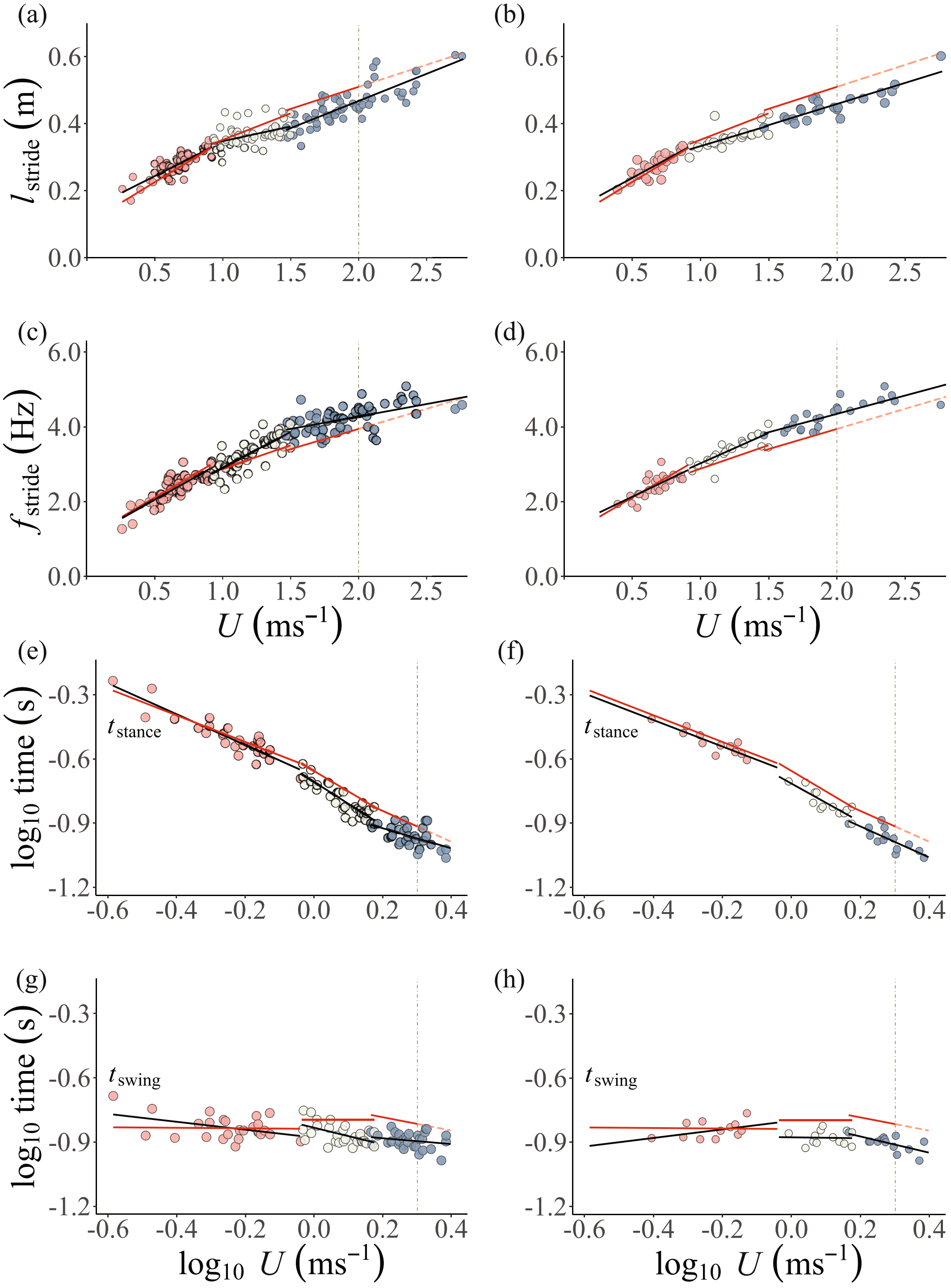

Figure 2. Kinematic parameters plotted against U for each gait - (**a**,**b**) l_{stride} against U; (**c**,**d**) f_{stride} against U; (**e**,**f**) $\log_{10} t_{stance}$ against $\log_{10} U$; and (**g**,**h**) $\log_{10} t_{swing}$ against $\mathrm{Log}_{10}\ U$. The left panels (a,c,e,g) represent 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 experiments[7]. 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 move[7]) and very high speeds (which are not aerobically sustainable for a long period of time[7]) 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 horses[65]. 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 animals[66]) 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. & Maloiy, 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 (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., Heliams, 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 inscriptus*) (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 mismathc 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. & Schmidtbleicher, 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., Merkens, 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 Quatermaster 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).

Acknowledgements

We thank John Lees for his contribution to the research project collecting the ptarmigan laboratory dataset. Nathan Thavarajah and Anna Marit Vik assisted with the collection of preliminary data used for refining field data collection techniques. The University of Tromsø and the University Centre in Svalbard provided logistical and field support. This work was financially supported by a Secretaría Nacional de Educación Superior Ciencia, Tecnología e Innovación del Ecuador (SENESCYT) award to A.M-G. and J.C., BBSRC grants (BB/G01138/1, BB/I021116/1) to J.C. and a Leverhulme Trust award (RPG-2012-759) to R.N.

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

Supplementary information accompanies this paper at https://doi.org/10.1038/s41598-019-47989-6.

Competing Interests: The authors declare no competing interests.

Supplementary Information

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

Andres C. Marmol-Guijarro[1], Robert L. Nudds[1], John C. Marrin[2], Lars P. Folkow[3] and Jonathan R. Codd[1*]

[1]Faculty of Biology, Medicine & Health, University of Manchester, Manchester, UK. [2]Faculty of Biological Science, University of Leeds, Leeds, UK. [3]Department of Arctic and Marine Biology, University of Tromsø – the Arctic University of Norway, Tromsø, Norway.

Contents

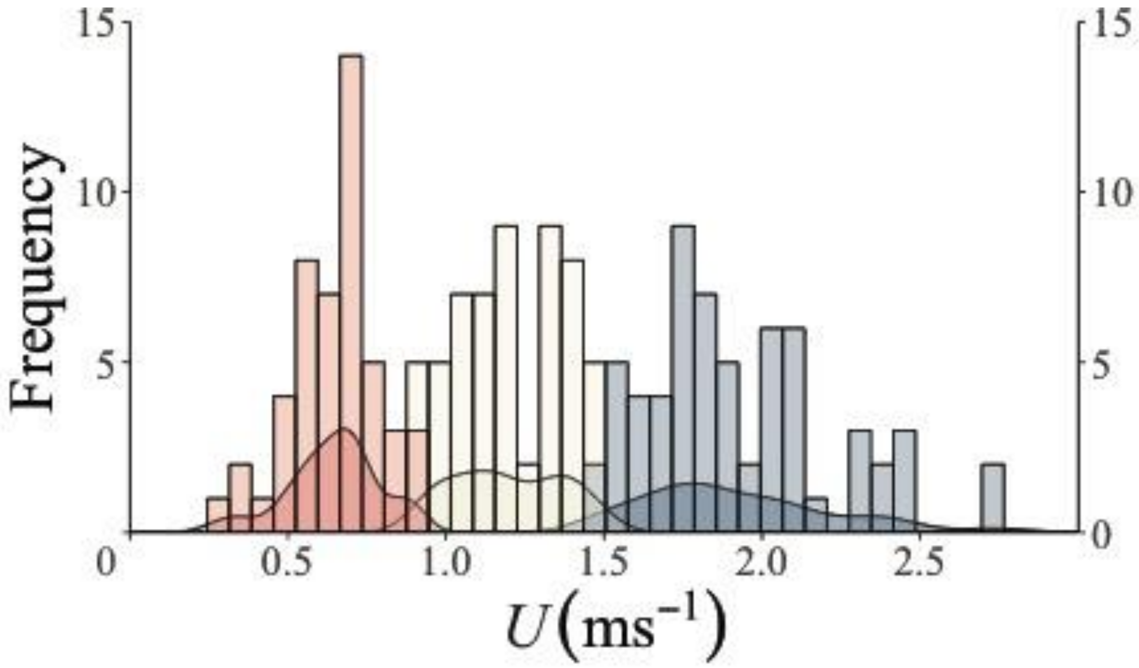

Figure S1. Self-selected speed (*U* ms^{-1}) frequency distribution across all trials. Walking, ground running and aerial running gaits are denoted by the red, white and blue bars, respectively. The birds demonstrate a preference for walking at a relatively fast speed around 0.7ms^{-1} and to a lesser extent aerial running around 1.7-1.85ms^{-1}. Generally, the birds infrequently moved at very slow (0.1-0.4ms^{-1}) and very high (>2.1ms^{-1}) speeds. There was no obvious preferred speed within the grounded running gait. Trials were binned into 0.07ms^{-1} speed increments across the full range. Axes show the frequency of trials.

Term	Hand test	Estimated Ram Resistance (Swiss rammsonde) (N)	Sample of footprint
	Object	range	
Soft	Four fingers	0–390	
Hard	Sharp pencil tip	> 390	

Table S1. Representative trackway footprints over snow of different hardness. Snow hardness measure are modified from [32].

Parameter	Covariate/ factor/ interaction	Model 1 d.f.	*F*	*P*	Model 2 d.f.	*F*	*P*	Model 13 d.f.	*F*	*P*	r^2
Walking											
l_{stride}	*U*	1, 44	0.431	0.668	1, 45	9.120	< 0.001	1, 46	9.287	< 0.001	0.65
	Year	1, 44	0.738	0.465	1, 45	1.649	0.106	*	*	*	
	Year × *U*	1, 44	-0.429	0.670	*	*	*	*	*	*	
f_{stride}	*U*	1, 44	-1.649	0.106	1, 45	8.270	< 0.001	1, 46	10.083	< 0.001	0.68
	Year	1, 44	-1.960	0.056	1, 45	-1.721	0.092	*	*	*	
	Year × *U*	1, 44	1.651	0.106	*	*	*	*	*	*	
Grounded running											
l_{stride}	*U*	1, 53	1.358	0.180	1, 54	3.910	< 0.001	1, 55	3.768	< 0.001	0.19
	Year	1, 53	1.176	0.245	1, 54	-1.176	0.245	*	*	*	
	Year × *U*	1, 53	1.357	0.180	*	*	*	*	*	*	
f_{stride}	*U*	1, 53	-1.448	0.154	1, 54	9.318	< 0.001	1, 55	9.620	< 0.001	0.62
	Year	1, 53	-1.289	0.203	1, 54	1.017	0.314	*	*	*	
	Year × *U*	1, 53	1.450	0.153	*	*	*	*	*	*	
Aerial Running											
l_{stride}	*U*	1, 57	-0.419	0.676	1, 58	11.461	< 0.001	1, 59	11.543	< 0.001	0.68
	Year	1, 57	-0.368	0.715	1, 58	0.343	0.733	*	*	*	
	Year × *U*	1, 57	0.422	0.675	*	*	*	*	*	*	
f_{stride}	*U*	1, 57	-0.005	0.996	1, 58	5.214	< 0.001	1, 59	5.268	< 0.001	0.31
	Year	1, 57	-0.029	0.977	1, 58	-0.158	0.875	*	*		
	Year × *U*	1, 57	0.006	0.995	*	*	*	*	*		

Table S2. Results of ANCOVAs testing for differences in l_{stride} and f_{stride} between the 2017 and 2018 seasons. l_{stride}, stride length; f_{stride}, stride frequency. Speed (*U*) is a covariate, Year is a fixed factor and Year × *U* is the interaction term within the model, d.f. are represented as (d.f., error d.f.). The adjusted r^2 values are reported for the third GLM analyses. In all cases the interaction term was not significant (Model 1) and was consequently removed from the model (Model 2). Similarly, no effect of year was found so the models were further simplified leaving only the speed term (effectively la regression analysis), which significantly affected l_{stride} and f_{stride} in all gaits (Model 3).

Gait	Parameter	model		Slope		Intercept	
		Field	Laboratory	z	p-value	z	p-value
Walk							
	l_{stride}	$0.127 + 0.222\,U$ ($t = 6.321$, $r^2 = 0.63$, $n = 25$, $p < 0.001$)	$0.102 + 0.246\,U$ ($t = 5.319$, $r^2 = 0.96$, $n = 3$, $p < 0.001$)	-0.426	0.667	0.705	0.478
	f_{stride}	$1.258 + 1.744\,U$ ($t = 5.208$, $r^2 = 0.54$, $n = 25$, $p < 0.001$)	$1.043 + 2.130$ ($t = 36.28$, $r^2 = 0.99$, $n = 3$, $p < 0.001$)	-1.137	0.271	0.941	0.347
	t_{stance}	$-0.666 – 0.619 \log_{10} U$ ($t = -6.257$, $r^2 = 0.80$, $n = 12$, $p < 0.001$)	$-0.646 – 0.623 \log_{10} U$ ($t = -7.368$, $r^2 = 0.98$, $n = 3$, $p < 0.086$)	0.040	0.992	-0.642	0.522
	t_{swing}	$-0.797 + 0.200 \log_{10} U$ ($t = 1.507$, $r^2 = 0.19$, $n = 12$, $p = 0.163$)	$-0.838 – 0.012 \log_{10} U$ ($t = -0.20$, $r^2 = 0.03$, $n = 3$, $p = 0.88$)	1.447	0.147	0.998	0.317
	DF	$0.871 – 0.330\,U$ ($t = -4.746$, $r^2 = 0.69$, $n = 12$, $p < 0.001$)	$0.858 – 0.281\,U$ ($t = -6.72$, $r^2 = 0.98$, $n = 3$, $p = 0.094$)	-0.589	0.555	0.261	0.795
Grounded running							
	l_{stride}	$0.211 + 0.122\,U$ ($t = 4.353$, $r^2 = 0.47$, $n = 23$, $p < 0.001$)	$0.194 + 0.158\,U$ ($t = 7.934$, $r^2 = 0.95$, $n = 5$, $p < 0.01$)	-0.888	0.373	–	–
	f_{stride}	$1.400 + 1.624\,U$ ($t = 6.737$, $r^2 = 0.68$, $n = 23$, $p < 0.001$)	$1.621 + 1.258\,U$ ($t = 5.728$, $r^2 = 0.92$, $n = 5$, $p < 0.05$)	1.203	0.230	–	–
	t_{stance}	$-0.715– 0.896 \log_{10} U$ ($t = -5.738$, $r^2 = 0.75$, $n = 13$, $p < 0.001$)	$-0.656 – 0.955 \log_{10} U$ ($t = -44.49$, $r^2 = 0.99$, $n = 5$, $p < 0.001$)	0.335	0.734	–	–
	t_{swing}	$-0.877 – 0.021 \log_{10} U$ ($t = 0.123$, $r^2 = 0.001$, $n = 13$, $p < 0.01$)	$-0.796 + 0.00 \log_{10} U$ ($t = 0$, $r^2 = 0.51$, $n = 5$, $p = 0.167$)	-0.117	0.904	–	–
	DF	$0.739 – 0.157\,U$ ($t = -3.442$, $r^2 = 0.52$, $n = 13$, $p < 0.001$)	$0.734 – 0.164\,U$ ($t = -18.18$, $r^2 = 0.99$, $n = 5$, $p < 0.001$)	0.140	0.889	–	–
Aerial Running							
	l_{stride}	$0.207 + 0.126\,U$	$0.247 + 0.131\,U$	-0.104	0.920	–	–

		($t = 8.034$, $r^2 = 0.75$, $n = 24$, $p < 0.001$)	($t = 2.484$, $r^2 = 0.75$, $n = 4$, $p = 0.131$)				
	f_{stride}	$2.384 + 0.981\ U$ ($t = 6.354$, $r^2 = 0.65$, $n = 24$, $p < 0.001$)	$1.788 + 1.078\ U$ ($t = 3.12$, $r^2 = 0.82$, $n = 4$, $p = 0.089$)	-0.256	0.795	–	–
	t_{stance}	$-0.770 - 0.726 \log_{10} U$ ($t = -4.403$, $r^2 = 0.62$, $n = 14$, $p < 0.01$)	$-0.698 – 0.723 \log_{10} U$ ($t = -3.32$, $r^2 = 0.85$, $n = 4$, $p = 0.08$)	-0.012	0.992	–	–
	t_{swing}	$-0.797 -0.380 \log_{10} U$ ($t = -2.839$, $r^2 = 0.4$, $n = 14$, $p = 0.24$)	$-0.722 – 0.311 \log_{10} U$ ($t = -1.71$, $r^2 = 0.59$, $n = 4$, $p = 0.23$)	-1.684	0.093	–	–
	DF	$0.539 -0.041\ U$ ($t = -1.449$, $r^2 = 0.15$, $n = 14$, $p = 0.045$)	$0.621 – 0.095\ U$ ($t = -1.992$, $r^2 = 0.67$, $n = 4$, $p < 0.185$)	0.967	0.332	–	–

Table S3. 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 for laboratory data and field data collected from birds moving over hard snow. 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.

Chapter 3

Does posture explain the kinematic differences in a grounded running gait between male and female Svalbard rock ptarmigan (*Lagopus muta hyperborea*) moving on snow?

This chapter is a draft of an article submitted to the journal of *Polar Biology:*

Marmol-Guijarro, A.C., Nudds, R., Folkow, L.P., Lees, J.J. and Codd, J.R. (in review). Does posture explain the kinematic differences in a grounded running gait between male and female Svalbard rock ptarmigan moving on snow? *Polar Biology*

Does posture explain the kinematic differences in a grounded running gait between male and female Svalbard rock ptarmigan (*Lagopus muta hyperborea*) moving on snow?

Andres Marmol-Guijarro[1], Robert Nudds[1], Lars Folkow[2], John Lees[3] & Jonathan Codd[1*]

[1]School of Biological Sciences, Faculty of Biology, Medicine & Health, University of Manchester, Manchester, UK. [2]Department of Arctic and Marine Biology, University of Tromsø - the Arctic University of Norway, Tromsø, Norway. [3]Department of Physics, Chemistry and Biology, Linköpings Universitet, Linköping, Östergötland, Sweden.

*Author for Correspondence:

Dr Jonathan Codd

e-mail: jonathan.codd@manchester.ac.uk

ORCID ID's:

Andres Marmol:	0000-0001-9316-540X
Robert Nudds:	0000-0002-7627-6324
Jonathan Codd:	0000-0003-0211-1786
Lars Folkow:	0000-0002-6580-9156
John Lees:	0000-0002-9627-1790

Declarations

Funding This research was supported by the Biotechnology and Biological Sciences Research Council (BBSRC), UK through awards to J.C. (BB/G011338/1, BB/I021116/1) and a grant from Secretaría de Educación Superior, Ciencia, Tecnología e Innovación (SENESCYT), Ecuador, awarded to A. M-G (AR2Q-000199-2016).

Conflicts of interest The authors declare no competing interests.

Ethics approval This project was conducted with ethical approval from the University of Manchester Ethics Committee and under research permits from the Governor of Svalbard Research in Svalbard (RiS) Project Numbers 10790, 11034 and 11248.

Consent to participate Not applicable.

Consent for publication Not applicable.

Availability of data and material The raw dataset generated during this project is available via the FigShare repository (https://doi.org/10.6084/m9.figshare.12205247).

Code availability Not applicable.

Authors contribution J.C. came up with the original concept and designed the study. J.C., A.M-G., R.N. L.F and J.L. all assisted in data collection in the field and laboratory, drafting, revision and approval of the final manuscript. A.M-G. and R.N. analysed the data.

Abstract

The majority of locomotor research is conducted on treadmills and few studies attempt to understand the differences between this and animals moving in the wild. For example, animals may adjust their gait kinematics or limb posture, to a more compliant limb, to increase stability of locomotion to prevent limb failure or falling on different substrates. Here, using video recordings, we compared locomotor parameters (speed range, stride length, stride frequency, stance duration, swing duration and duty factor) of female Svalbard rock ptarmigan (*Lagopus muta hyperborea*) moving in the wild over snow to previous treadmill-based research. We also compared the absolute and body size (body mass and limb length) corrected values of kinematic parameters to published data from males to look for any sex differences across walking and grounded running gaits. Our findings indicate that the kinematics of locomotion are largely conserved between the field and laboratory in that none of the female gaits were drastically affected by moving over snow, except for a prolonged swing phase at very slow walking speeds, likely due to toe dragging. Comparisons between the sexes indicate that the differences observed during a walking gait are likely due to body size. However, sexual dimorphism in body size could not explain the disparate grounded running kinematics of the female and male ptarmigan, which might be linked to a more crouched posture in the females. Our findings provide insight into how males and females moving *in situ* may use different strategies to alleviate the effects of a variable substrate.

Keywords: Arctic, sexual dimorphism, biomechanics, substrate

Introduction

Although terrestrial animals moving in the real world almost never experience stable substrate conditions, locomotion studies are overwhelmingly conducted through treadmill experiments (e.g. Abourachid 2000; Abourachid and Renous 2000; Nudds et al. 2010; Rubenson et al. 2004; Tickle et al. 2010; Watson et al. 2011). Attempts have been made to understand the influence of substrates, including the incorporation of additional factors affecting locomotion such as substrate friction coefficients with the feet (Cappellini et al. 2010; Clark and Higham 2011), substrate compliance (Lejeune et al. 1998) and/or substrate irregularities (Birn-Jeffery and Daley 2012; Daley and Biewener 2006; Daley et al. 2007; Daley et al. 2006). It is only by direct comparison, however, that the real effect(s) of substrate variations can be ascertained. For example, reductions in stride frequency (f_{stride}) and increases in stride length (l_{stride}) for a given speed (U) have both been reported in rodents and humans when moving ground and on treadmills (Herbin et al. 2007; Riley et al. 2008). When running humans also experienced greater moments acting around the limb joints due to increased ground reaction forces (GRF) caused by the relatively stiffer natural ground compared to the more compliant treadmill belt (Riley et al. 2008). On slippery substrates, the low frictional coefficient between the substrate and the feet makes it challenging to attain enough GRF, increasing the risk of missing the step and falling (Cappellini et al. 2010; Clark and Higham 2011). This is mitigated by ensuring that the centre of mass (COM) remains close to or directly above the supporting limb via reductions in the retraction angle of the limb, resulting in smaller l_{stride} in avian (Clark and Higham 2011) and non-avian bipeds (Cappellini et al. 2010). Unexpected changes in substrate can trigger the proprioceptive responses of limb muscles that alter limb-posture to facilitate either recovery of energy through elastic recoil or to absorb/produce mechanical energy depending on how the foot lands on the ground (Daley and Biewener 2006; Daley and Biewener 2011; Daley et al. 2007). Intrinsic factors such as differences between sexes can also have significant effects on the metabolic cost and kinematics of locomotion (Lees et al. 2012a). Generally, however, data documenting sex-specific locomotor characteristics are lacking, particularly for species moving over natural substrates *in situ* in their own habitats.

A broad range of experimental locomotor data demonstrates that limb posture is a major factor influencing limb biomechanics, locomotor energetics and the effectiveness of energy saving mechanisms (Reilly et al. 2007). Defining stability as “the ability of a system to return to a steady-state, periodic gait after a perturbation” following Full et al. (2002), comparative studies suggest that the more crouched postured species are inherently more stable and manoeuvrable during locomotion compared to species with relatively more upright and stiffer limbs (Daley and Usherwood 2010; Gatesy and Biewener 1991). This greater stability is a result of proportionally longer stance times (t_{stance}) that alleviate and redistribute GRF acting over the limb (Alexander and Jayes 1983; Andrada et al. 2013; Gatesy and Biewener 1991). Often, crouched-postured species also use bouncing gaits with duty factors (DF) greater than 0.5, meaning they grounded run with no aerial phase which is thought to improve stability (Abourachid and Renous 2000; Alexander and Jayes 1983; Andrada et al. 2013; Daley and Usherwood 2010; Gatesy and Biewener 1991); however, to our knowledge empirical data is lacking. Thus, it is possible that a more stable species with a more crouched posture would experience only minor changes in kinematics parameters when walking over natural substrates relatively to those over uniform ground.

Structural (Biewener 1989), physiological (Usherwood 2013) and biomechanical (Daley and Usherwood 2010) factors must combine to determine the limb posture of animals. The scaling of morphological components (i.e. muscles and bones) and related biomechanical concepts (i.e. stress and strain) are thought to drive the phenomenon whereby smaller species tend to have a more crouched posture and larger species have more upright limbs (Alexander and Jayes 1983; Biewener 1989; Gatesy and Biewener 1991; Jenkins 1971). Relatively small species have proportionally longer – i.e. the sum of all the leg segments – crouched limbs that move over a greater range of angles during the stance phase (t_{stance}) (Gatesy and Biewener 1991), allowing for higher duty factors (DF) that optimize the volume of active muscle to power locomotion (Usherwood 2013). These generalities hold true across a number of distantly related taxa, including members of the mammalian families of canids, felids, mustelids and ceratomorphids (Alexander and Jayes 1983; Biewener 1989), and avian representatives of the galliformes and palaeognates (Gatesy and Biewener 1991). However, any scaling effects are complex and not always uniform for phylogenetically close taxa or at an intraspecific level. For example, in felids, limb posture remains uniform among 9 species despite differing in body mass up to 41-fold (Day and Jayne 2007). Conversely, in cercopithecine monkeys of comparable body size, Polk (2002) found that extended limb postures were often associated to longer limb segments. Interestingly, size-dependent shifts in posture towards increased erectness with increasing body size is not always the case. In fact, among nine species of varanid lizards, including the small *Varanus brevicauda* (7.6 g) and the large *Varanus komodoensis* (40 kg), the largest species of the clade compensate for larger stresses of being larger by increasing the muscle mass and physiological cross-sectional area (PCSA; which is positively correlated with the muscle force output) of the muscles at the hindlimb joints (Dick and Clemente 2016).

The Svalbard rock ptarmigan (*Lagopus muta hyperborea*) is an ideal model species for examining limb posture during locomotion as its locomotor performance has been extensively studied, including comparative work spanning the laboratory and field (Marmol-Guijarro et al. 2019). Svalbard ptarmigan are also interesting as treadmill-based studies in these birds demonstrate that there is strong sexual selection towards improved locomotor performance in males compared to females (Lees et al. 2012a). Males use walking, grounded, and aerial running gaits with energy savings upon the transition to aerial running (Nudds et al. 2011). In contrast, females do not use an aerial running gait and their locomotion is *circa* 34% per kg more metabolically expensive than males moving at the same speed (Lees et al. 2012a). These differences in male and female performance are thought to result from sexual selection acting on the males, likely related to agonistic encounters with other males to secure a breeding territory (Unander and Steen 1985). To our knowledge, comparable studies analysing walking kinematics and limb posture in birds have only been made in leghorn chickens on treadmills (*Gallus gallus domesticus*). When comparing limb posture between sexes of large and bantam chickens, postural sex differences are only found in the larger variety, with females having a more erect limb posture despite being smaller than males, relatively, whereas no differences were found between both sexes of the small variety (Rose et al. 2016b; Rose et al. 2015). Whether if postural changes become apparent at the onset of maturity in the leghorns is unclear; however, evidence of this has been reported in the Chacma baboons *Papio hamadryas ursinus*, where adult males walk with more upright limbs than comparatively lighter females and younglings (Patel et al. 2013). In the case of leghorn, males experience proportionally larger increases in limb muscle mass than females (Rose et al. 2016a). This sex-specific difference may cause postural changes particularly in males at the onset of maturity. Similar to leghorns, the disparities in locomotor performance and size between male and female Svalbard ptarmigan are less evident in juveniles, which have comparable kinematics and energetics (Lees et al. 2012b). Adult male ptarmigan, however, are 6% heavier and possess longer limbs (172.7 mm) than adult females (153.2 mm) (Lees et al. 2012a; Steen and Unander 1985) which might lead to potential differences in limb posture.

Recently we compared locomotor kinematics in male Svalbard rock ptarmigan when moving on a treadmill and in the wild under natural conditions (Marmol-Guijarro et al. 2019).

Overall, the kinematics of locomotion were conserved when the birds were walking slowly and aerial running, however important differences were found during grounded running. When moving on snow with a grounded running gait, the limb kinematics of male ptarmigan showed a reduction in l_{stride} and an increase in f_{stride}, presumably because of an early retraction of the limb moments before the foot lands on the ground. By making this adjustment males would be capable of stabilizing their body, if needed, after an unexpected perturbation caused by the snowy substrate (Daley and Biewener 2006; Daley et al. 2006; Seyfarth et al. 2003). Females in the wild would be affected by snow as well; however, it is unclear if they will alter kinematic adjustments in response to the uneven and highly variable snowy substrate, irrespectibly of their gait.

Redressing the lack of comparable wild data for female ptarmigan was the principal aim of our current research. Accordingly, here, we compare the gait kinematics of female Svalbard rock ptarmigan moving *in situ* over snowy substrates to a previous report on females moving on treadmills (Lees et al. 2012a), to determine how substrate affects their locomotion. We also test how comparable are the effects of snow over the limb kinematics between female ptarmigan with the data previously published for wild male ptarmigan by Marmol-Guijarro et al. (2019). Given that the males of this species are larger than the females, strategies to negotiate with snow would be dynamically comparable if the spatial (i.e. l_{stride}) and temporal (i.e. f_{stride}, t_{stance} and t_{swing}) kinematic parameters of the limb are scalable after accounting for body size (Alexander and Jayes 1983). As snow is a common factor affecting locomotion in both sexes, we hypothesize that walking and grounded running in wild female ptarmigan be dynamically similar to the kinematics of the wild males. In other words, females should use shorter but faster strides, with reduced periods of absolute t_{stance} to support the body within each stride (Abourachid and Renous 2000; Alexander and Jayes 1983; Gatesy and Biewener 1991), all of them scalable to the limb kinematics of the males.

Material and methods

The terrestrial locomotion of wild female Svalbard ptarmigan *(L. muta hyperborea, n* = 58) moving over snow in Adventdalen and adjacent side valleys (78° 18’ 13’’ N, 15° 38’ 30’’ E) in Spitzbergen on the Svalbard archipelago was examined through video recordings during spring (April-May) in 2017, 2018, and 2019, coinciding with the beginning of the breeding season. During this period the midnight sun was already present, the birds are at their lowest seasonal body weight and females are not egg bearing (Steen and Unander 1985;

Stokkan et al. 1986). Females were distinguished from males by the presence of a relatively thin dark eye stripe, their reduced supra-orbital red combs, and by their quieter ‘kee-ah kee-ah’ calls (as opposed to the thicker eye stripe, pronounced combs and characteristic loud ‘aarr-aa-ka-ka’ calls in males). Each video recording consisted of filming a bird moving parallel across the camera frame (held at a fixed height and distance from the subject during recording) over level ground, at either 25 frames per second (fps) with a SONY® Handycam HDR-XR250 during the 2017 season or at 100 fps with a SONY® Cyber-shot RX10 III (SONY® Corporation) during the 2018 and 2019 seasons. Immediately after the bird had moved out of camera shot, a 1 metre scale bar was carried into the frame and held directly over the trackways left by the bird in order to measure *U*. Pseudo-replication of the data was avoided by marking data location sites with GPS and using each location only once, as the Svalbard ptarmigan are highly territorial during the breeding season (Stokkan et al. 1986).

From the 58 video recordings obtained, f_{stride} was calculated from 1-3 consecutive strides and l_{stride} derived by dividing *U* by f_{stride}. t_{stance}, t_{swing}, and *DF* were also calculated from the high-speed (100 fps) recordings. We considered the beginning of stance immediately after foot was fully loaded on the ground, while the end of stance was marked immediately after the limb began protraction. From the high-speed recordings we also estimated the mechanical energy (the sum of the potential (E_p) and kinetic (E_k) energies) of the COM using the same method for male ptarmigans as described in Marmol-Guijarro et al. (2019). A mean body mass of 476.7 g for the females was obtained from literature (Lees et al. 2012a). Previous treadmill research by our group found that females are restricted to walking and grounded running gaits with a subsequent lower top speed (Lees et al. 2012a) than males, which can make use of an additional aerial running gait (Marmol-Guijarro et al. 2019; Nudds et al. 2011). Gaits were determined by the fluctuations in potential and kinetic energy of the COM (Cavagna et al. 1977). Grounded and aerial running were further identified by the presence of an aerial phase (i.e. $DF < 0.5$). The analyses of the video recordings were conducted in Tracker® v.5.1.2 (Open Source Physics).

Prior to data analyses, all data points for each wild female ptarmigan were allocated to a specific gait based in phase relationship of E_p and E_k of the COM: in a walking gait E_p and E_k fluctuate out of phase, whilst in a grounded running gait E_p and E_k fluctuate in phase. Gait changes occur at *U* ranging from 0.85 to 0.95 ms^{-1}. For analysis in this paper, the data from females moving on treadmill reported by Lees et al. (2012a) was placed into either a walking or grounded running gait based on the speed ranges of the wild females. We first analysed the kinematics of locomotion of female ptarmigan moving *in situ* over snowy ground and compared it to the corresponding treadmill data using linear models (LM). LM were then used to test whether limb kinematics within each gait changed in a similar way in both sexes (using male data from Lees et al. (2012a) and Marmol-Guijarro et al. (2019)) when moving over snowy substrates *in-situ* using U as a covariate. Initially, both the slope and the intercept were tested for differences. The resulting model was then simplified by removing the interaction term (sex × U) if it was non-significant (i.e. similar slopes), and the LM was rerun to test only for differences in the intercepts. Shapiro-Wilks tests were used to ensure the residuals of the linear regressions and LMs approximated a normal distribution. To conform to the assumption of normally distributed data, in some cases kinematic parameters were transformed to $\log_{10}$.

Male ptarmigan are larger than females and differences in body mass and limb length are known to affect leg kinematics. Therefore, two sets of sex comparisons were done. The first set was analysed using the absolute value for each kinematic parameter regressed against U, where body mass and limb length effects were not considered. Then to account for size effects and test if male and female ptarmigan move in dynamically similar way, the second analysis used transformed kinematic parameters by relating them to hip height (h_{hip}), taken from Lees et al. (2012a), and gravity (g), following Alexander and Jayes (1983): stride length ($\hat{l}_{\mathrm{stride}} = l_{\mathrm{stride}}/h_{\mathrm{hip}}$), stride frequency ($\hat{f}_{\mathrm{stride}} = f_{\mathrm{stride}}/\sqrt{g/h_{\mathrm{hip}}}$), stance ($\hat{t}_{\mathrm{stance}} = t_{\mathrm{stance}}/\sqrt{h_{\mathrm{hip}}/g}$) and swing ($\hat{t}_{\mathrm{swing}} = t_{\mathrm{swing}}/\sqrt{h_{\mathrm{hip}}/g}$), and $\hat{U}$ ($U/\sqrt{h_{\mathrm{hip}} \times g}$) as the speed covariate. DF is dimensionless and was therefore not corrected when regressed against $\hat{U}$. All the statistical analyses were conducted in R v. 3.6.6 “Holding the Windsock” (R Core Team 2020) and the results are summarized in Tables 1, 2 and S1.

Results

Comparison of absolute values for wild and treadmill locomotion kinematics in females

When compared to the previous treadmill studies (Lees et al. 2012a) females did have a higher top speed in the wild, increasing by up to 8% to a maximum of 1.63 ms^{-1} (Fig. 1) but in line with treadmill studies they never displayed an aerial running gait (Fig. 1A). Overall locomotor kinematics for the female ptarmigan are similar in both walking and grounded running gaits when moving under laboratory and field conditions.

Within the walking gait, l_{stride} and f_{stride} increased linearly with increasing U (Fig. 1B & C; Table 1). t_{stance} decreased curvilinearly with U and DF decreased linearly with U (Fig. 1A & D; Table 1). The only difference between the two groups was that t_{swing} was slightly higher in females walking in the wild at the slowest speeds and decreased at a faster rate with *U* than in females walking on treadmills (Fig. 1D; Table 1).

For grounded running, l_{stride} and f_{stride} increased linearly with *U* (Fig. 1B & 1C; Table 1). t_{stance} and t_{swing} decreased linearly and curvilinearly with increasing *U*, respectively (Fig. 1D; Table 1). Similar to the walking gait, *DF* decreased linearly with *U* (Fig. 1A; Table 1).

Comparison of absolute values for wild kinematics between females and males

For the walking gait, l_{stride} and f_{stride} increased linearly with increasing *U* at the same rate in males and females. However, l_{stride} and f_{stride} were lower (14%) and higher (16%) across all walking speeds in females (Fig. 2A & B; Table 2), respectively. With increasing *U*, t_{stance} and t_{swing} decreased curvilinearly at the same rate for both sexes. t_{stance} was shorter across all speeds in females; however, t_{swing} was similar for both sexes at all speeds (Fig. 2C; Table 2). Consequently, *DF* is lower in females at the slowest speeds relatively to the *DF* of males but becomes similar at the fastest walking speeds for both sexes (Fig. 2D; Table 2).

Within the grounded running gait, females showed lower l_{stride} at the slowest grounded running *U* that progressively became similar to the ones observed in the males as they moved faster. The opposite was true for f_{stride}, where females took faster strides at the slowest grounded running *U*, that became comparable to the f_{stride} values observed in males as they moved faster (Fig. 2A & B; Table 2). t_{stance} and t_{swing} decreased curvilinearly with increasing *U* and was similar across all values of *U* for both sexes (Fig. 2C; Table 2). Therefore, *DF* was also similar at all speeds in both sexes (Fig. 2D; Table 2).

Body size-corrected kinematics of wild females and wild males

After accounting for body mass and limb length, most of the differences between sexes reported above during the walking gait disappeared, whereas differences in $\hat{t}_{\text{swing}}$ became apparent. $\hat{l}_{\text{stride}}$ and $\hat{f}_{\text{stride}}$ increased linearly with, and were similar at all values of, $\hat{U}$ for males and females (Fig. 2E & F; Table 2). $\hat{t}_{\text{stance}}$ decreased curvilinearly with $\hat{U}$, and again no differences were detected between the sexes (Fig. 2G, Table 2). $\hat{t}_{\text{swing}}$ decreased curvilinearly with $\hat{U}$ at the same rate for each sex. Across all $\hat{U}$, however, females had a greater $\hat{t}_{\text{swing}}$ (Fig. 2G, Table 2). Concordant with the non-size-corrected results above, females had a lower *DF* at lower $\hat{U}$ than the males, but their *DF* converged at the highest $\hat{U}$ (Fig. 2H, Table 2). Thus, the differences in l_{stride}, f_{stride} and t_{stance}, could be attributed to the unequal body mass and limb lengths of males and females, because those differences disappeared after size correction.

In contrast to the walking gait data, all sex differences identified in the relationships between the absolute kinematic parameters and U within a grounded running were conserved after accounting for the effects of body mass and limb length. $\hat{l}_{\mathrm{stride}}$ increased curvilinearly with $\hat{U}$ and was longer in males at lower $\hat{U}$, but, conversely, longer in females at higher $\hat{U}$ (Fig. 2E; Table 2). $\hat{f}_{\mathrm{stride}}$ increased with $\hat{U}$. Males had a higher $\hat{f}_{\mathrm{stride}}$ at higher $\hat{U}$ than females, but their $\hat{f}_{\mathrm{stride}}$ converged at the lowest grounded running gait $\hat{U}$ (Fig. 2F, Table 2). $\hat{t}_{\mathrm{stance}}$ and $\hat{t}_{\mathrm{swing}}$ decreased in a curvilinear manner with increasing $\hat{U}$ and decreased at a similar rate in males and females. Females, however, had greater $\hat{t}_{\mathrm{stance}}$ and $\hat{t}_{\mathrm{swing}}$ than the males across all $\hat{U}$ (Fig. 2G; Table 2). Despite these differences, DF was similar in each sex and decreased linearly with increasing $\hat{U}$ in both (Fig. 2H, Table 2). In contrast to the sex differences in the absolute values for the walking gait, body size cannot explain the kinematic differences in grounded running between male and female ptarmigan.

Discussion

Generally, walking in females, aside from t_{swing}, was not greatly affected by moving over snow relative to on a treadmill (Fig. 1). The robustness of a walking gait over snow was found previously in males (Marmol-Guijarro et al. 2019) where an increased stability is achieved via passive mechanics of the musculoskeletal system (Jindrich and Full 2002) (Jindrich and Full 2002) in tandem with the presence of a period of double support, thereby contributing to lower lateral displacements of the centre of mass (COM) after by a medio lateral perturbations compared to a running gait (Qiao et al. 2012; Qiao and Jindrich 2014). The greater absolute t_{swing} observed in the wild females at very slow walking U, compared to females on treadmills, could be caused by a reduction in the toe clearance. Toe dragging was observed in the trackways associated with very slow, which would increase the length of time it took to swing the limb (see Fig. S1), although snow hardness and/or depth may also be important. Toe dragging may be the best option, as increasing toe clearance by lifting the foot clear of the snow during each stride could potentially impose greater energetic penalties for each stride (Gates et al. 2012; Wu and Kuo 2016). The absence of an effect on t_{swing} at faster speeds likely reflects the fact that toe dragging is not an option when moving faster as the risk of falling, limb failure or injury becomes too great (Gates et al. 2012; Schulz 2011).

Interestingly, and unlike the findings for male ptarmigan (Marmol-Guijarro et al. 2019), there were no differences in the kinematics of a grounded running gait for females in the wild when compared to the treadmill. This result was surprising as faster gaits are usually more susceptible to destabilization of the COM because of the relatively greater time spent with only one limb on the ground (Qiao et al. 2012; Qiao and Jindrich 2014), particularly when moving faster over a highly irregular substrate like snow. Birds minimize the risk of falling by a reduction of l_{stride} and an increase in f_{stride}, achieved by an earlier retraction of the limb just before the stance phase (Bhatt et al. 2005; Birn-Jeffery and Daley 2012; Cappellini et al. 2010; Clark and Higham 2011; Daley and Biewener 2006; Daley et al. 2006), that ensures that the COM passes over the supporting limb (Seyfarth et al. 2003). Similar adjustments have also been reported in a number of avian species when negotiating obstacles and/or drops, including the guinea fowl (*Numida meleagris*) (Birn-Jeffery et al. 2014; Daley and Biewener 2006; Daley et al. 2006), the pheasant (*Phasianus colchinus*) (Birn-Jeffery and Daley 2012; Birn-Jeffery et al. 2014), the bobwhite (*Colinus virginianus*), the turkey (*Meleagris gallopavo*) and ostriches (*Struthio camelus*) (Birn-Jeffery et al. 2014) or when locomotion occurs over other slippery surfaces as shown in the guinea fowl (Clark and Higham 2011) and in humans (Bhatt et al. 2005; Cappellini et al. 2010). The Svalbard ptarmigan males are thought to adjust their limb kinematics in this way to negotiate with snowy substrate while using grounded running (Marmol-Guijarro et al. 2019). Generally, grounded running is thought to improve locomotor stability due to longer supporting phases (Andrada et al. 2013; Gatesy and Biewener 1991), while still recovering energy through the elastic elements of the limb (Nudds et al. 2011; Rubenson et al. 2004). Grounded running is also associated with other benefits like an increased stability of the head (Hancock et al. 2007) and a reduction in the bouncing of non-locomotor tissues (Daley and Usherwood 2010). It is puzzling therefore as to why the female ptarmigan are not modifying their limb kinematics during grounded running over snow when all these potential effects could be beneficial. We believe it is likely that the differential influences of snow on a grounded running gait for males and females can be explained by differences in limb compliance. If female ptarmigan had a more compliant limb during grounded running relative to males, this may explain why their kinematics were less affected at increasing speeds over an inherently unstable substrate. Therefore, by examining sex differences between the kinematics of walking and grounded running it should be possible to detect whether any disparities are caused solely by sexual dimorphism in body mass and limb length or if the apparent robustness of female locomotion over snow is explained by differences in limb posture.

Sex differences in locomotion over snow

Males are up to 6% heavier and have longer limbs (Lees et al. 2012a; Steen and Unander 1985) than females. Therefore, if the two sexes are to move in a dynamically similar way and the absolute kinematics and hip heights scale with body mass and limb length (Alexander and Jayes 1983), the rates of change in the kinematic parameters with increasing *U* should remain similar. Except for t_{swing} and *DF*, all the absolute kinematic parameters during a walking gait in male and female ptarmigan are in line with the differences associated with body size for birds (Abourachid and Renous 2000; Gatesy and Biewener 1991). The smaller females had smaller absolute l_{stride}, and greater absolute f_{stride} and absolute t_{stance} at any given *U* compared to the males (Fig. 2A, B & C). The differences in the absolute l_{stride}, f_{stride} and t_{stance}, however, all disappeared when comparisons were made using body mass and limb length-corrected values for any given relative speed $\hat{U}$ (Fig. 2E, F & G). Therefore, male and female ptarmigan are using a dynamic similar walking gait where body size has a major influence on the kinematic parameters.

Conversely, male and female ptarmigan do not appear to move in a dynamically similar way within a grounded running gait. As the differences in the absolute l_{stride} and absolute f_{stride} between males and females when using a grounded running gait persisted after correcting for body size (body mass and limb length), a difference appeared in size-corrected $\hat{t}_{\text{stance}}$. Differences, such as these, in limb posture are often associated with a departure from dynamic similarity (Alexander and Jayes 1983; Gatesy and Biewener 1991). The greater $\hat{l}_{\text{stride}}$ of the females at the top end of the speed range during grounded running, may be attributed to a greater excursion of a more crouched limb in females relative to males (Fig. 2E). Changes in limb posture may also explain the lower $\hat{f}_{\text{stride}}$ of the females for almost all the range of grounded running $\hat{U}$ (Fig. 2F). A more crouched posture of the females is also supported by the greater $\hat{t}_{\text{stance}}$ across grounded running $\hat{U}$ (Gatesy and Biewener 1991) (Fig. 2G). Adjusting their $\hat{t}_{\text{stance}}$ would confer additional stability to females (Andrada et al. 2013; Gatesy and Biewener 1991), which might explain why they do not change their kinematic parameters in the same way as males do when moving on snow.

The relatively longer $\hat{t}_{\text{swing}}$ of the female ptarmigan for all walking and grounded running $\hat{U}$ (Fig. 2G) can likely be explained by departures in the mass proportions of each of the limb segments when compared to ptarmigan males. Experiments on limb loading in birds demonstrate that if the distal portion is heavier relative to the proximal portion, for example with loads added equivalent to 5% of their body mass, then these birds face difficulties in decelerating the swinging limb as the extra load caused greater moments of inertia, increasing t_{swing} (Tickle et al. 2010). Similarly, a study of three species of shore birds revealed that $\hat{t}_{\text{swing}}$ was longer in the species that naturally possessed limbs with heavier distal portions (Kilbourne et al. 2016). In the case of the female ptarmigan, the longer $\hat{t}_{\text{swing}}$ might be explained by departures in mass of the proximal limb segments (the femoral and the tibiotarsal regions) with females having smaller muscles, relative to the males. This would make it more challenging for the females to counter the moments of inertia of the swinging limb, if the mass of the distal limb segment in both sexes is proportional. Yet, data on joint kinematics in the ptarmigan is needed to test this hypothesis.

Sexual dimorphism in limb posture is evident in leghorn chicken, where females have a more upright posture compared to the males (Rose et al. 2016b; Rose et al. 2015). In leghorns the more upright limbs reduce the work that muscles must produce and bones must resist due to a proportionally greater visceral mass of females compared to males, without decreasing t_{stance} (Rose et al. 2016b). However, this is the opposite of what we see in the female ptarmigan, which have a more crouched posture compared to the males. These differences are likely explained by important differences between how female leghorns and ptarmigan move. In contrast with female ptarmigan, the female leghorns are not capable of grounded running, at least on treadmills, and all the sex differences in their locomotor kinematics were found during a walking gait (Rose et al. 2016b). Moreover, female leghorns have been artificially selected to be in a permanently gravid state able to lay eggs all year (Mitchell et al. 1931; Rose et al. 2016b), whereas female ptarmigan breed once a year normally in June (Stokkan et al. 1986). Therefore, female leghorns must support 1.32 times larger reproductive organs for longer; maximum ovaries mass in the female ptarmigan is 34.60 g in June (Mitchell et al. 1931; Stokkan et al. 1986). Conversely, the ptarmigan females in this study were sampled at the end of April/beginning of May, at the onset of ovarian development prior egg laying (Stokkan et al. 1986). As a result, the female ptarmigan in this study were free from the constraint of having to support any extra weight, which means that joint moments can be reduced enough to make crouched postures attainable, thus allowing for longer stance periods, lower power demands (Usherwood 2013) and greater locomotor stability. Furthermore, the risks of bone fracture in ptarmigan females might be lower, as bone calcium deficits are expected to be negligible at this time of the year. Bone fracture is a particular risk for Leghorn hens as they often suffer from osteoporosis as a result of the permanent transfer of calcium to the egg shell (Whitehead 2004).

Implications for limb architecture and muscle anatomy

From an anatomical perspective, the limbs of the female ptarmigan may not be as suited to generating force in the way males do in order to run faster. The PCSA of a muscle is directly related to the forces that muscles, in this case of the pelvic limbs, can produce and depends directly on the mass and volume of the muscle and the length and angle of pennation of the fascicles within that muscle. In leghorns, males have a greater PCSA on several locomotor muscles, including the ilitibialis cranialis and lateralis, the ilifibularis, and the flexor cruris medialis and lateralis pars pelvica, at the onset of maturity compared to females, conferring them an improved locomotor performance (Rose et al. 2016b; Rose et al. 2016c). The Svalbard ptarmigan appear to fit this general pattern with a higher U achieved by males under both treadmill and wild conditions (Lees et al. 2012a). Higher U are likely due to a greater PSCA and more upright posture of the males. It is particularly interesting that wild females' top speed only increased by 8 % (from 1.5 to 1.62 ms^{-1}) compared to the speed achieved running on treadmills (Fig. 1). Whereas in males the differences are greater for the wild individuals that could achieve up to a 34% increase in top speed (from 2 to 2.76 ms^{-1}) (Marmol-Guijarro et al. 2019). These differences between females and males may be related to the relative composition of fibre types in the ptarmigan limb muscles. Indeed, sex differences in fibre type composition are common on many muscles of a number of species. For example, in mice hindlimb the expression levels of the myosin heavy chain isoform for type-IIB fibres (fast glycolytic) are higher in females compared to males in the soleus (64% in females vs. 42% in males) and the tibialis lateralis muscles (75% in females vs. 61% in males), whilst in the plantaris muscle higher levels of the type-IIB isoform are observed in males (84%) than in females (63%) (Haizlip et al. 2015). Similarly in humans, the vastus lateralis muscle located in the thigh show higher percentages of type-I myosin isoforms (slow oxidative) in females (41%) than in males (34%), while type-IIA isoform is higher in males (46%) than in females (36%) (Staron et al. 2000) . In the tropical golden collared manakin (*Manacus vitellinus*), 49% of the fibres in the scapulohumeralis caudalis and 47% of the fibres in the supracoracoides in the males correspond to fast oxidative glycolytic and fast oxidative fibres compared to only 4% and 2% in the females, respectively; as these muscles are key for the wing snaping behaviour of males during courtship (Schultz et al. 2001). Similar to the manakin, sexual selection favouring higher proportions of fast twitch fibres on the hindlimb muscles of the ptarmigan males provides further support to the improved locomotor capacity show by them compared to females. On the other hand, a greater proportion of slow oxidative fibres would explain the greater $\hat{t}_{\mathrm{stance}}$ observed for the during grounded running in females, as they would find challenging to produce enough force to move faster and restricting them from using aerial gaits.

Future Directions

There is a marked seasonal variation in body mass in the Svalbard rock ptarmigan over the year (Steen and Unander 1985; Stokkan et al. 1986). In particular for females, it would be interesting to study the locomotion their throughout breeding cycle, in particular when they are at their heaviest prior to egg laying, and throughout winter, when they double their body weight seasonally to further test some of these hypotheses. Sampling across the range of seasonal mass fluctuations would enable us to tease apart the influence of mass gain specifically associated with reproductive effort and that associated with overwintering survival. These data would be particularly interesting in the Svalbard ptarmigan as males have adaptations that mitigate the influence of winter mass gain, meaning they move more efficiently in terms of the metabolic cost of locomotion, albeit over a reduced speed range (Lees et al. 2010). It is unknown if females show the same adaptations.

At the muscular level, a detailed analysis of the muscle architecture of the limb, including PSCA measures, fibre typing and limb proportions, of the male and the female ptarmigan remains to be done.

Comparisons between laboratory and field datasets are challenging. Snow by its own nature is a highly variable substrate, where a number of physical properties relevant for terrestrial locomotion, including snow harness, humidity, stratification and depth, might drastically change at very short spatiotemporal scale. For the sake of this study, we have considered here snow to be a more uniform substrate; however, research on the effects of snow properties upon Svalbard ptarmigan locomotion is underway (Marmol-Guijarro et al. *in progress*). Moreover, studying the wild ptarmigan locomotor kinematics through video recordings depends on the ability to identify temporal events (i.e. t_{stance}) that can be hindered either because foot landing and lifting may occur in deep snow or simply because the frame rate used for recording may not precisely capture such event. This results in estimation errors particularly affecting DF (Fig. S2). With the development of smaller and more powerful batteries, bio-loggers that allow the study of key ecological, behavioural and physiological aspects of wild birds may be used to link these traits to adaptations in the locomotor system.

For example, bio-loggers that are capable of detecting the time that the GRF acts on the feet may give a more accurate detection of foot landing and take-off. These types of loggers have been already used to analyse the locomotor biomechanics in other species including ostriches (Daley et al. 2016), cheetah (Wilson et al. 2013), and elephants (Ren and Hutchinson 2008). Moreover, they could provide valuable information regarding underlying evolutionary constraints leading to disparate locomotor capabilities in males and females in terms of locomotor biomechanics and energetics. Overall, our study adds new data on sex differences in locomotion and the kinematic mechanisms used by birds to improve stability while moving over snow.

Acknowledgements

We would like to thank the Governor of Svalbard's office (Sysselmannen på Svalbard) for facilitating this research, granting our fieldwork permits and for logistical support. The University of Tromsø provided access to the Adventdalen Field Station, field and logistical support. We would also like to thank three anonymous reviewers for their comments that greatly improved this manuscript.

References

Abourachid A (2000) Bipedal locomotion in birds: the importance of functional parameters in terrestrial adaptation in Anatidae. Can J Zool 78:1994-1998. https://doi.org/10.1139/z00-112

Abourachid A, Renous S (2000) Bipedal locomotion in ratites (Paleognatiform) examples of cursorial birds. Ibis 142:538-549. https://doi.org/10.1111/j.1474-919X.2000.tb04455.x

Alexander RM, Jayes AS (1983) A dynamic similarity hypothesis for the gaits of quadrupedal mammals. J Zool 201:135-152. https://doi.org/10.1111/j.1469-7998.1983.tb04266.x

Andrada E, Rode C, Blickhan R (2013) 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

Bhatt T, Wening JD, Pai YC (2005) Influence of gait speed on stability: recovery from anterior slips and compensatory stepping. Gait Posture 21:146-156. https://doi.org/10.1016/j.gaitpost.2004.01.008

Biewener AA (1989) Scaling body support in mammals: limb posture and muscle mechanics. Science 245:45-48. https://doi.org/10.1126/science.2740914

Birn-Jeffery AV, Daley MA (2012) Birds achieve high robustness in uneven terrain through active control of landing conditions. J Exp Biol 215:2117. https://doi.org/10.1242/jeb.065557

Birn-Jeffery AV, Hubicki CM, Blum Y, Renjewski D, Hurst JW, Daley MA (2014) Don't break a leg: running birds from quail to ostrich prioritise leg safety and economy on uneven terrain. J Exp Biol 217:3786. https://doi.org/10.1242/jeb.102640

Cappellini G, Ivanenko YP, Dominici N, Poppele RE, Lacquaniti F (2010) Motor patterns during walking on a slippery walkway. J Neurophysiol 103:746-760. https://doi.org/10.1152/jn.00499.2009

Cavagna GA, Heglund NC, Taylor CR (1977) 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

Clark AJ, Higham TE (2011) Slipping, sliding and stability: locomotor strategies for overcoming low-friction surfaces. J Exp Biol 214:1369. https://doi.org/10.1242/jeb.051136

Daley MA, Biewener AA (2006) Running over rough terrain reveals limb control for intrinsic stability. Proc Natl Acad Sci USA 103:15681. https://doi.org/10.1073/pnas.0601473103

Daley MA, Biewener AA (2011) 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 B Biol Sci 366:1580-1591. https://doi.org/10.1098/rstb.2010.0338

Daley MA, Channon AJ, Nolan GS, Hall J (2016) 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

Daley MA, Felix G, Biewener AA (2007) Running stability is enhanced by a proximo-distal gradient in joint neuromechanical control. J Exp Biol 210:383. https://doi.org/10.1242/jeb.02668

Daley MA, Usherwood JR (2010) Two explanations for the compliant running paradox: reduced work of bouncing viscera and increased stability in uneven terrain. Biol Lett 6:418-421. https://10.1098/rsbl.2010.0175

Daley MA, Usherwood JR, Felix G, Biewener AA (2006) 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

Day LM, Jayne BC (2007) Interspecific scaling of the morphology and posture of the limbs during the locomotion of cats (Felidae). J Exp Biol 210:642. https://doi.org/10.1242/jeb.02703

Dick TJM, Clemente CJ (2016) How to build your dragon: scaling of muscle architecture from the world's smallest to the world's largest monitor lizard. Front Zool 13:8. https://doi.org/10.1186/s12983-016-0141-5

Full RJ, Kubow T, Schmitt J, Holmes P, Koditschek D (2002) Quantifying dynamic stability and maneuverability in legged locomotion. Integr Comp Biol 42:149-157. https://doi.org/10.1093/icb/42.1.149

Gates DH, Wilken JM, Scott SJ, Sinitski EH, Dingwell JB (2012) Kinematic strategies for walking across a destabilizing rock surface. Gait Posture 35:36-42. https://doi.org/10.1016/j.gaitpost.2011.08.001

Gatesy SM, Biewener AA (1991) 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

Haizlip KM, Harrison BC, Leinwand LA (2015) Sex-Based Differences in Skeletal Muscle Kinetics and Fiber-Type Composition. Physiology 30:30-39. https://doi.org/10.1152/physiol.00024.2014

Hancock JA, Stevens NJ, Biknevicius AR (2007) 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

Herbin M, Hackert R, Gasc J-P, Renous S (2007) 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

Jenkins FA (1971) Limb posture and locomotion in the Virginia opossum (*Didelphis marsupialis*) and in other non-cursorial mammals. J Zool 165:303-315. https://doi.org/10.1111/j.1469-7998.1971.tb02189.x

Jindrich DL, Full RJ (2002) Dynamic stabilization of rapid hexapedal locomotion. J Exp Biol 205:2803-2823.

Kilbourne BM, Andrada E, Fischer MS, Nyakatura JA (2016) Morphology and motion: hindlimb proportions and swing phase kinematics in terrestrially locomoting charadriiform birds. J Exp Biol 219:1405-1416. https://doi.org/10.1242/jeb.124081

Lees JJ, Nudds R, Stokkan K-A, Folkow L, Codd J (2010) 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

Lees JJ, Nudds RL, Folkow LP, Stokkan KA, Codd JR (2012a) Understanding sex differences in the cost of terrestrial locomotion. Proc Biol Sci 279:826-832. https://doi.org/10.1098/rspb.2011.1334

Lees JJ, Stokkan K-A, Folkow LP, Codd JR (2012b) Locomotor development in the Svalbard rock ptarmigan (*Lagopus muta hyperborea*). Polar Biol 35:867-874. https://doi.org/10.1007/s00300-011-1131-x

Lejeune TM, Willems PA, Heglund NC (1998) Mechanics and energetics of human locomotion on sand. J Exp Biol 201:2071-2080.

Marmol-Guijarro AC, Nudds RL, Marrin JC, Folkow LP, Codd JR (2019) Terrestrial locomotion of the Svalbard rock ptarmigan: comparing field and laboratory treadmill studies. Sci Rep 9:11451. https://doi.org/10.1038/s41598-019-47989-6

Mitchell H, Hamilton T, Card L (1931) A technical study of the growth of White Leghorn chickens. Univ Ill Agric Expt Stn Bull 367:81-139.

Nudds RL, Folkow LP, Lees JJ, Tickle PG, Stokkan KA, Codd JR (2011) Evidence for energy savings from aerial running in the Svalbard rock ptarmigan (*Lagopus muta hyperborea*). Proc Biol Sci 278:2654-2661. https://doi.org/10.1098/rspb.2010.2742

Nudds RL, Gardiner JD, Tickle PG, Codd JR (2010) Energetics and kinematics of walking in the barnacle goose (*Branta leucopsis*). Comp Biochem Physiol A Mol Integr Physiol 156:318-324. https://doi.org/10.1016/j.cbpa.2010.01.023

Patel BA, Horner AM, Thompson NE, Barrett L, Henzi SP (2013) Ontogenetic scaling of fore- and hind limb posture in wild Chacma baboons (*Papio hamadryas ursinus*). PLoS One 8:e71020. https://doi.org/10.1371/journal.pone.0071020

Polk JD (2002) Adaptive and phylogenetic influences on musculoskeletal design in cercopithecine primates. J Exp Biol 205:3399.

Qiao M, Hughes M, Jindrich DL (2012) Response to medio-lateral perturbations of human walking and running. Paper presented at the American Society of Biomechanics Annual Meeting, Gainsville, Florida,

Qiao M, Jindrich DL (2014) Compensations during unsteady locomotion. Integr Comp Biol 54:1109-1121. https://doi.org/10.1093/icb/icu058

R Core Team (2020) R: a language and environment for statistical computing, R version 3.6.3 edn. R Foundation for Statistical Computing, Vienna, Austria

Reilly SM, McElroy EJ, Biknevicius AR (2007) Posture, gait and the ecological relevance of locomotor costs and energy-saving mechanisms in tetrapods. Zoology 110:271-289. https://doi.org/10.1016/j.zool.2007.01.003

Ren L, Hutchinson JR (2008) The three-dimensional locomotor dynamics of African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants reveal a smooth gait transition at moderate speed. J R Soc Interface 5:195-211. https://doi.org/10.1098/rsif.2007.1095

Riley PO, Dicharry JAY, Franz J, Croce UD, Wilder RP, Kerrigan DC (2008) A kinematics and kinetic comparison of overground and treadmill running. Med Sci Sports Exerc 40:1093-1100. https://doi.org/10.1249/mss.0b013e3181677530

Rose KA, Bates KT, Nudds RL, Codd JR (2016a) Ontogeny of sex differences in the energetics and kinematics of terrestrial locomotion in leghorn chickens (*Gallus gallus domesticus*). Sci Rep 6:24292. https://doi.org/10.1038/srep24292

Rose KA, Codd JR, Nudds RL (2016b) Differential sex-specific walking kinematics in leghorn chickens (*Gallus gallus domesticus*) selectively bred for different body size. J Exp Biol 44:jeb.139709. https://doi.org/10.1242/jeb.139709

Rose KA, Nudds RL, Butler PJ, Codd JR (2015) Sex differences in gait utilization and energy metabolism during terrestrial locomotion in two varieties of chicken (*Gallus gallus domesticus*) selected for different body size. Biology Open:1-10. https://doi.org/10.1242/bio.013094

Rose KA, Nudds RL, Codd JR (2016c) Variety, sex and ontogenetic differences in the pelvic limb muscle architectural properties of leghorn chickens (*Gallus gallus domesticus*) and their links with locomotor performance. J Anat 228:952-964. https://doi.org/10.1111/joa.12460

Rubenson J, Heliams DB, Lloyd DG, Fournier PA (2004) Gait selection in the ostrich: mechanical and metabolic characteristics of walking and running with and without an aerial phase. Proc R Soc Lond B Biol Sci 271:1091-1099. https://doi.org/10.1098/rspb.2004.2702

Schultz DJ, Hertel F, Bauch M, Schlinger BA (2001) Adaptations for rapid and forceful contraction in wing muscles of the male golden-collared manakin: sex and species comparisons. J Comp Physiol A 187:677-684. https://doi.org/10.1007/s00359-001-0239-9

Schulz BW (2011) Minimum toe clearance adaptations to floor surface irregularity and gait speed. J Biomech 44:1277-1284. https://doi.org/10.1016/j.jbiomech.2011.02.010

Seyfarth A, Geyer H, Herr H (2003) Swing-leg retraction: a simple control model for stable running. J Exp Biol 206:2547-2555. https://doi.org/10.1242/jeb.00463.

Staron RS et al. (2000) Fiber type composition of the vastus lateralis muscle of young men and women. J Histochem Cytochem 48:623-629. https://doi.org/10.1177/002215540004800506

Steen JB, Unander S (1985) Breeding biology of the Svalbard rock ptarmigan *Lagopus mutus hyperboreus*. Ornis Scandinavica 16:191-197. https://doi.org/10.2307/3676630

Stokkan K-A, Sharp PJ, Unander S (1986) The annual breeding cycle of the high-arctic svalbard ptarmigan (*Lagopus mutus hyperboreus*). Gen Comp Endocrinol 61:446-451. https://doi.org/10.1016/0016-6480(86)90232-7

Tickle PG, Richardson MF, Codd JR (2010) Load carrying during locomotion in the barnacle goose (*Branta leucopsis*): The effect of load placement and size. Comp Biochem Physiol A Mol Integr Physiol 156:309-317. https://doi.org/10.1016/j.cbpa.2010.01.022

Unander S, Steen JB (1985) Behaviour and Social Structure in Svalbard Rock Ptarmigan *Lagopus mutus hyperboreus*. Ornis Scandinavica (Scandinavian Journal of Ornithology) 16:198-204. https://doi.org/10.2307/3676631

Usherwood JR (2013) Constraints on muscle performance provide a novel explanation for the scaling of posture in terrestrial animals. Biol Lett 9:20130414. https://doi.org/10.1098/rsbl.2013.0414

Watson RR, Rubenson J, Coder L, Hoyt DF, Propert MWG, Marsh RL (2011) Gait-specific energetics contributes to economical walking and running in emus and ostriches. Proc Biol Sci 278:2040-2046. https://doi.org/10.1098/rspb.2010.2022

Whitehead CC (2004) Overview of bone biology in the egg-laying hen. Poult Sci 83:193-199. https://doi.org/10.1093/ps/83.2.193

Wilson AM, Lowe JC, Roskilly K, Hudson PE, Golabek KA, McNutt JW (2013) Locomotion dynamics of hunting in wild cheetahs. Nature 498:185-189. https://doi.org/10.1038/nature12295

Wu AR, Kuo AD (2016) Determinants of preferred ground clearance during swing phase of human walking. J Exp Biol 219:3106. https://doi.org/10.1242/jeb.137356

Figures

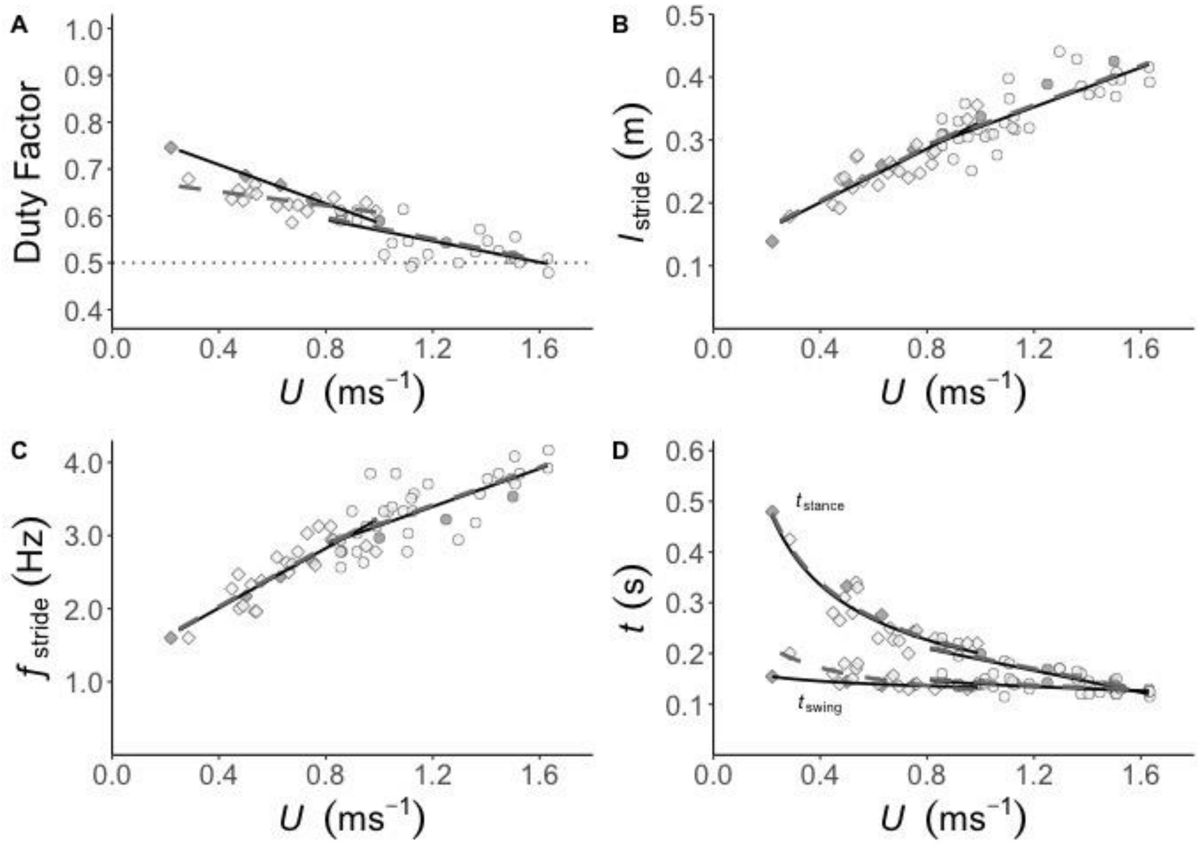

Fig. 1 Female kinematic parameters plotted against speed (U). DF (A), l_{stride} (B), f_{stride} (C) and t_{stance} and t_{swing} (D) are plotted against U for females moving in the wild (dashed line and white points) compared to females moving on treadmills (solid line and grey points) during walking (rhomboids) and grounded running (circles). The results of the linear models with the best-fine line equations are summarized in table 1.

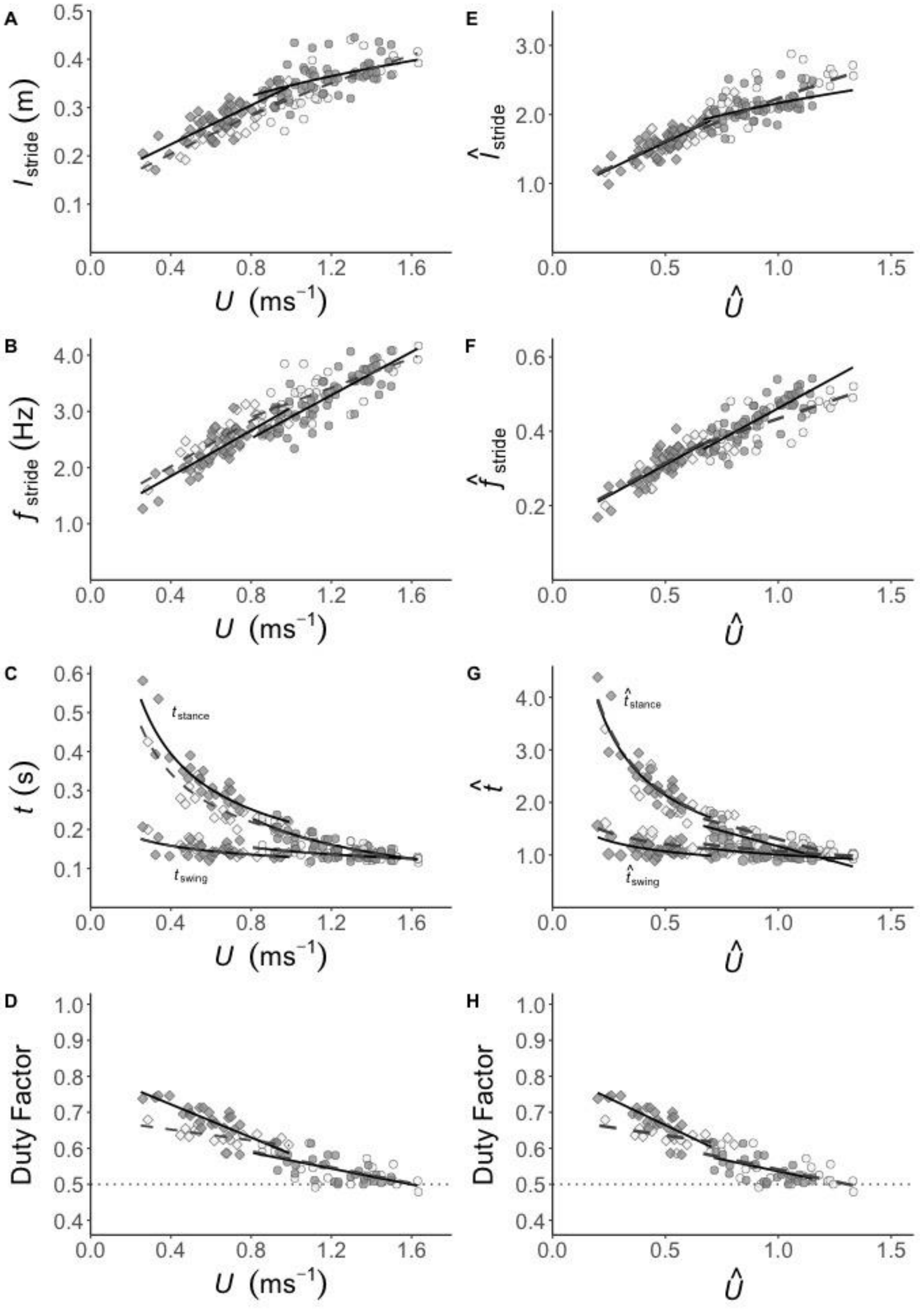
A
l_{stride} (m)
0.1
0.2
0.3
0.4
0.5
U (ms^{-1})
0.0
0.4
0.8
1.2
1.6
E
$\hat{l}_{\mathrm{stride}}$
1.0
2.0
3.0
$\hat{U}$
0.0
0.5
1.0
1.5
B
f_{stride} (Hz)
1.0
2.0
3.0
4.0
U (ms^{-1})
F
$\hat{f}_{\mathrm{stride}}$
0.2
0.4
0.6
$\hat{U}$
C
t (s)
0.1
0.2
0.3
0.4
0.5
0.6
t_{stance}
t_{swing}
U (ms^{-1})
G
$\hat{t}$
1.0
2.0
3.0
4.0
$\hat{t}_{\mathrm{stance}}$
$\hat{t}_{\mathrm{swing}}$
$\hat{U}$
D
Duty Factor
0.4
0.5
0.6
0.7
0.8
0.9
1.0
U (ms^{-1})
H
Duty Factor
$\hat{U}$

Fig. 2 Kinematic parameters plotted against speed (U) and relative speed ($\hat{U}$), compensated for body size (body mass and limb length), for each gait and both sexes. l_{stride} (A), f_{stride} (B), t_{stance} and t_{swing} (C) and Duty Factor (D), and the body-size-compensated correlates (please see text for definitions), $\hat{l}_{\mathrm{stride}}$ (E), $\hat{f}_{\mathrm{stride}}$ (F), $\hat{t}_{\mathrm{stance}}$ and $\hat{t}_{\mathrm{swing}}$ (G), and Duty Factor (H) are plotted against U (left column) and $\hat{U}$ (right column), respectively, for females (dashed line and white points) and males (solid line and grey points) when walking (rhomboids) and grounded running (circles) *in situ* over snowy substrate. Male data from. The results of the linear models with the best-fine line equations are summarized in table 2.

Table 1. Results of the linear models investigating differences in the absolute kinematics between female ptarmigan locomoting on treadmills and in the field.

Gait	Parameter	Final model	R^2	Equations
Walking	l_{stride}	U ($F_{1,\,24} = 81.769$; $P < 0.001$)	0.764	♂ & ♀ = $0.214\ U + 0.115$
	f_{stride}	U ($F_{1,\,24} = 73.663$; $P < 0.001$)	0.744	♂ & ♀ = $2.041\ U + 1.193$
	$\log_{10} t_{\mathrm{stance}}$	Log$_{10}$ U ($F_{1,\,18} = 75.568$; $P < 0.001$)	0.797	♂ & ♀ = $0.200\ U^{-0.564}$
	$\log_{10} t_{\mathrm{swing}}$	Log$_{10}$ U ($F_{1,\,16} = 7.576$; $P < 0.0001$) sex ($F_{1,\,16} = 5.650$; $P < 0.05$) Log$_{10}$ U × sex ($F_{1,\,16} = 4.851$; $P < 0.05$)	0.575	♂ = $0.133\ U^{-0.098}$ ♀ = $0.127\ U^{-0.332}$
	Duty Factor	U ($F_{1,\,16} = 35.36$; $P < 0.01$) sex ($F_{1,\,16} = 12.937$; $P < 0.01$) U × sex ($F_{1,\,16} = 6.891$; $P < 0.05$)	0.733	♂ = $-\,0.207\ U + 0.792$ ♀ = $-\,0.075\ U + 0.682$
Grounded running	l_{stride}	U ($F_{1,\,34} = 55.191$; $P < 0.001$)	0.608	♂ & ♀ = $0.157\ U + 0.164$
	f_{stride}	U ($F_{1,\,34} = 40.303$; $P < 0.001$)	0.529	♂ & ♀ = $1.297\ U + 1.839$
	t_{stance}	U ($F_{1,\,24} = 55.484$; $P < 0.001$)	0.686	♂ & ♀ = $-\,0.108\ U + 0.296$
	$\log_{10} t_{\mathrm{swing}}$	Log$_{10}$ U ($F_{1,\,24} = 7.0584$; $P < 0.05$)	0.195	♂ & ♀ = $0.140\ U^{-0.213}$
	Duty Factor	U ($F_{1,\,24} = 21.409$; $P < 0.001$)	0.449	♂ & ♀ = $-\,0.113\ U + 0.682$

Table 2. Results of the linear models investigating differences in kinematics between male and female ptarmigan.

<table>
<tr><td colspan="5">Kinematic comparison with absolute values</td></tr>
<tr><th>Gait</th><th>Parameter</th><th>Final model</th><th>R^2</th><th>Equations</th></tr>
<tr><td>Walking</td><td>l_{stride}</td><td>U ($F_{1,\,67} = 137.419$; $P < 0.001$)
sex ($F_{1,\,67} = 10.736$; $P < 0.001$)</td><td>0.689</td><td>♂: $= 0.202\,U + 0.143$
♀: $= 0.202\,U + 0.123$</td></tr>
<tr><td></td><td>f_{stride}</td><td>U ($F_{1,\,67} = 149.940$; $P < 0.001$)
sex ($F_{1,\,67} = 11.125$; $P < 0.01$)</td><td>0.698</td><td>♂: $= 2.036\,U + 1.032$
♀: $= 2.036\,U + 1.205$</td></tr>
<tr><td></td><td>$\log_{10} t_{\text{stance}}$</td><td>$\text{Log}_{10}\,U$ ($F_{1,\,39} = 140.057$; $P < 0.001$)
sex ($F_{1,\,39} = 34.525$; $P < 0.001$)</td><td>0.808</td><td>♂: $= 0.218\,U^{-0.647}$
♀: $= 0.190\,U^{-0.647}$</td></tr>
<tr><td></td><td>$\log_{10} t_{\text{swing}}$</td><td>$U$ ($F_{1,\,40} = 14.349$; $P < 0.001$)</td><td>0.286</td><td>♂ & ♀ $= 0.131\,U^{-0.234}$</td></tr>
<tr><td></td><td>Duty Factor</td><td>U ($F_{1,\,39} = 42.223$; $P < 0.001$)
sex ($F_{1,\,39} = 34.947$; $P < 0.001$)
$U \times$ sex ($F_{1,\,39} = 10.611$; $P < 0.01$)</td><td>0.674</td><td>♂: $= -\,0.230\,U + 0.814$
♀: $= -\,0.075\,U + 0.682$</td></tr>
<tr><td>Grounded running</td><td>l_{stride}</td><td>U ($F_{1,\,84} = 58.446$; $P < 0.001$)
sex ($F_{1,\,84} = 11.127$; $P < 0.01$)
$U \times$ sex ($F_{1,\,84} = 4.869$; $P < 0.05$)</td><td>0.451</td><td>♂: $= 0.346\,U^{0.291}$
♀: $= 0.318\,U^{0.532}$</td></tr>
<tr><td></td><td>f_{stride}</td><td>U ($F_{1,\,84} = 117.949$; $P < 0.001$)
sex ($F_{1,\,84} = 2.269$; $P = 0.136$)
$U \times$ sex ($F_{1,\,84} = 4.358$; $P < 0.05$)</td><td>0.583</td><td>♂: $= 1.925\,U + 0.979$
♀: $= 1.309\,U + 1.851$</td></tr>
<tr><td></td><td>$\log_{10} t_{\text{stance}}$</td><td>$\text{Log}_{10}\,U$ ($F_{1,\,50} = 130.3$; $P < 0.001$)</td><td>0.717</td><td>♂ & ♀ $= 0.189\,U^{-0.872}$</td></tr>
<tr><td></td><td>$\log_{10} t_{\text{swing}}$</td><td>$\text{Log}_{10}\,U$ ($F_{1,\,50} = 17.883$; $P < 0.001$)</td><td>0.249</td><td>♂ & ♀ $= 0.144\,U^{-0.302}$</td></tr>
<tr><td></td><td>Duty Factor</td><td>U ($F_{1,\,50} = 33.96$; $P < 0.001$)</td><td>0.393</td><td>♂ & ♀ $= -\,0.111\,U + 0.677$</td></tr>
<tr><td colspan="5">Body size (body mass and limb length)-corrected kinematic comparison</td></tr>
<tr><td>Walking</td><td>$\hat{l}_{\text{stride}}$</td><td>$\hat{U}$ ($F_{1,\,68} = 145.18$; $P < 0.001$)</td><td>0.676</td><td>♂ & ♀ $= 1.571\,\hat{U} + 0.810$</td></tr>
</table>

	$\hat{f}_{\text{stride}}$	$\hat{U}$ ($F_{1,\,68}$ = 147.39; P < 0.001)	0.679	♂ & ♀ = 0.332 $\hat{U}$ + 0.144
	$\log_{10}\hat{t}_{\text{stance}}$	Log$_{10}$ $\hat{U}$ ($F_{1,\,40}$ = 153.83; P < 0.001)	0.789	♂ & ♀ = 1.351 $\hat{U}^{-0.662}$
	$\log_{10}\hat{t}_{\text{swing}}$	Log$_{10}$ $\hat{U}$ ($F_{1,\,38}$ = 19.028; P < 0.001) sex ($F_{1,\,38}$ = 6.343; P < 0.05)	0.363	♂: = 0.901 $\hat{U}^{-0.245}$ ♀: = 1.016 $\hat{U}^{-0.245}$
	Duty Factor	$\hat{U}$ ($F_{1,\,37}$ = 40.928; P < 0.001) sex ($F_{1,\,37}$ = 34.947; P < 0.001) $\hat{U}$ × sex ($F_{1,\,37}$ = 11.907; P < 0.01)	0.674	♂: = – 0.299 $\hat{U}$ + 0.814 ♀: = – 0.092 $\hat{U}$ + 0.682
Grounded running	$\log_{10}\hat{l}_{stride}$	Log$_{10}$ $\hat{U}$ ($F_{1,\,84}$ = 58.446; P < 0.001) sex ($F_{1,\,84}$ = 8.539; P < 0.05) Log$_{10}$ $\hat{U}$ × sex ($F_{1,\,84}$ = 4.869; P < 0.05)	0.441	♂: = 2.164 $\hat{U}^{0.291}$ ♀: = 2.231 $\hat{U}^{0.532}$
	$\hat{f}_{\text{stride}}$	$\hat{U}$ ($F_{1,\,84}$ = 116.187; P < 0.001) sex ($F_{1,\,84}$ = 3.098; P = 0.082) $\hat{U}$ × sex ($F_{1,\,84}$ = 7.456; P < 0.01)	0.587	♂: = 0.333 $\hat{U}$ + 0.130 ♀: = 0.200 $\hat{U}$ + 0.231
	$\log_{10}\hat{t}_{\text{stance}}$	Log$_{10}$ $\hat{U}$ ($F_{1,\,49}$ = 108.936; P < 0.001) sex ($F_{1,\,49}$ = 1.374; P = 0.247)	0.680	♂: = – 1.168 $\hat{U}$ + 2.333 ♀: = – 1.168 $\hat{U}$ + 2.468
	$\log_{10}\hat{t}_{\text{swing}}$	Log$_{10}$ $\hat{U}$ ($F_{1,\,49}$ = 17.494; P < 0.001) sex ($F_{1,\,49}$ = 2.809; P < 0.05)	0.264	♂: = 1.005 $\hat{U}^{-0.300}$ ♀: = 1.071 $\hat{U}^{-0.300}$
	Duty Factor	$\hat{U}$ ($F_{1,\,50}$ = 31.456; P < 0.001)	0.374	♂ & ♀ = 0.669 $\hat{U}$ – 0.133

Electronic Supplementary Material

Does posture explain the kinematic differences in a grounded running gait between male and female Svalbard rock ptarmigan (*Lagopus muta hyperborea*) moving on snow?

Polar Biology

Andres Marmol-Guijarro[1], Robert Nudds[1], Lars Folkow[2], John Lees[3] & Jonathan Codd[1*]

[1]School of Biological Sciences, Faculty of Biology, Medicine & Health, University of Manchester, Manchester, UK. [2]Department of Arctic and Marine Biology, University of Tromsø - the Arctic University of Norway, Tromsø, Norway. [3]Department of Physics, Chemistry and Biology, Linköpings Universitet, Linköping, Östergötland, Sweden.

*Author for Correspondence:

Dr Jonathan Codd

e-mail: jonathan.codd@manchester.ac.uk

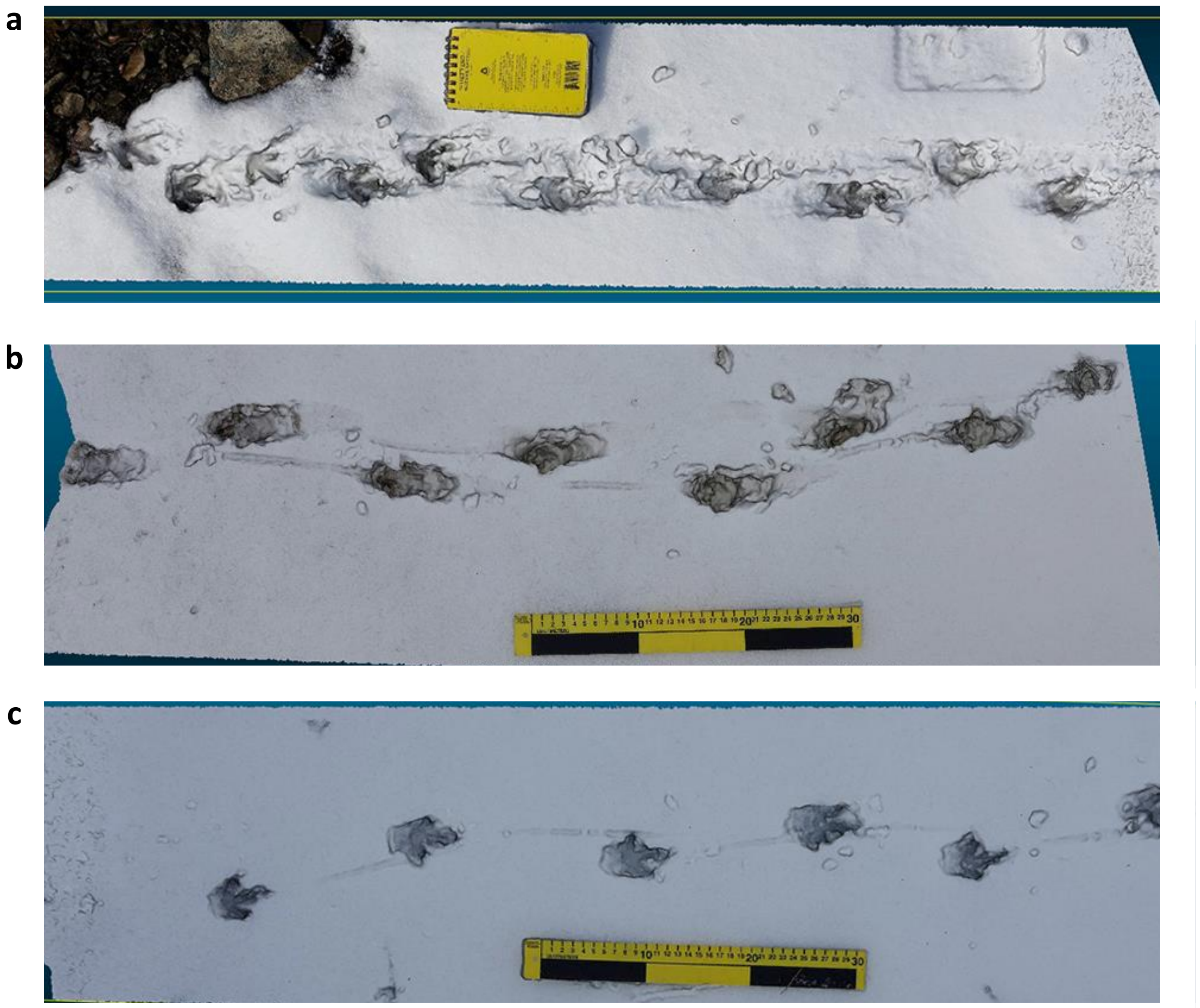

Fig. S1. Examples of tracks highlighting incidences of toe dragging for female ptarmigan moving soft snow at very slow (a, U = 0.5 ms^{-1}) and faster (b and c, U = 0.68 & 1.5 ms^{-1} respectively) locomotion speeds. Toe dragging in snow may decelerate the swinging limb, thus increasing $\boldsymbol{t}_{\mathbf{swing}}$. Toe dragging decreases with increasing U.

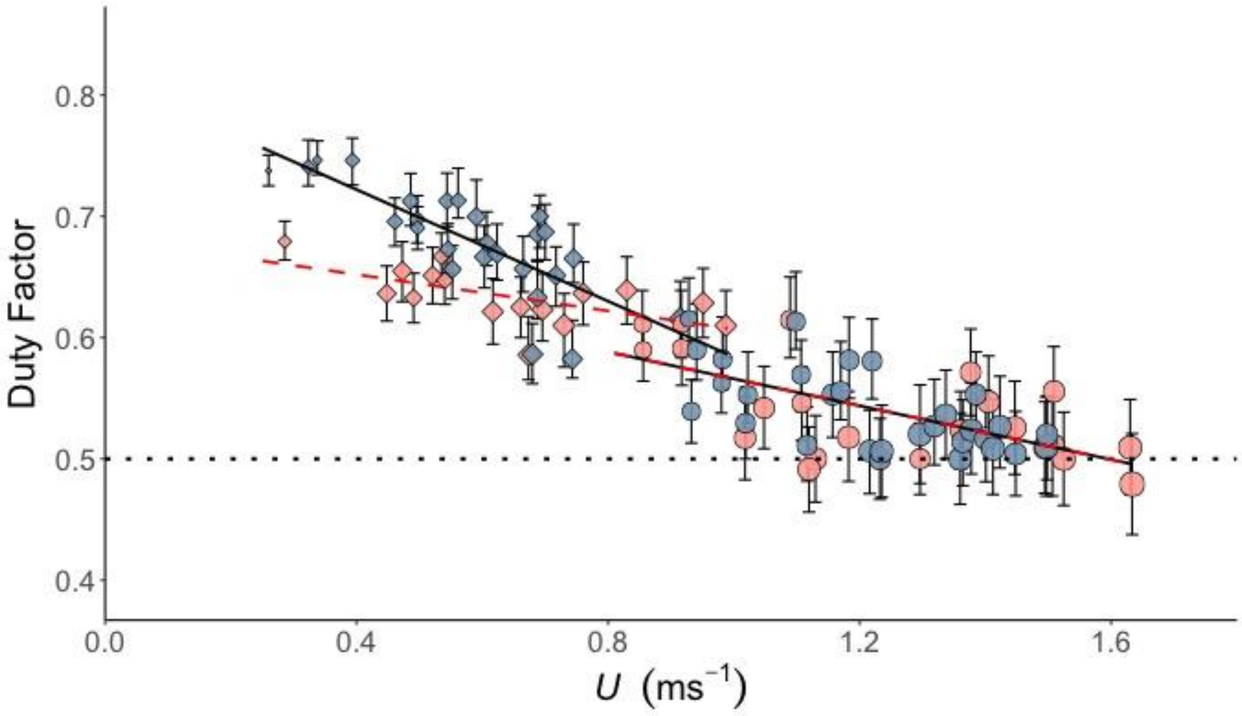

Fig. S2. Precision-related issues in Duty Factor (*DF*) estimates. *DF* is plotted against speed (*U*) for females (red points and dashed red lines) and males (blue points and solid lines) while walking (rhomboids) and grounded running (circles) over snow. The relative size of each point represents the error estimates in *DF*, the larger being associated with larger errors. The error bars represent the upper and lower limits if the beginning or the ending of t_{stance} was delayed by one hundredth of a second (one frame). All data points and limits were obtained from videos recorded at 100 fps using the same manual technique described in the method section of the paper. *DF* lower than 0.5 (0.48 and 0.49, respectively) were recorded in two females and would technically be classified to an aerial running gait. However, at these *U*, t_{stance} and t_{swing} vary only in a few hundredths of second, which is at the limit of the accuracy that can be obtained from the video recordings. For example, if the foot lifting of these two females occurs only one hundredth of a second (a frame) later, *DF* would become 0.52 as suggested by the upper limits of the error bars and would be reassigned to a grounded running gait. Determining foot landing or lifting when the bird’s feet sink into the substrate can be challenging.

Chapter 4

Potential evidence for route choice through snow in the Svalbard rock Ptarmigan

This chapter is a draft of an article in preparation for submission to *The Journal of Integrative Organismal Biology:*

Marmol-Guijarro, A.C., Nudds, R., Folkow, L.P., Sellers, W., Falkingham, P. and Codd, J.R. (in preparation). Potential evidence for route choice through snow in the Svalbard rock Ptarmigan

Potential evidence for route choice through snow in the Svalbard rock ptarmigan

Andres Mármol-Guijarro[1], Robert Nudds[1], Lars Folkow[2], William Sellers[3], Peter Falkingham[4] & Jonathan Codd[1*]

[1]School of Biological Sciences, Faculty of Biology, Medicine & Health, University of Manchester, Manchester, UK; [2]Department of Arctic & Marine Biology, University of Tromsø – the Arctic University of Norway, Tromsø, Norway; [3]School of Earth & Environmental Sciences, Faculty of Science & Engineering, University of Manchester, Manchester, UK; [4]School of Biological and Environmental Sciences, Liverpool John Moores University, Liverpool, UK; [5]Civil Engineering Department, Montana State University, Montana, USA

* corresponding author

jonathan.codd@manchester.ac.uk

Keywords: Arctic, snow properties, terrestrial locomotion, footprints, speed

Running title: Evidence of route choice in ptarmigan

Abstract

Snow supportiveness is linked to the metabolic cost of locomotion, as it influences the depth to which the foot of a moving animal will sink. As track depth increases animals typically reduce their speed to minimise any potential energetic imbalance. Here we examine how self-selected speed in the Svalbard rock ptarmigan is affected by snow supportiveness and subsequent footprint depth measured using thin-blade penetrometry and 3D photogrammetry, respectively. Our findings indicate that snow supportiveness and footprint depth are poor estimators of speed (r^2 = 0.149) and stride length (r^2 = 0.106). Interestingly, the ptarmigan in our study rarely sunk to depths beyond the intertarsal joint, regardless of the speed, suggesting that at this relatively shallow depth any increased cost is manageable. 3D reconstructions also indicate that the ptarmigan may exploit the compressive nature of snow to generate thrust during stance, as a trend towards greater foot rotations in deeper footprints was found. In support of the theory that animals should choose routes that minimise energy costs, our results suggest that the ptarmigan are selecting snow patches that are supportive enough to prevent large foot sinking depths, however, it is unclear what mechanisms they may be using to do this.

Animals traverse complex environments with heterogenous terrain, where obstacles and variations in substrate, such as ground compliance and roughness, are commonplace. Under such conditions, animals adjust the way they move to maintain stability, manoeuvrability and grip to prevent falls and injures (Birn-Jeffery and Daley 2012; Clark and Higham 2011; Daley et al. 2006; Li et al. 2012; Wilson et al. 1991). Animals will also modulate the speed they move at and the route taken, in relation to the energy landscape (Alexander 2000; Shepard et al. 2013). Snow is a common substrate across the temperate and circumpolar regions of the planet. It permanently covers up to 10% of the earth's surface, and during winter in the northern hemisphere, may extend over 60% of the available surface (Hornberger and Winter 2009). Snow is a fascinating and variable substrate to consider in relation to animal locomotion. When fresh and dry, snow behaves as a fluidizing granular material (Hagenmuller et al. 2014; Nicot 2004), however, temperature increases, rainfall, gravity and external loadings over time can all lead to changes in the mechanical properties of the snow, creating a spectrum of snow types ranging from very soft, dry snow to crusted hardened layers, to slippery icy layers (Bruland et al. 2004; Nicot 2004). Variability in snow properties can occur rapidly over large and small scales both temporally and spatially.

Any changes in snow properties ultimately shape the fitness of the animals that must move over this substrate, as it influences access to food (Descamps et al. 2017; Hansen et al. 2013), reproductive success (Descamps et al. 2017; Hansen et al. 2013) and the metabolic cost of locomotion (Crête and Larivière 2003; Fancy and White 1987; Heinonen et al. 1959; Ramaswamy et al. 1966). In terms of animal movement any increase in the metabolic cost of locomotion over snow is significant; particularly in areas where snow cover is abundant and there would appear to be a selective advantage for animals opting for specific behavioural strategies to minimise the increase in cost (Shepard et al. 2013). For example, arctiodactyls, including the mule deer (*Cervus americanus*) and moose (*Alces alces*), self-select snow pathways where foot sinking depth does not exceed 66% of the height to the chest (Kelsall 1969). Similarly, coyotes (*Canis latrans*) and grey wolves (*Canis lupus*) are known to exploit human-made compressed snow paths to travel more efficiently (Crête and Larivière 2003; Droghini and Boutin 2018b). Many species, including humans, will self-select slower speeds (U), relative to when moving over firm ground, to mitigate the increased energetic costs of moving on deep snow with a natural “firm-ground” pace (Crête and Larivière 2003; Parker et al. 1984; Ramaswamy et al. 1966). Specific anatomical adaptations have also evolved to mitigate the energetic cost increase caused by moving through snow, such as relatively longer limbs and larger foot areas. Relatively longer foot edge lengths may also be advantageous, although empirical evidence of this has only been obtained on natural granular media other than snow (Falkingham et al. 2010). Having a ‘snowshoe’ foot is an effective adaptation for moving over unsupportive snow. For example, the relatively large feet of moose facilitate movement in areas where snow depth exceeds 70 cm, whilst deer, with their relatively narrow feet, do not move on snow where they might sink deeper than 40 cm because locomotion is severely impeded (Kelsall 1969). A similar relationship is found in lynx (*Lynx canadiensis*) which inhabit places with deeper snow when compared to the coyote (*C. latrans*), with their relatively small feet (Murray and Boutin 1991). A snowshoe foot lowers the pressure applied to the substrate. A common adaptation for moving over snow seen in birds such as the Adélie penguins (*Pygoscelis adeliae*) is switching to a “toboggan” gait, to spread their body weight more evenly when the snow is non-supportive and deep (Wilson et al. 1991).

The Svalbard rock ptarmigan (*Lagopus muta hyperborea*) is endemic to Svalbard and is the only bird that permanently lives in this Archipelago. *Lagopus* (from the Latin *lagōpūs,* from the ancient Greek *lagṓ* for 'hare' and *poús* 'foot') refers to the feathered foot densely covered in semiplume feathers (Höhn 1977), that in combination with wider and longer claws in winter (Lees et al. 2014) creates a snowshoe which is thought to reduce foot loadings by increasing foot area (Höhn 1977). Ptarmigan face extreme environmental conditions, with temperatures below freezing from September to May and snow cover that persists from October until April-May (Mortensen et al. 1983). Ptarmigan regularly commute over snowy ground and are therefore an ideal species for studying the effects of snow properties on locomotion. Although they can fly, they are predominantly a ground-dwelling bird, with males capable of three terrestrial gaits; walking, grounded running, and aerial running at higher speeds (Nudds et al. 2011). Juvenile ptarmigan rapidly develop adult-like locomotor capacities prior to winter (Lees et al. 2012b). Males gain weight before the onset of winter, which restricts them to walking and grounded running gaits; however, they can carry this extra fat (up to 32% of body mass (Mortensen et al. 1983)) at no additional metabolic cost (Lees et al. 2010).

It is widely accepted that animals select optimal routes on which to move principally to reduce the associated energetic costs of movement (Alexander 2000), however there is a general paucity of studies examining animal movement in the wild to test these hypotheses (Marmol-Guijarro et al. 2019; Shepard et al. 2013). Here, we investigated movements of free-ranging Svalbard rock ptarmigan in the Arctic and test hypotheses about how snow depth and supportiveness affect track profile, stride length and the speed of locomotion and ultimately route choice. We used 3D photogrammetry to measure foot sinking depth and footprint morphology. We hypothesized that speed will decrease as track depth increases on softer, deeper snow and that there should be evidence of route choice to avoid deeper snow that would be more energetically costly to move over.

Methods

Data from 14 males was obtained during a fieldtrip to Adventdalen (78° 13’18’’ N, 15° 38’ 30’’ E) and the surrounding side valleys in the Svalbard Archipelago from the 18th of April to the 3rd of May 2019. In spring, the midnight sun is already present, and the ground is snow covered. Ptarmigan body mass changes seasonally and males are at their summer weights at this time (Mortensen et al. 1983). Males were identified by their secondary sexual characteristics (distinctive red supraorbital comb, a thick black eye-stripe and calls). Birds were recorded moving at self-selected speed (U) at 100 frames per second using a SONY® Cyber-Shot RX10 III (SONY® Corporation, Japan) camera on a tripod parallel to the direction of movement at a fixed height and position. Immediately after the bird was out of the shot, a 1 metre scale bar was placed in frame, and over the trackway, to allow distance calibration so U could be determined using Tracker® v. 5.1.3 (Open Source Physics). A trackway consisted of at least 2 to 4 footprints (i.e. 1-3 strides). A stride consisted of two subsequent footfalls from the same foot (e.g. left footprint to the next left footprint). Gaits were allocated for a given speed; 0.26 to 0.91 ms^{-1} (walking) 0.92 to 1.48 ms^{-1} (grounded running) and 1.45 to 2.76 ms^{-1} (aerial running), respectively using (Marmol-Guijarro et al. 2019). Additional tracks made by the same birds immediately before and/or after the video field of view were also photographed when available (Figure 1A). For these trackways, stride length (l_{stride}) was used as a predictor of U for walking and aerial running speeds (Marmol-Guijarro et al. 2020). l_{stride} was measured using ImageJ v. 1.52q (Schneider et al. 2012). Grounded running U was not predicted because of the high error associated to the predictions based on l_{stride} and the lack of certainty of gait identification (Marmol-Guijarro et al. 2020).

3D Reconstructions and footprint depth analysis

After each video recording, 60 photographs were taken of each trackway from different angles, with a scale bar placed beside the tracks. Then, these photographs were imported into Agisoft Metashape software to generate the 3D models. “Very High Quality” settings were used for image alignment and mesh generation, and texture files were produced. 3D models were exported as .OBJ files and then imported to CloudCompare v. 2.10.2 to measure the footprint depths (D). Prior to the measurements, the footprints for each stride were cropped from the main model to the level of the snow surface. In the majority of trackways where the foot morphology was well preserved, depth measurements from the impressions of Toe II, Toe III, Toe IV and the metatarso-phalangeal joint (MTP) were taken (Figure 1C). In a few deep footprints, the toe regions collapsed after the foot was lifted. In such cases *h* was taken from the deepest, most distal portion that remained. A mean footprint depth value ($\overline{D}$) from two successive footprints was taken and a total of 121 strides with measured U and 186 strides with l_{stride}-only were analysed from the 3D reconstructions. Previous studies have suggested foot subsurface rotation on granular substrates of varying depths (Li et al. 2012; Turner et al. 2020) and this is an important measure of the functional movements of the foot through any substrate (Turner et al. 2020). To examine this the angle of the Toe III – MTP segment relative to the surface was measured (Figure 1D).

Measuring snow supportiveness

Snow supportiveness (R_{snow}) was measured using a modified thin-blade force gauge set-up (Borstad and McClung 2011) as a proxy for snow hardness to provide a measure of the resistiveness of the snow. Using a SPK-FMG-008A Chatillon® force probe attached to a Chatillon® DFE2-002 force gauge 10 ± 0.01 N (Ametek Inc. Florida, USA), 10 readings were taken at equidistant points (Figure 1B) closely beside each track by letting the probe penetrate into the snow up to a fixed depth (1cm) under its own weight.

Data Analysis

All variables were normalised using a $\log_{10}$ transformation prior to analyses to ensure that the data met the normality assumptions of the statistical tests used. Quantile-quantile plots were used to confirm this: a normal distribution is achieved if the residuals lie close to the line of best fit of the plot. A linear mixed model (full model -FM) was fitted with $\log_{10} U$ as the dependent variable and $\log_{10} R_{\text{snow}}$ and $\log_{10} \overline{D}$ as independent fixed variables including the interaction term ($\log_{10} R_{\text{snow}} \times \log_{10} \overline{D}$). The individual contribution of each bird was also included in the statistical model as random effects to account for repeated measures in some individuals. A second linear mixed model using the same independent variables as above was also performed with $\log_{10} l_{\text{stride}}$ as the dependent variable. For both dependent variables the FM models were simplified to assess, which statistical model (combination of independent variable) described the data best. Three statistical models in addition to the FM were used. The main effects model (MM) included only fixed effect variables with no interaction term. RM (the snow supportiveness model) refers to a linear mixed model only containing the independent variable $\log_{10} R_{\text{snow}}$. The footprint depth model (DM) refers to a linear mixed model only containing the independent variable $\log_{10} \overline{D}$. The random effect, individual, was retained in all of the statistical models. In order to assess which model best fits our data, first, we analysed the AIC_c of all models to estimate the likelihood of the models (p_i) to effectively minimize the AIC_c. Where AIC_c did not discriminate clearly between statistical models - i.e. if the AIC_c of the i^{th}- model is not significantly different from AIC_c of the model with the lowest score (Burnham and Anderson 2004) - the model which explained the largest amount of variation (highest r^2) was considered best. Thus, a model with the lowest AIC_c score or with a significantly comparable AIC_c to the lowest AIC_c and the largest amount of variation explained was selected as the best model. Although included for completeness (Table 1), the statistical models containing only the intercept were excluded as they would imply that the data is not influenced by any independent variable. To compare the mean subsurface rotation of the foot between varying depth profiles, we binned all data into 0.5cm depth ranges and performed a Kruskal-Wallis test and a post hoc pairwise Dunn's test to explore the differences between depth profiles. All the statistical analyses were conducted in R v. 3.6.3 (R Core Team 2020), using the lme4 (Bates et al. 2015) and the MuMIn (Bartón 2020) packages to generate the mixed models and to estimate their associated r^2, respectively. We used the Kruskal-Wallis built-in R function for the foot rotation comparisons, and the Dunn's Test function of the FSA (Ogle et al. 2020) package in R.

Results

The effect of $\boldsymbol{R_{\mathrm{snow}}}$ and $\boldsymbol{\overline{D}}$ on $\boldsymbol{U}$

The FM had the lowest AIC_c score and the highest r^2 explaining 14.9% of the total variation in U (Table 1). The effect of R_{snow} on U was not consistent across $\overline{D}$ ($t_{104} = -3.42$, $p < 0.001$) (Figure S1). At high values of R_{snow}, U has no effect on $\overline{D}$

whereas at low values of R_{snow}, $\overline{D}$ increases linearly with U. At intermediate values of R_{snow}, $\overline{D}$ again increases with U, but at a lower incremental rate. The U increased with increasing $\overline{D}$ ($t_{104} = 3.58$, $p < 0.001$), but decreased with increasing R_{snow} ($t_{104} = -3.44$, $p < 0.001$). The intercept (0.864) of the FM differed from zero ($t_{104} = 3.36$, $p < 0.001$). This, however, has little biological meaning here as it suggests that birds move at 7.32 ms^{-1} when R_{snow} and $\overline{D}$ are zero, which is approximately 2.3 times the highest documented U for the Ptarmigan [29]. Considerably, more variation (31.9%), than explained by the fixed effects in U, was explained by differences among individuals (random effect).

The effect of $\boldsymbol{R_{\text{snow}}}$ and $\boldsymbol{\overline{D}}$ on $\boldsymbol{l_{\text{stride}}}$

Again, the FM provided the best fit to the data explaining 10.6 % of the variation in l_{stride} and having an AIC_c not significantly different from that of the statistical model (DM) with the lowest AIC_c (Table 1). The results for l_{stride} were similar to those for U. The effect of R_{snow} on l_{stride} was not consistent across $\overline{D}$ ($t_{167} = -3.41$, $p < 0.001$) showing a similar pattern across $\overline{D}$ at different levels of R_{snow} to that found for U (Figure S2); l_{stride} increased with increasing $\overline{D}$ ($t_{167} = 3.30$, $p < 0.001$) and decreased concomitantly with increasing R_{snow} ($t_{167} = -2.95$, $p < 0.001$). Again, the intercept ($t_{167} = -5.15$, $p < 0.001$) by itself lacks any biological relevance. The amount of variation in l_{stride} accounted for by the main-effects (10.6%) was once again lower than that accounted for by the random effect, individual (31.4%).

Foot subsurface rotation at different $\boldsymbol{\overline{D}}$

Our data (Figure 2 and Table 2) suggest that the ptarmigan foot rotates to a greater extent when pushed deeper into the snow ($X^2 = 81.2$ d.f. = 6, $p < 0.001$). The foot has very little subsurface rotation 1.07° (SD ± 2.61°) when penetrating at the shallowest depths (0-0.5 cm depth) and rotates detectably less than at all deeper profiles. Other than at the shallowest depth profile, and although the angle of rotation increases progressively with depth profile, no other depth profile category is statistically discreet from all others (Figure 2 and Table 2).

Discussion

Effects of snow depth and supportiveness upon speed

Our study hypothesised that the ptarmigan travel speed would tend to decrease with decreasing snow supportiveness (R_{snow}) and increasing fooprint depth ($\overline{D}$). However, contrary to our hypothesis, U and l_{stride} were only weakly affected by $\overline{D}$ and snow R_{snow} in our models (r^2 = 0.149 and r^2 = 0.106 for U and l_{stride}, respectively). Thus, our data indicate that ptarmigan use similar speed ranges even when moving over snow that offers reduced structural support and that allows the foot to sink to variable depths. This contrasts to the only other data that exist for bipedal locomotion; studies of humans (Heinonen et al. 1959; Ramaswamy et al. 1966) show a reduction in U as sinking depth increases. Reductions in self-selected U are observed in other species, albeit quadrupedal mammals, to keep the energetic cost of moving in deep snow acceptable (Crête and Larivière 2003; Droghini and Boutin 2018a; Fancy and White 1987; Parker et al. 1984). These previous studies also report a positive association between the cost of locomotion and $\overline{D}$. For example, when $\overline{D}$ reaches 30% of the brisket height in elk (*Cervus elaphus nelsoni*), mule deer (*Odocoileus hemionus*), white-tail deer (*Odocoileus virginianus*) and the barren ground caribou (*Rangifer tarandus granti*), the net energy costs of locomotion increases from 12 to 34% (Fancy and White 1987; Mattfeld 1974; Parker et al. 1984). However, if the feet of these species sink to 60% of the brisket height, the energetic costs could span from 111 to 137% of that for a firm substrate, and beyond this point energy costs increase asymptotically (Fancy and White 1987; Mattfeld 1974; Parker et al. 1984). A 100% increase in the energy cost of locomotion has also been reported for coyote-sized dogs moving through 35 cm deep snow [15] – i.e. 77% of the chest height of a coyote (Murray and Boutin 1991).

In our study the ptarmigan $\overline{D}$ rarely exceeded 3.71 cm of depth, approximating the mean height to the intertarsal joint of the ptarmigan males (Lees, et al., unpublished data) and only two incidences during our study (*n* = 182) exceeded this depth (4.15 and 4.48 cm in two different males). These $\overline{D}$ correspond to 21.4 % (25.9 % in the case of the extreme value) of the total leg length reported for the Svalbard ptarmigan males elsewhere, although as Lees and colleagues (Lees et al. 2012a) pointed out these values may be underestimated due to the crouched posture of the ptarmigan limb. If it is assumed that similar increases in the cost of locomotion occur in the ptarmigan as in humans – the only other biped for which energetic data on snow of varying depth is available –, sinking 25% of the ptarmigan leg length into the snow would imply an increase of more than 2-fold in the cost of locomotion compared to firm ground. We did not quantify the energy expenditure of the birds in relation to movement over varying snow depths; however, the fact that the ptarmigan in our study rarely exceeded the intertarsal joint, and that up to this depth there was no evidence that it was affecting U, indicates that it is possible that the increase in the energetic cost of locomotion is manageable up to this depth but may increase rapidly if the foot sinks much further. Additional energy savings might also be obtained at bouncing gaits by the ptarmigan as a result of their avian morphology (i.e. horizontally oriented trunk, crouched hindlimb, etc.) (Watson et al. 2011). The snowshoe-like feet of the ptarmigan also contribute to minimise underfoot pressures, preventing them from sinking deeper into the snow, which translates into further energy savings. In humans, for instance, savings of up to 50 % of the energy being expended are possible compared to moving without snowshoes (Knapik et al. 1997; Rogers et al. 1965), despite the limitations of carrying a long and heavy device on the feet upon leg kinematics (Browning et al. 2012). In birds generally, and ptarmigan specifically, the avian foot enables a large surface area during stance, but it can also flex into a much smaller area during swing which decrease snow resistance. Hence, it is likely that the energetic costs of locomotion in the ptarmigan are less pronounced than in humans at comparable footprint depths.

In comparison to the ptarmigan, on the other hand, it appears that human bipeds might be less efficient when walking through deep snow. A study of military personnel, walking at self-selected U, reported a 120% increase in the metabolic cost of locomotion when subjects sank 30% of the leg length into snow compared to moving over firm ground (Ramaswamy et al. 1966) – a 4-10 fold increase compared to ungulates sinking to an equivalent proportion. The disproportionate increase in the energetic costs of locomotion in humans compared to quadruped mammals may be attributed to the morphological and kinematic differences between both locomotor modes, in particular the greater energetics cost of swinging limbs reported in humans (Pontzer 2007), which may also apply to ground dwelling birds (Marsh et al. 2004). Bipedal locomotion is only seen obligatorily in humans and birds and occasionally in apes (Alexander 2004); although, it is widely accepted that no animal moves in a similar way to humans (Alexander 2004). So, while it is interesting to look for parallels between humans and the ptarmigan, it is worth remembering that there are good reasons why human bipedal locomotion cannot be considered representative. We are not aware of any comparable data from other bird species for direct comparison.

Our study was conducted during the early spring months in Svalbard. Before the onset of winter, the Svalbard ptarmigan increase their body mass by 30-50% and this extra mass is maintained until early spring of the following year (Stokkan et al. 1986). This extra mass would translate into higher foot loading being transferred to the snow which would increase foot sinking depth. Intriguingly, previous work from our group found that despite the additional body mass the metabolic cost of locomotion is lower in winter (Lees et al. 2010) which, in light of the findings of this current study, we speculate could indicate an adaptation to mitigate the increased costs of the feet sinking at relatively greater depths during the heavier winter snowfalls. However, further study would be required to assess if there is evidence for any avoidance of very deep soft snow areas, for example using GPS tags together with measurements of the associated metabolic costs (Shepard et al. 2013).

Our models indicate that a large portion of the variance is explained by individuals (repeated measures), which may reflect the necessity to better control for the confounding effects of body size and mass. The gold standard in this approach that would enable this to be quantified would be to measure these parameters in each individual bird being recorded, however this is logistically difficult in a field setting. However, Stokkan and colleagues (Stokkan et al. 1986) found that, at the time of year our current study were conducted, body weight varies by about 30g in wild caught birds so this may not be a major issue. Comparable data on body size are not available.

Footprint Morphology

The 3D reconstructions of the footprints suggest greater foot rotations in deeper footprints (Figure 2, Table 2). Similar foot kinematics have been seen in guineafowl [32] and zebra-tailed lizards (Li et al. 2012) moving on granular media, indicating increased rotation of toe III below the surface with increasing depth (Turner et al. 2020). The ptarmigan may also be taking advantage of the compressive nature of snow by forming a densely packed and supportive snow layer beneath the rotating foot, generating enough ground reaction forces to move forward and leaving a well-defined footprint. A similar phenomenon has been reported in sea turtle hatchlings, where a supportive region of natural sand is created beneath the edge of the flipper after stance and during flipper rotation for thrust (Mazouchova et al. 2010). Irrespectively of the substrate, however, it appears that footprint rotation *within* the substrate may be an additional source of energetic cost.

There is a large source of variation within all the depth profiles included in this study. One possible explanation for this might be related to the snow cover stratification, where layers of snow beneath the surface may vary in their physical properties directly affecting foot rotation and support. For example, a denser layer of snow buried under a layer of fresh new snow at a given depth, or a relatively thin layer of snow above *terra firma*, might prevent subsurface foot rotation, as it would provide enough support during the ptarmigan’s stance phase. Rocks or other debris may also prevent foot subsurface rotations by keeping one or more toes at shallower depths than the metatarsophalangeal joint, if the ptarmigan stand on them. In the same way, foot subsurface rotation may not be accurately estimated in the footprints showing signs of snow collapse. These two factors may obscure a potential relationship between subsurface foot rotation with l_{stride} and U. When plotted together (Figure S3), a positive trend (differences between l_{stride} ranges are statistically non-significant –

Table S1) between foot rotations and l_{stride} is suggested from 0.15 to 0.35 m but no association is evident at longer l_{stride}. A similar positive trend is observed between foot rotation and U up to 1 ms^{-1} (Figure S4), and again it becomes highly variable at higher speeds (grounded running and aerial running). Angle, however, is only detectably different at the lowest speed (Table S2). The lack of an association between foot rotation angle and higher U and l_{stride}, may, in part, be because of low sample sizes at these higher non-walking (grounded and aerial running) speeds.

Conclusion

Our data provide evidence that the Svalbard ptarmigan moving over snow of varying depth may be preferentially choosing to move on routes through the snow that aren't deep enough to affect locomotion speed and therefore help them avoid increases in the energetic cost of locomotion. Evidence from other animals suggests that this strategy may be widespread as animals seek to maintain their energy balance (Wall et al. 2006). They also raise an interesting question about what feedback mechanisms the birds (and indeed all animals) are using to identify regions of any substrate that are supportive enough to keep sinking depths reasonable, for example under the intertarsal threshold identified here for the ptarmigan. It would clearly be advantageous if they could identify which areas of the substrate would provide less support and therefore potentially require more energy to move over. Options for detecting variations in substrate would likely be limited to visual cues or through learnt trial and error behaviour.

Ethics: All experimental procedures and methods conducted in this study were performed under ethical approval from the University of Manchester Animals Ethics Committee in accordance with the Animal (Scientific Procedures) Act 1986 and under research permits from the Governor of Svalbard. Research in Svalbard (RiS) Project Numbers 10790, 11034 and 11248.

Data accessibility: processed data and code available from figshare digital repository (https://figshare.com/s/709457add73cf386c65a)

Authors Contribution: J.C. designed the study with assistance of A.M.-G., R.N., W.S., P.T., C.B. and L.F. A.M.-G. and J.C. conducted the study in the field and interpreted the findings. A.M.-G. and R.N. analysed the data. All authors were involved in the drafting, revision and approval of the final manuscript.

Competing Interest Statement: The authors declare that we have no competing interest.

Funding: This research was supported by a Secretaría Nacional de Educación Superior Ciencia, Tecnología e Innovacíon del Ecuador (SENESCYT) award to A.M.-G and J.C. (ARQ2-000199-2016); and the Biotechnology and Biological Sciences Research Council (BBSRC) to J.C. (BB/G01138/1).

Acknowledgements: Access to the Adventdalen Field Station and logistical support was provided by the University of Tromsø. We would like to thank Chris Borstad for his advice and training in using the force gauge for snow classifications. We would also like to thank the Governor of Svalbard's (Sysselmannen) office for permission to conduct these studies.

Footnotes: Electronic supplementary material is available online at https://figshare.com/s/4b12322d1d2b3c7a3718

References

Alexander RM. 2000. Walking and running strategies for humans and other mammals. In: Blake PW, Domenici P, editors. Biomechanics in Animal Behaviour. Oxford: BIOS Scientific Publishers. p. 49-58.

Alexander RM. 2004. Bipedal animals, and their differences from humans. J Anat. 204(5):321-330.

Bartón K. 2020. MuMIn: Multi-Model Inference. R package version 1.43.17. Vienna: R Foundation for Statistical Computing.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. J Stat Softw. 67(1):48.

Birn-Jeffery AV, Daley MA. 2012. Birds achieve high robustness in uneven terrain through active control of landing conditions. J Exp Biol. 215(12):2117.

Borstad CP, McClung DM. 2011. Thin-blade penetration resistance and snow strength. J Glaciol. 57(202):325-336.

Browning RC, Kurtz RN, Kerherve H. 2012. Biomechanics of walking with snowshoes. Sports Biomech. 11(1):73-84.

Bruland O, Liston GE, Vonk J, Sand K, Killingtveit Å. 2004. Modelling the snow distribution at two high arctic sites at Svalbard, Norway, and at an alpine site in central Norway. Hydrol Res. 35(3):191-208.

Burnham KP, Anderson DR. 2004. Multimodel inference: Understanding AIC and BIC in model selection. Sociol Method Res. 33(2):261-304.

Clark AJ, Higham TE. 2011. Slipping, sliding and stability: locomotor strategies for overcoming low-friction surfaces. J Exp Biol. 214(8):1369.

Crête M, Larivière S. 2003. Estimating the costs of locomotion in snow for coyotes. Can J Zool. 81(11):1808-1814.

Daley MA, Usherwood JR, Felix G, Biewener AA. 2006. Running over rough terrain: Guinea fowl maintain dynamic stability despite a large unexpected change in substrate height. J Exp Biol. 209(1):171.

Descamps S, Aars J, Fuglei E, Kovacs KM, Lydersen C, Pavlova O, Pedersen ÅØ, Ravolainen V, Strøm H. 2017. Climate change impacts on wildlife in a High Arctic archipelago – Svalbard, Norway. Glob Chang Biol. 23(2):490-502.

Droghini A, Boutin S. 2018a. The calm during the storm: Snowfall events decrease the movement rates of grey wolves (*Canis lupus*). PLoS One. 13(10):e0205742.

Droghini A, Boutin S. 2018b. Snow conditions influence grey wolf (*Canis lupus*) travel paths: The effect of human-created linear features. Can J Zool. 96(1):39-47.

Falkingham PL, Margetts L, Manning PL. 2010. Fossil vertebrate tracks as paleopenetrometers: confounding effects of foot morphology. Palaios. 25(6):356-360.

Fancy SG, White RG. 1987. Energy expenditures for locomotion by barren-ground caribou. Can J Zool. 65(1):122-128.

Hagenmuller P, Chambon G, Flin F, Morin S, Naaim M. 2014. Snow as a granular material: Assessment of a new grain segmentation algorithm. Granul Matter. 16(4):421-432.

Hansen BB, Grøtan V, Aanes R, Sæther B-E, Stien A, Fuglei E, Ims RA, Yoccoz NG, Pedersen ÅØ. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the high Arctic. Science. 339(6117):313.

Heinonen AO, Karvones MJ, Ruosteenoja R. 1959. The energy expenditure of walking on snow at various depths. Ergonomics. 2(4):389-394.

Höhn EO. 1977. The “snowshoe effect” of the feathering on ptarmigan feet. Condor. 79(3):380-382.

Hornberger G, Winter TC. 2009. Snow and Ice. In: Likens GE, editor. Encyclopedia of Inland Waters. Oxford: Academic Press. p. 773.

Kelsall JP. 1969. Structural adaptations of moose and deer for snow. J Mammal. 50(2):302-310.

Knapik J, Hickey C, Ortega S, Nagel J, de Pontbriand R. 1997. Energy cost of walking in four types of snowshoes. Paper presented at: Proceedings of the Human Factors and Ergonomics Society Annual Meeting. SAGE Publications Inc.

Lees JJ, Folkow LP, Nudds RL, Codd JR. 2014. The effects of season and sex upon the morphology and material properties of keratin in the Svalbard rock ptarmigan (*Lagopus muta hyperborea*). J Therm Biol. 44:126-130.

Lees JJ, Nudds R, Stokkan K-A, Folkow L, Codd J. 2010. Reduced metabolic cost of locomotion in Svalbard rock ptarmigan (*Lagopus muta hyperborea*) during winter. PLoS One. 5:e15490.

Lees JJ, Nudds RL, Folkow LP, Stokkan KA, Codd JR. 2012a. Understanding sex differences in the cost of terrestrial locomotion. Proc R Soc B: Biol Sci. 279(1729):826-832.

Lees JJ, Stokkan K-A, Folkow LP, Codd JR. 2012b. Locomotor development in the Svalbard rock ptarmigan (*Lagopus muta hyperborea*). Polar Biol. 35:867-874.

Li C, Hsieh ST, Goldman DI. 2012. Multi-functional foot use during running in the zebra-tailed lizard (*Callisaurus draconoides*). J Exp Biol. 215(18):3293.

Marmol-Guijarro A, Nudds R, Folkow L, Codd J. 2020. Examining the accuracy of trackways for predicting gait selection and speed of locomotion. Front Zool. 17(1):17.

Marmol-Guijarro AC, Nudds RL, Marrin JC, Folkow LP, Codd JR. 2019. Terrestrial locomotion of the Svalbard rock ptarmigan: Comparing field and laboratory treadmill studies. Sci Rep. 9(1):11451.

Marsh RL, Ellerby DJ, Carr JA, Henry HT, Buchanan CI. 2004. Partitioning the energetics of walking and running: Swinging the limbs is expensive. Science. 303(5654):80.

Mattfeld GF. 1974. The energetics of winter foraging by white-tailed deer: A perspective on winter concentration. [Syracuse]: State university of New York.

Mazouchova N, Gravish N, Savu A, Goldman DI. 2010. Utilization of granular solidification during terrestrial locomotion of hatchling sea turtles. Biol Lett. 6(3):398-401.

Mortensen A, Unander S, Kolstad M, Blix AS. 1983. Seasonal changes in body composition and crop content of Spitzbergen ptarmigan *Lagopus mutus hyperboreus*. Ornis Scand. 14:144-148.

Murray DL, Boutin S. 1991. The influence of snow on lynx and coyote movements: does morphology affect behavior? Oecologia. 88(4):463-469.

Nicot F. 2004. Constitutive modelling of snow as a cohesive-granular material. Granul Matter. 6(1):47-60.

Nudds RL, Folkow LP, Lees JJ, Tickle PG, Stokkan KA, Codd JR. 2011. Evidence for energy savings from aerial running in the Svalbard rock ptarmigan (*Lagopus muta hyperborea*). Proc R Soc B: Biol Sci. 278(1718):2654-2661.

Ogle DH, Wheeler P, Dinno A. 2020. FSA: fisheries stock analysis.

Parker KL, Robbins CT, Hanley TA. 1984. Energy expenditures for locomotion by mule deer and elk. J Wildl Manage. 48(2):474-488.

Pontzer H. 2007. Predicting the energy cost of terrestrial locomotion: a test of the LiMb model in humans and quadrupeds. J Exp Biol. 210(3):484.

R Core Team. 2020. R: a language and environment for statistical computing. R version 3.6.3. Vienna, Austria: R Foundation for Statistical Computing.

Ramaswamy SS, Dua GL, Raizada GP, Dimri GP, Viswanathan KR, Madhaviah J, Srivastava TN. 1966. Effects of looseness of snow on energy expenditure in marching on snow-covered ground. J Appl Physiol. 21(6):1747-1749.

Rogers TA, Buck AC, Klopping JC. 1965. Studies on the energy cost of level cross-country travel in the Arctic. Fort Wainwright, Alaska. No. AAL-TR-65-9.

Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image analysis. Nat Methods. 9(7):671-675.

Shepard ELC, Wilson RP, Rees WG, Grundy E, Lambertucci SA, Vosper SB. 2013. Energy landscapes shape animal movement ecology. Am Nat. 182(3):298-312.

Stokkan KA, Mortensen A, Blix AS. 1986. Food intake, feeding rhythm, and body mass regulation in Svalbard rock ptarmigan. Am J Physiol. 251:R264-R267.

Turner ML, Falkingham PL, Gatesy SM. 2020. It's in the loop: shared sub-surface foot kinematics in birds and other dinosaurs shed light on a new dimension of fossil track diversity. Biol Lett. 16(7):20200309.

Wall J, Douglas-Hamilton I, Vollrath F. 2006. Elephants avoid costly mountaineering. Curr Biol. 16(14):R527-R529.

Watson RR, Rubenson J, Coder L, Hoyt DF, Propert MWG, Marsh RL. 2011. Gait-specific energetics contributes to economical walking and running in emus and ostriches. Proc R Soc B: Biol Sci. 278(1714):2040-2046.

Wilson RP, Culik B, Adelung D, Coria NR, Spairani HJ. 1991. To slide or stride: when should Adélie penguins (*Pygoscelis adeliae*) toboggan? Can J Zool. 69(1):221-225.

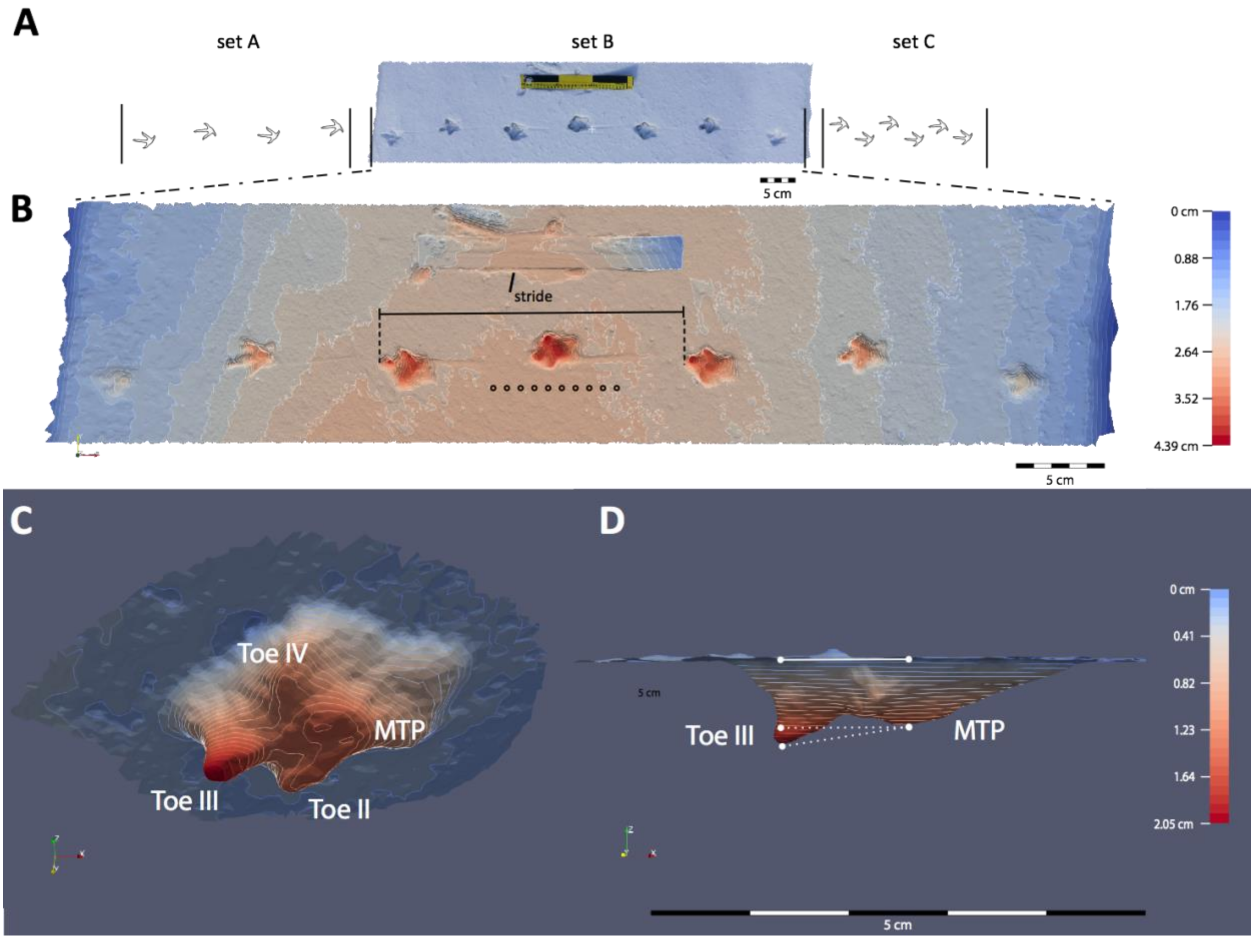

Figure 1. Schematic representation of the footprint analysis in the field. All footprints were taken only from one side. (A) represent three sets of continuous footprints where set A and set C were not video recorded, whilst set B was. A 30 cm scale bar was placed alongside each footprint set and up to 10 force penetration measurements were taken, as a proxy of snow supportiveness (R_{snow}) (the dots on B). After 3D reconstruction (B), l_{stride} was measured from the tip of toe III of two continuous footprints. (C) $\overline{D}$ was then estimated as the mean depth at four different footprint landmarks corresponding to toe II, toe III, toe IV and MTP joint. Finally, the angle between toe III – MTP segment to the surface was measured as a proxy of foot subsurface rotation (D).

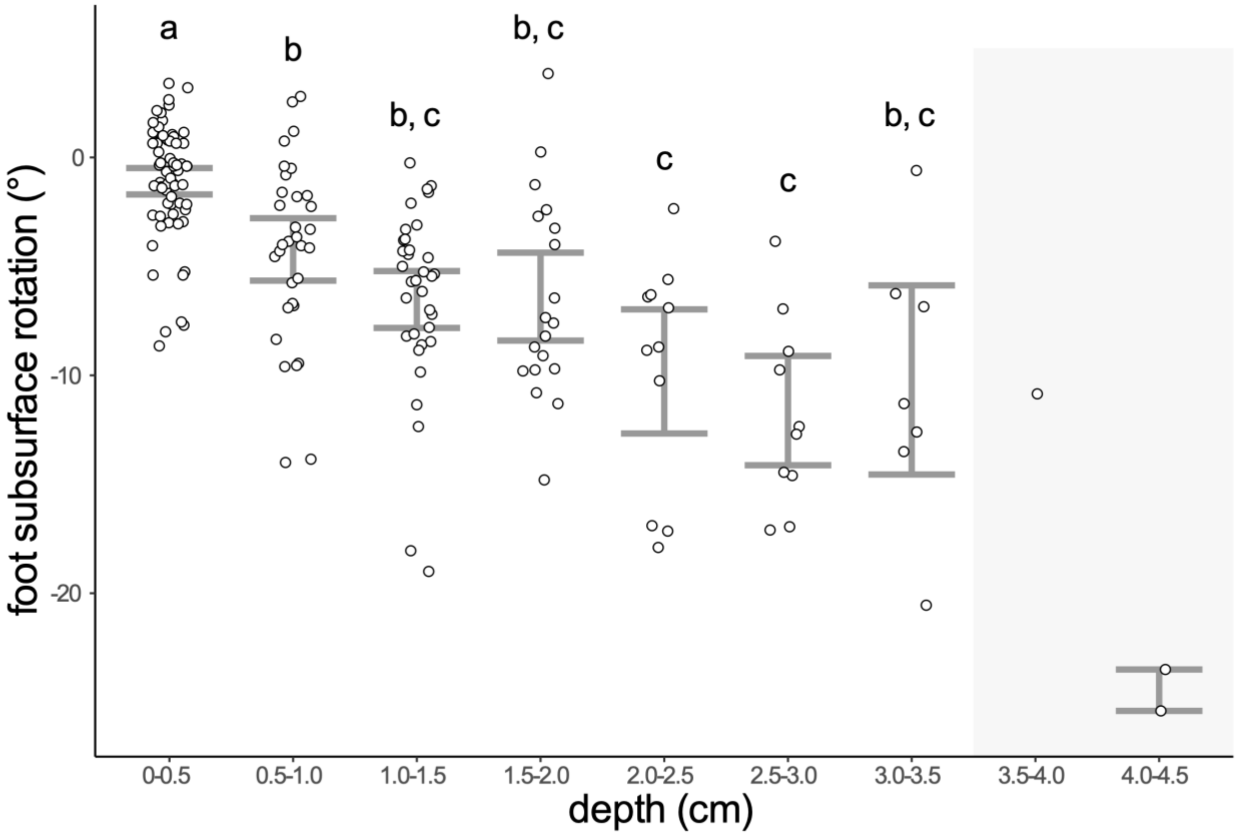

Figure 2. Subsurface rotation of the feet at varying snow depth profiles. Each snow depth profile is binned into 0.5 cm bins from 0 to 4.5 cm. “a”, “b” and “c” represent similarities in foot subsurface rotation based on pairwise Dunn’s tests comparisons (Table S3) between all depth profiles. Data points within the grey shaded area were not included in the analyses due to a low sample size.

Table 1. Model selection describing the influence of footprint sinking depth ($\overline{D}$) and snow supportiveness (R_{snow}) on estimates of speed (U) and stride length (l_{stride}). FM refers to the linear mixed models (LMM) including both R_{snow} and $\overline{D}$ as independent variables and the interaction term ($R_{\text{snow}} \times \overline{D}$). The MM refers to the LMMs exploring the main effects of R_{snow} and $\overline{D}$ as independent variables without the interaction term. RM and DM are LMMs where R_{snow} and $\overline{D}$ are analysed independently as single variables. LMMs where neither of the independent variables influenced l_{stride} and U are represented only by the intercept.

Model	*K*	AIC$_c$	Δ AIC	AIC$_{wt}$	*p*$_i$	r^2
Log$_{10}$ U						
Intercept	3	-36.44	0	0.412	1	-
Intercept + log$_{10}$ $\boldsymbol{R_{\text{snow}}} \times$ log$_{10}$ $\boldsymbol{\overline{D}}$ (FM)	**6**	**-35.83**	**0.613**	**0.303**	**0.960**	**0.149**
Intercept + log$_{10}$ $\overline{D}$ (DM)	4	-34.76	1.686	0.177	0.462	0.044
Intercept + log$_{10}$ R_{snow} (RM)	4	-33.52	2.92	0.096	0.249	0.038
Intercept + log$_{10}$ R_{snow} + log$_{10}$ $\overline{D}$ (MM)	5	-29.33	7.112	0.012	0.033*	0.050
Log$_{10}$ l_{stride}						
Intercept + log$_{10}$ $\overline{D}$ (DM)	4	-297.02	0	0.41	1	0.052
Intercept	3	-296.73	0.29	0.355	0.827	-
Intercept + log$_{10}$ $\boldsymbol{R_{\text{snow}}} \times$ log$_{10}$ $\boldsymbol{\overline{D}}$ (FM)	**6**	**-295.61**	**1.402**	**0.204**	**0.562**	**0.106**
Intercept + log$_{10}$ R_{snow} + log$_{10}$ $\overline{D}$ (MM)	4	-290.92	6.097	0.019	0.050*	0.053
Intercept + log$_{10}$ R_{snow} (RM)	4	-289.87	7.15	0.011	0.028*	0.009

K = the number of parameters within the model.

p$_i$-values indicate if the statistical model's AIC$_c$ differs from the model with the lowest AIC$_c$.

r^2 corresponds to the explained variance of the fixed effects within the model.

Bold text indicates the best linear mixed effect model based on the largest r^2 and an AIC$_c$ score not significantly different from the model with the lowest AIC$_c$.

Ptarmigan individual identity was included as random factor (1|bird id) in all the statistical models to account for repeated measures.

Table 2. Mean foot subsurface rotation angles at different depth profiles.

Depth profile (cm)	*n*	Angle (°)	95% Confidence Intervals	
			Lower percentile	Upper percentile
0-0.5	66	1.08 ± 2.62 [a]	0.47	1.71
0.5-1.0	32	4.24 ± 4.15 [b]	2.85	5.66
1.0-1.5	34	6.41 ± 4.18 [bc]	5.13	7.86
1.5-2.0	19	6.48 ± 4.64 [bc]	4.42	8.45
2.0-2.5	11	9.75 ± 5.27 [c]	6.90	12.80
2.5-3.0	10	11.76 ± 4.34 [c]	9.09	14.20
3.0-3.5	7	10.24 ± 6.38 [bc]	5.89	14.60
3.5-4.0	1	10.85	-	-
4.0-4.5	2	24.5 ± 1.34	23.5	25.4

[a,b,c] represent similarities in angle between depth profiles determined using Dunn's test pairwise comparisons of each profile.

Data in the shaded areas were not included in the analyses because of their low *n*.

Electronic Supplementary Material

Potential evidence for route choice through snow in the Svalbard rock ptarmigan

Andres Mármol-Guijarro[1], Robert Nudds[1], Lars Folkow[2], William Sellers[3], Peter Falkingham[4] & Jonathan Codd[1*]

[1]School of Biological Sciences, Faculty of Biology, Medicine & Health, University of Manchester, Manchester, UK; [2]Department of Arctic & Marine Biology, University of Tromsø – the Arctic University of Norway, Tromsø, Norway; [3]School of Earth & Environmental Sciences, Faculty of Science & Engineering, University of Manchester, Manchester, UK; [4]School of Natural Sciences, Liverpool John Moores University, Liverpool, UK.

***Corresponding author:** Dr. Jonathan Codd

Email: jonathan.codd@manchester.ac.uk

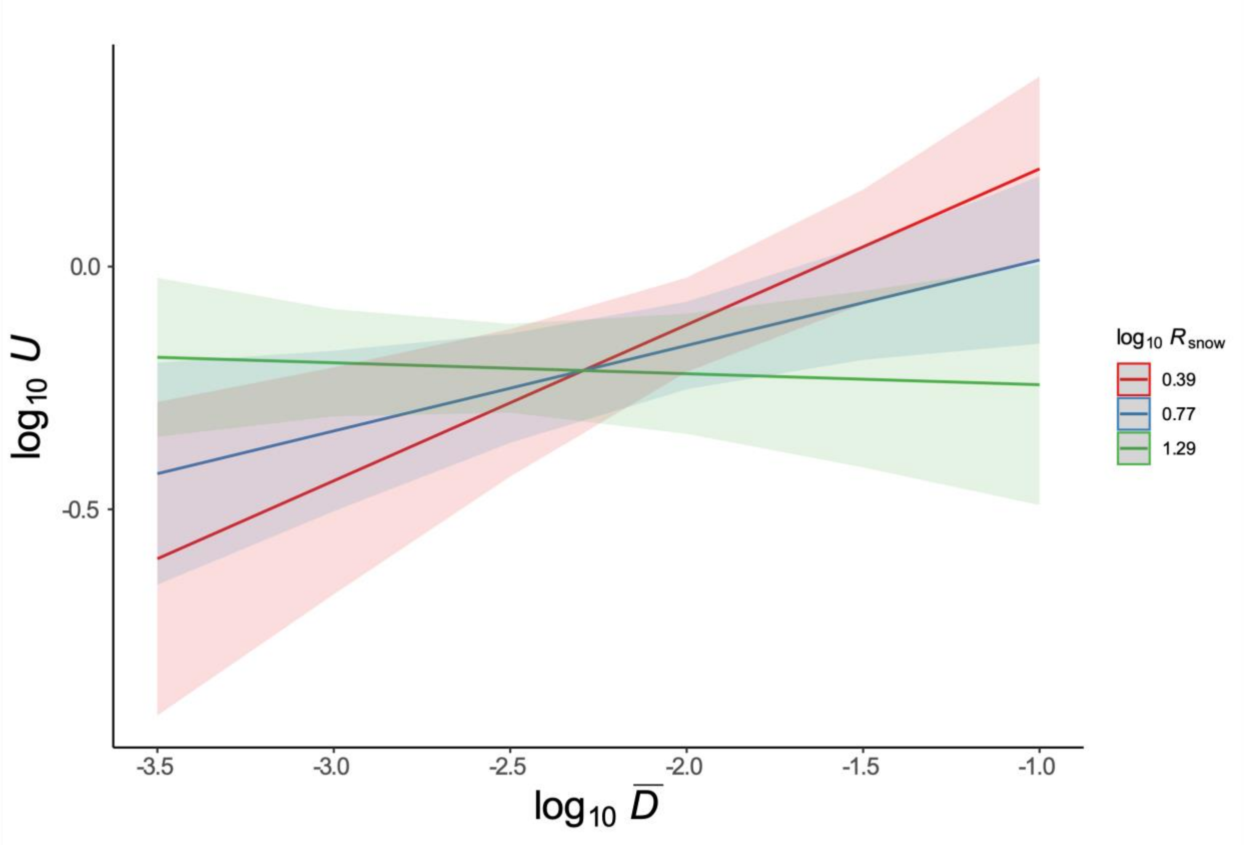

Figure S1. Interaction plot for the linear mixed model (full Model-FM) predicting the $\log_{10}$ of speed (U) from mean footprint depth ($\overline{D}$) and snow supportiveness (R_{snow}). The lines of best fit represent the slope between U and $\overline{D}$ at the first (red), second (blue) and third (green) quartiles of R_{snow}. The shaded areas represent the 95% confidence intervals of the slopes.

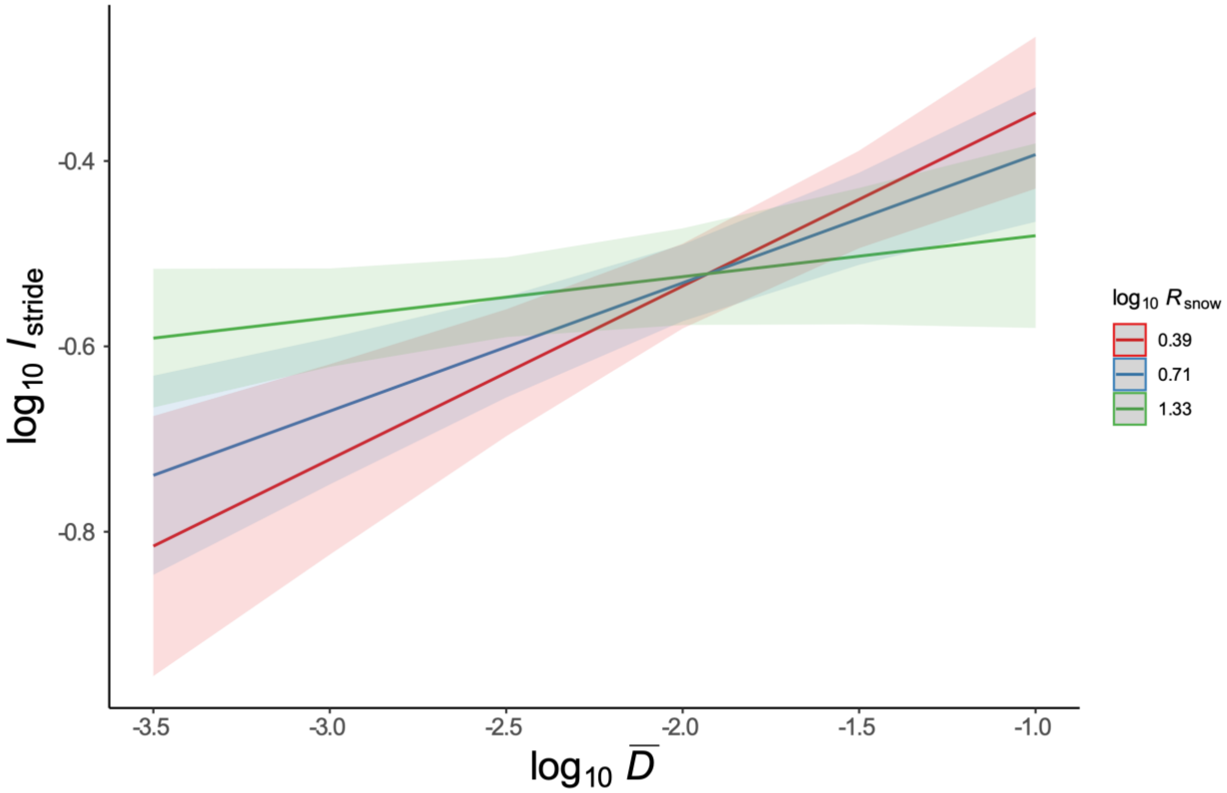

Figure S2. Interaction plot for the linear mixed model (full Model-FM) predicting the $\log_{10}$ of stride length (l_{stride}) from mean footprint depth ($\overline{D}$) at different values of snow supportiveness (R_{snow}). The lines of best fit represent the slope between U and $\overline{D}$ at the first (red), second (blue) and third (green) quartiles of R_{snow}. The shaded areas represent the 95% confidence intervals of the slopes.

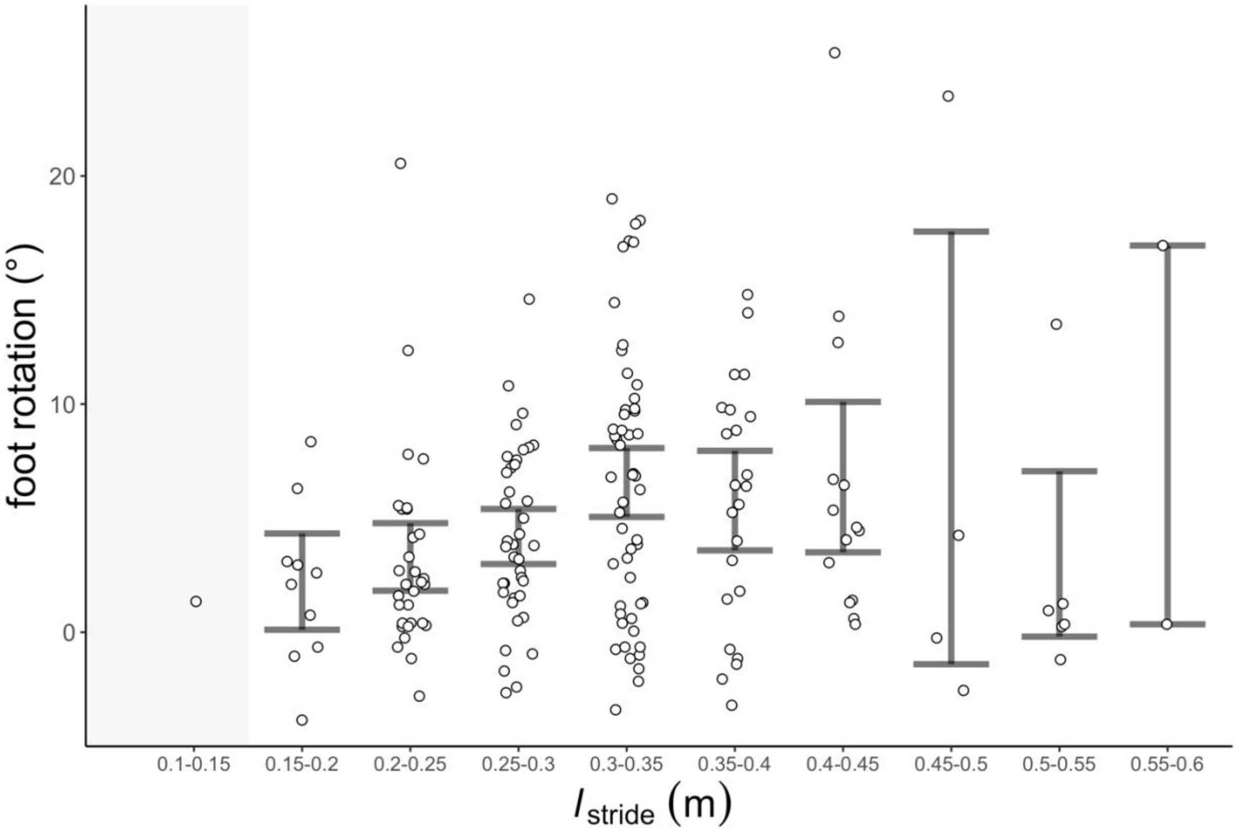

Figure S3. Subsurface rotation of the feet at different stride lengths (l_{stride}). l_{stride} was binned into 0.05 m bins from 0.10 to 0.60 m. No differences among the l_{stride} bins were found based on a pairwise Dunn's tests. Bars indicate the confidence intervals of the mean for each l_{stride} bin. Data points within the shaded area were not included in the analyses due to low sample sizes.

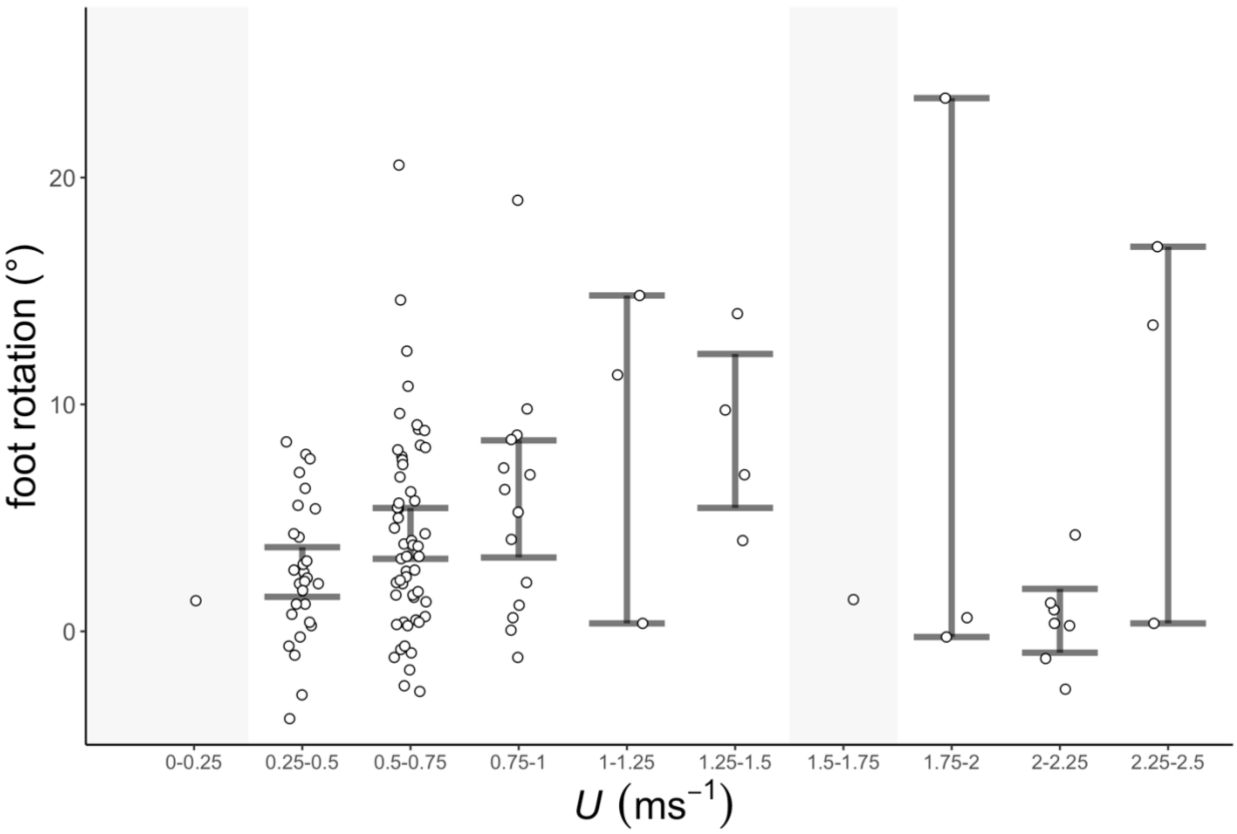

Figure S4. Subsurface rotation of the feet at different speeds (*U*). *U* was binned into 0.25 m bins from 0 to 2.5 ms^{-1}. No differences among *U* bins were found based on a pairwise Dunn's tests. Bars indicate the confidence intervals of the mean for each *U* bin. Data points within the shaded area were not included in the analyses due to low sample sizes.

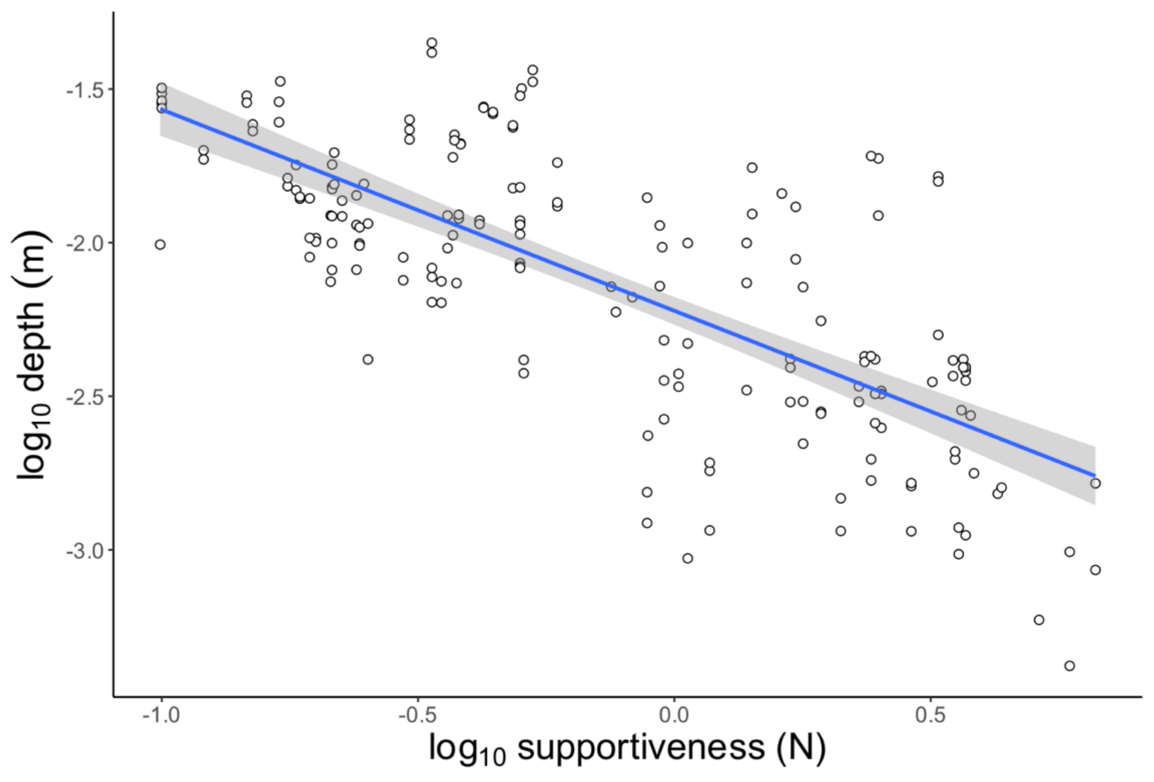

Figure S5. The base 10 logarithm of footprint depth plotted against the base 10 logarithm of snow supportiveness. As snow compliance increases (right side of the x-axis), footprint depth decreases (lower side of the y-axis), which is indicated by the line of best fit (solid blue) drawn over the data points. Similar results have been previously reported for humans walking on sand by Bates et al. (2013) The shaded area represents the 95% confidence intervals of the slope.

Table S1. Mean foot subsurface rotation at different ranges of l_{stride}.

l_{stride} (m)	*n*	Angle (°)	95% Confidence Intervals	
			Lower percentile	Upper percentile
0.10-0.15	1	1.35	-	-
0.15-0.20	10	2.06 ± 3.55 [a]	0.02	4.24
0.20-0.25	31	3.19 ± 4.46 [a]	1.78	4.85
0.25-0.30	39	4.22 ± 3.84 [a]	3.04	5.44
0.30-0.35	52	6.55 ± 5.98 [a]	4.98	8.18
0.35-0.40	23	5.67 ± 5.24 [a]	3.55	7.77
0.40-0.45	14	6.45 ± 6.81 [a]	3.46	10.20
0.45-0.50	4	6.24 ± 11.85 [a]	-1.40	17.60
0.50-0.55	6	2.52 ± 5.45 [a]	-0.19	7.06
0.55-0.60	2	8.65 ± 11.74 [a]	0.35	17.00

[a] indicates similarities between l_{stride} bins determined using pairwise comparisons (Dunn's tests) of each profile.

Data in shaded areas were not included in the analyses due to a low *n.*

Table S2. Mean foot subsurface rotation at different ranges of *U*.

U (ms^{-1})	*n*	Angle (°)	95% Confidence Intervals	
			Lower percentile	Upper percentile
0-0.25	1	1.35	-	-
0.25-0.50	10	2.62 ± 3.12 [a]	1.49	3.76
0.50-0.75	31	4.26 ± 4.46 [a]	3.09	5.46
0.75-1.00	39	5.60 ± 5.22 [a]	3.16	8.46
1.00-1.25	52	8.82 ± 7.54 [a]	0.35	14.80
1.25-1.50	23	8.66 ± 4.26 [a]	5.44	12.20
1.50-1.75	14	1.40	-	-
1.75-2.00	4	7.95 ± 13.47 [a]	-0.25	23.50
2.00-2.25	6	0.47 ± 2.13 [a]	-0.94	1.98
2.25-2.50	2	10.27 ± 8.76 [a]	0.35	17.00

[a] represents similarities between l_{stride} bins determined by pairwise comparisons (Dunn's tests) of each profile using the *p*-adjusted values.

Data on shaded areas were not included into analysis due to their low *n.*

Table S3. Dunn's test pairwise comparisons output for foot rotation over different (binned) depth profiles summarised in Figure 2 and table 2.

Comparison	*Z*	*p*	*p* - adjusted
0-0.5 vs. 0.5-1	-3.49	4.82E-04	1.69E-03
0-0.5 vs. 1-1.5	-4.98	6.40E-07	4.48E-06
0.5-1 vs. 1-1.5	-1.12	0.262	0.324
0-0.5 vs. 1.5-2	-4.38	1.19E-05	6.26E-05
0.5-1 vs. 1.5-2	-1.28	0.199	0.279
1-1.5 vs. 1.5-2	-0.34	0.732	0.768
0-0.5 vs. 2-2.5	-5.13	2.83E-07	2.98E-06
0.5-1 vs. 2-2.5	-2.63	0.008	0.020
1-1.5 vs. 2-2.5	-1.89	0.059	0.103
1.5-2 vs. 2-2.5	-1.48	0.140	0.210
0-0.5 vs. 2.5-3	-5.78	7.33E-09	1.54E-07
0.5-1 vs. 2.5-3	-3.34	0.001	0.002
1-1.5 vs. 2.5-3	-2.64	0.008	0.022
1.5-2 vs. 2.5-3	-2.18	0.029	0.061
2-2.5 vs. 2.5-3	-0.66	0.506	0.591
0-0.5 vs. 3-3.5	-4.11	3.88E-05	1.63E-04
0.5-1 vs. 3-3.5	-2.12	0.034	0.065
1-1.5 vs. 3-3.5	-1.49	0.137	0.221
1.5-2 vs. 3-3.5	-1.18	0.238	0.313
2-2.5 vs. 3-3.5	0.08	0.940	0.940
2.5-3 vs. 3-3.5	0.66	0.507	0.560

References

Bates KT, Savage R, Pataky TC, Morse SA, Webster E, Falkingham PL, Ren L, Qian Z, Collins D, Bennett MR et al. 2013. Does footprint depth correlate with foot motion and pressure? J R Soc Interface. 10(83):20130009.

Chapter 5

Examining the accuracy of trackway for predicting gait preferences and speed of locomotion

This chapter is a reprint of an article published in *Frontiers in Zoology:*

Marmol-Guijarro, A.C., Nudds, R., Folkow, L.P. and Codd, J.R. (2020). Examining the accuracy of trackway for predicting gait selection and speed of locomotion. *Frontiers in Zoology* 17, 17 (https://doi.org/10.1186/s12983-020-00363-z).

Marmol-Guijarro *et al. Frontiers in Zoology* (2020) 17:17
https://doi.org/10.1186/s12983-020-00363-z

Frontiers in Zoology

RESEARCH Open Access

Examining the accuracy of trackways for predicting gait selection and speed of locomotion

Andres Marmol-Guijarro[1], Robert Nudds[1], Lars Folkow[2] and Jonathan Codd[1*]

Abstract

Background: Using Froude numbers (*Fr*) and relative stride length (stride length: hip height), trackways have been widely used to determine the speed and gait of an animal. This approach, however, is limited by the ability to estimate hip height accurately and by the lack of information related to the substrate properties when the tracks were made, in particular for extinct fauna. By studying the Svalbard ptarmigan moving on snow, we assessed the accuracy of trackway predictions from a species-specific model and two additional *Fr* based models by ground truthing data extracted from videos as the tracks were being made.

Results: The species-specific model accounted for more than 60% of the variability in speed for walking and aerial running, but only accounted for 19% when grounded running, likely due to its stabilizing role while moving faster over a changing substrate. The error in speed estimated was 0–35% for all gaits when using the species-specific model, whereas *Fr* based estimates produced errors up to 55%. The highest errors were associated with the walking gait. The transition between pendular to bouncing gaits fell close to the estimates using relative stride length described for other extant vertebrates. Conversely, the transition from grounded to aerial running appears to be species specific and highly dependent on posture and substrate.

Conclusion: Altogether, this study highlights that using trackways to derive predictions on the locomotor speed and gait, using stride length as the only predictor, are problematic as accurate predictions require information from the animal in question.

Keywords: Gait, Locomotion, Arctic, Biomechanics, Snow, Track, Speed

Background

Understanding what speeds of locomotion animals choose during interactions with conspecifics (i.e. social or reproductive behaviour), other species (i.e. predation or predator avoidance), and when moving through an often-changing environment is paramount to better understanding their biology. Studies of terrestrial animal locomotion, however, are overwhelmingly conducted under laboratory conditions using treadmills [1]. Treadmill studies have facilitated great insight into the biomechanics of locomotion and using this approach the correlation between kinematic parameters like stride length (l_{stride}), stride frequency (f_{stride}) stance (t_{stance}) and swing (t_{swing}) time with speed (U) has been widely reported in the literature across a range of species. For example; treadmill kinematic data exists on a wide range of mammals including polar bears [2]; horses [3]; otters [4]; deer [5] cats [6], rodents [7, 8] and monkeys [9]. However, perhaps the most comprehensive research into animal locomotion has been conducted in birds [10–17]. The focus on avian biomechanics is likely due to birds evolutionary link to their theropod ancestors, being

---

* Correspondence: jonathan.codd@manchester.ac.uk
[1] Faculty of Biology, Medicine & Health, University of Manchester, Manchester, UK
Full list of author information is available at the end of the article

bipedal, easy to train, experimentally tractable and exibiting a wide range of adaptations. For example, the Svalbard rock ptarmigan (*Lagopus muta hyperborea*) has been extensively studied for locomotor adaptations related to energy savings upon gait change [18], sexual selection [19], efficient load carriage [20] and ontogeny [21].

Studying the locomotion of wild animals in their natural enviroment can be challenging, many animals are elusive and fieldwork can be protracted, expensive and prone to a wide range of factors that cannot be controlled. Trackways are one way to circumvent these issues and may provide insight into the biology of animals in the absence of the animal themselves. To this end, tracks have been used to help understand aspects of extinct fauna such as their diversity, the description of new ichnotaxa, and to gain inference into morphological, behavioural, and ecological aspects of the trackmakers (e.g. [22–26]). Trackways have also provided evidence of key evolutionary events such as the transition of tetrapods from water to land ([27], see [28]) and the first bipedal hominids (e.g. [29–31]). Outside of the evolutionary insights, perhaps the most common usage of the information gleaned from trackways relates to gait selection and speed (e.g. [23, 32–35]). An established concept for extracting speed (and gait) from trackways uses the *Fr* [10, 36], defined as:

$$Fr = \frac{U^2}{gh} \tag{1}$$

Where U is speed, g is the acceleration due to gravity and h is the functional hip height. Fr is a dimensionless number that by equalising the centripetal to gravitational force ratio allows the locomotion of terrestrial animals to be compared equally across all sizes. Geometrically similar animals of different sizes will move in a dynamically similar way at any given Fr. In practice, not all animals are geometrically similar, but it was argued that despite this, the ratio of stride length (l_{stride}) to h gave a highly predictable relationship across a broad size range of mammals and birds [10, 11]. By using this empirically derived relationship with the Fr concept, it was further suggested [10] that the forward U of a terrestrial animal can be calculated from:

$$U = 0.25 g^{0.5} l_{\text{stride}}{}^{1.67} h^{-1.17} \tag{2}$$

Fr may also allow the U at which gait transition occurs (e.g. walking to running) to be estimated [36]. Alexander [10] and Thulborn [37] suggest that gaits will shift from walking to a bouncing gait (e.g. trotting) when l_{stride}/h reaches 2.0, and the transition from trotting to running (or galloping) at an l_{stride}/h of 2.9. Eq. 2 is therefore probably applicable to walking animals only [38]. For highspeed gaits where l_{stride}/h is greater than 2.9 the following is advocated as being more appropriate for estimating U [23, 38]:

$$U = \left[gh \left(\frac{l\text{stride}}{1.8\ h} \right)^{2.56} \right]^{0.5} \tag{3}$$

For trotting U is better estimated by the mean of predictions derived from eqs. 2 & 3 [23]. Irrespective of the equation used, the reliability of estimates of U may be compromised if there is lack of certainty on h –in particular in extinct animals where h is not available [39–42]– and the use of l_{stride} boundaries that may not be compatible with bipedal gaits [39]. Trackways are therefore restricted in the information that they can provide as much of the information needed for accurate locomotion analysis, such as leg morphology and stride frequency, depends on data from the animal itself. It is worth remembering that anecdotally the vast majority of extant animal movement does not leave evidential tracks. Aside from seeing occasional footprints in the sand or on muddy ground, overwhelmingly animals are not moving over substrates where their feet will leave lasting impressions. An exception to this is locomotion over snow which will, in the vast majority of cases, leave tracks. Regions of the world, like the Arctic are seasonally covered in snow which provides an opportunity to examine trackways and the kinematics of locomotion in context of the real-world influence of variations in substrate. Svalbard rock ptarmigan are endemic to the high Arctic Archipelago of Svalbard meaning they spend approximately half a year locomoting over snow and they are also one of the few species in which a comprehensive laboratory treadmill dataset exists which can be used for comparison. Recently one of the first comparisons of the kinematics of locomotion under field and laboratory treadmill conditions was undertaken in the Svalbard rock ptarmigan [1]. The kinematics of locomotion were conserved for ptarmigan moving in the field and during laboratory treadmills studies but only for walking and aerial running gaits. Important differences were found when the birds were grounded running, with the birds taking faster and shorter steps in the field when compared to the movement on the treadmill. These kinematic differences were attributed to differing substrate when moving over snow compared to a treadmill belt [1]. Our ptarmigan studies also highlighted the importance of understanding the influence substrate can have on locomotion [1]. Studies in extant animals have demonstrated that substrate can influence the neuromuscular control of locomotion to maintain stability [43–45] and can affect the energetic cost [46, 47] and the speed [48] of locomotion. Furthermore, despite the obvious links between trackways and the ground, substrate is rarely considered when inferences into speed and gait are made from tracks. Not taking any potential effect of substrates into account is surprising as information derived from tracks depends more on the substrate properties than other potentially important variables like the anatomy of the foot itself [49]. Substrate effects can be difficult to assess under some situations. For example, the water content of the substrate at the time of trackway formation is uncertain. However, when substrate is considered it is most often examined in terms of the formation of the physical tracks themselves (see [49]). Consideration of substrates and tracks has also been used to demonstrate that in extant species foot morphology can vary with stance and gait [50, 51] and highlighted the interaction of the feet with different sedimentary substrates [52, 53].

The principle objective of our study was to develop a species-specific model to examine gait and speed predictions directly from l_{stride} of trackways of the Svalbard rock ptarmigan. The accuracy of these trackway derived speed predictions and gait transitions was determined by ground truthing data extracted from videos of the birds taken as the tracks were being made. Finally, a comparison between the predictions obtained using our ptarmigan species-specific model and existing *Fr* based models [10, 23, 38] were made to elucidate the accuracy of each approach. Further, we discuss how reliable information extracted from trackways is for examining the predicted speed of locomotion in both extant and extinct animals.

Results

As expected, U increased linearly with increasing l_{stride} across all gaits (Fig. 1a, b), although the amount of variation in U explained by l_{stride} during grounded running was much lower than that for the other two gaits (walking: $F_{1,\ 46} = 86.25$, $r^2 = 0.64$, $p < 0.001$; grounded running: $F_{1,\ 54} = 14$, $r^2 = 0.19$, $p < 0.001$; aerial running: $F_{1,\ 59} = 133.2$, $r^2 = 0.69$, $p < 0.001$). For walking trackways, the corresponding regression model predicts ptarmigan walking speeds in the range 0.49 ± 0.18 to 0.80 ± 0.18 ms^{-1}. For the grounded running trackways, the model predicts birds using speeds that range from 1.07 ± 0.33 to 1.36 ± 0.33 ms^{-1}. The predictions of U for aerial running suggest ptarmigan use this gait in a speed range from 1.57 ± 0.34 to 2.74 ± 0.37 ms^{-1} (Fig. 1).

Predicted U for each of the 50 birds in this study, were more accurate using our model than those of Alexander [10] and Thulborn and Wade [23]. The error (Eq. 4) associated with predictions derived from the ptarmigan specific model for the 50 birds within all gaits were between 0 and 30% (mean error = 11.8, SD = ± 8.2), except one that was 35% (Fig. 2). In contrast, the errors related to the predicted U from Alexander [10] and Thulborn and Wade [23] were 0 to 55% (Alexander: mean error = 14.4, SD = ± 11.0; Thulborn & Wade: mean error = 17.0, SD = ± 13.8), in both cases (Fig. 2). Within the three gaits, walking was associated to the largest errors, although they had less variation.

Discussion

The ptarmigan specific model for the walking and aerial running gait accounted for a moderate amount of the variation in U (64 and 69%, respectively), and for the grounded running gait was lower, accounting for less that 20% of the variation. The inability to predict U for the grounded running gait with any confidence is likely due to the influence of substrate, which particularly effects this intermediate gait [1]. All terrestrial locomotion involves interaction with a substrate. The slow walking speeds, however, are thought to negate the influence of substrate on locomotion kinematics as they provide greater resistance to external ground perturbations acting on the centre of mass [54, 55] whilst fast running speeds where only possibly over hard substrates anyway [1]. The reason there is much more variability in U during the grounded running gait which reduces the ability to make accurate predictions is that a grounded running gait is used as a mechanism to move faster while also maintaining stability, by cancelling the effects of uneven ground and a changing substrate through increased times of contact of the foot to the ground and a more compliant leg [11, 45, 56]. For ptarmigan moving over snow, modifications in l_{stride} during grounded running are required to prevent falls [1] since shorter steps improve locomotion over slippery surfaces by keeping the centre of mass above the supporting limbs [57, 58].

The ptarmigan specific model represents the best-case scenario in terms of using l_{stride} to predict speed in that we were able to match these data to accurate morphological measurements of hip height and also to double check predictions against real speeds calculated from simultaneous video recordings. Despite these advantages the ability to predict speeds still lacks of accuracy, likely accounted for by the inherent variation in kinematic parameters within a gait (as demonstrated in Fig. 1a). After comparing the error estimates between the predicted U of the three models (Alexander [10] and Thulborn and Wade [23] and the current study) against the measured U from the 50 video-recordings, the error associated with the predictions were lower using our model. This result is not surprising, as our models were built upon previously measured and validated data for the three gaits specifically from Svalbard ptarmigan. Therefore, it deals only with the uncertainty associated with the

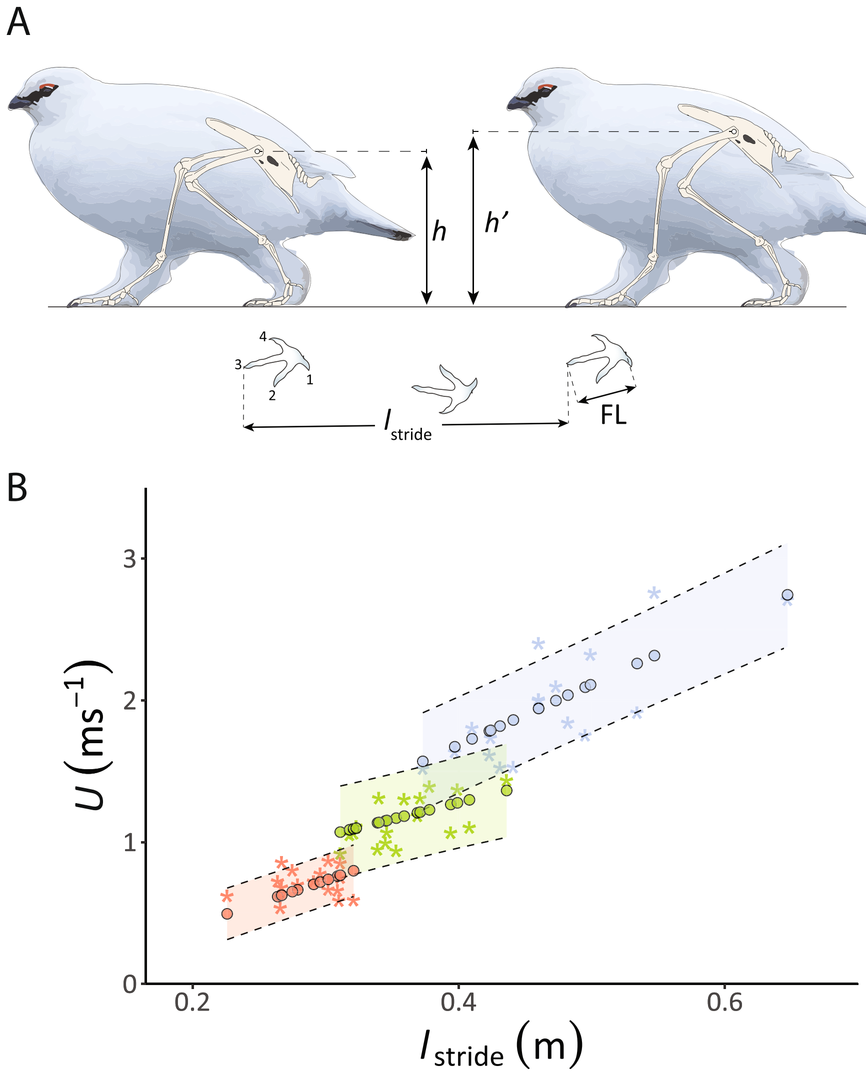

Fig. 1 Trackways of the Svalbard Rock Ptarmigan. **a** length (FL), Stride length (l_{stride}) and Hip Height (*h*) are used to estimate speed. *h* is the distance to the top of the hip perpendicular to ground. This measurement however, is entirely dependent on accurate joint angles of the leg bones. As illustrated, a small alteration in joint angle results in different hip height measurements ($h < h'$). It has been suggested that four times FL can be used as a proxy of effective hip height however this method is also prone to error when applied to extinct animals where there is no information on the joint angles. Digits are numbered 1–4 for analysis as indicated. **b** Speed (*U*) predictions from stride length (l_{stride}) using the ptarmigan species-specific model. The stars represent the data determined from video recordings and the filled circles represent the predicted value for a given l_{stride} for 50 birds calculated from trackways that corresponded to the video recordings. Red, green and blue represent walking, grounded running and aerial running gaits, respectively. The coloured area delimited by the dashed lines represents the predictive interval for the lines of best fit (corresponding to the filled circles) described by the following equations: $U = 3.20\ l_{\text{stride}} - 0.23$ (walking), $U = 2.34\ l_{\text{stride}} + 0.34$ (grounded running) and for aerial running is $U = 4.29\ l_{\text{stride}} - 0.03$ (aerial running)

intraspecific variation within the Svalbard ptarmigan. On the other hand, the equations from Alexander [10] and Thulborn and Wade [23] were derived from kinematic data of several extant taxa, most of them quadrupedal mammals, that possess diverse geometries and move in a subtly different way. Despite the relatively low error for the ptarmigan speed estimates using the three models (up to 55% in our study compared to up to 200% reported elsewhere [59–61]) they would still lead to inaccurate predictions on the metabolic cost of locomotion, in particular at walking speed where the predictions would change drastically [18].

Identifying gaits in the absence of the animal solely from footprints is challenging if no other information is available. However, approximations of the relative l_{stride} and the dimensionless *Fr* before a gait change was suggested by Alexander [10] as a means that allowed researchers to infer which gait an animal was using. Alexander [10], in his paper on dinosaur footprints, proposed that the transition from a walking gait to trotting

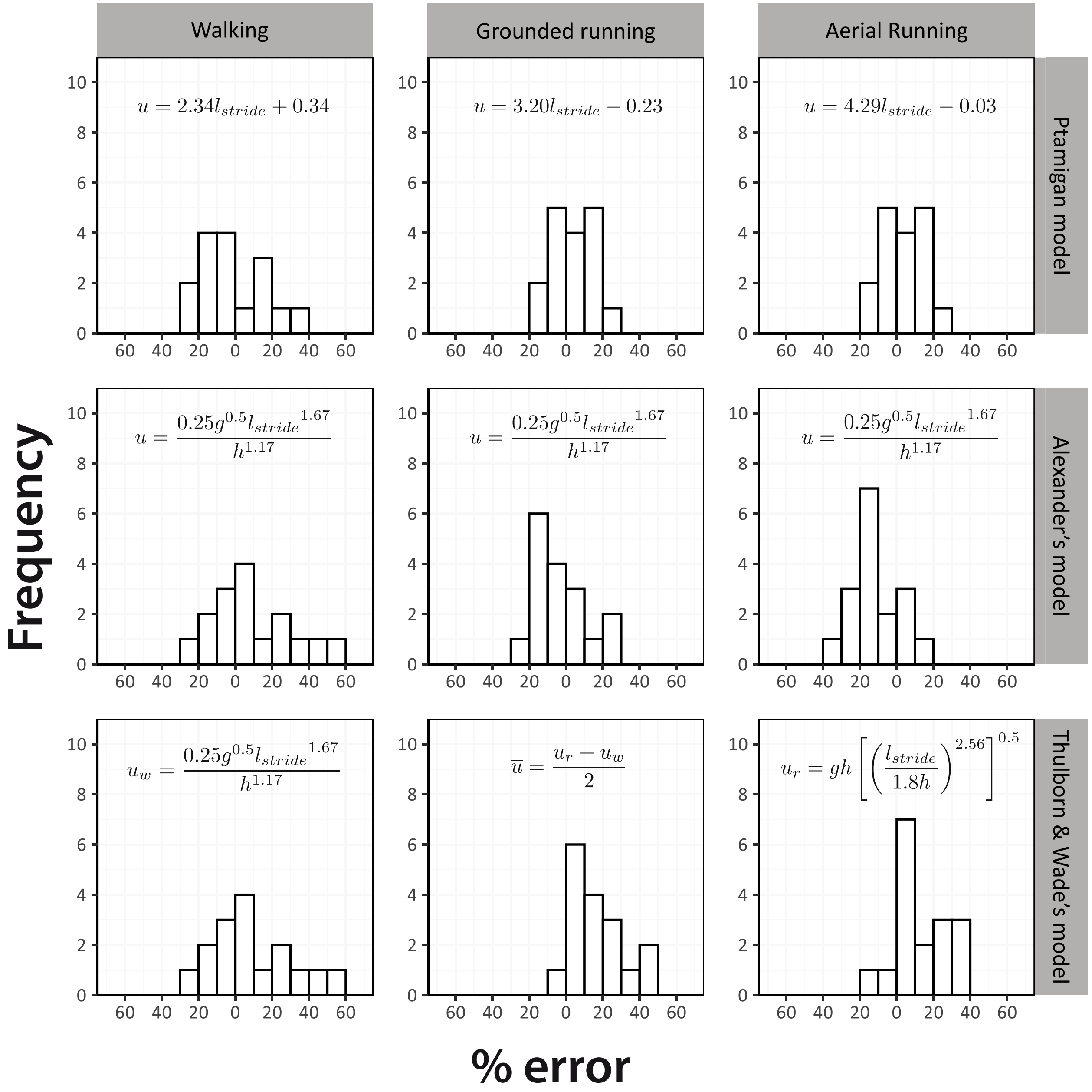

Fig. 2 Error estimation for the ptarmigan species-specific regression models and the Alexander (1976), and Thulborn, and Wade (1984) *Fr* derived equations. Bars to the left of zero represent estimations of *U* below the measured *U*, and vice versa. Note that the error estimates from Alexander (1976) and Thulborn, and Wade (1984) for walking gaits are identical because they use the same equation for this gait. Errors have been binned to 10

or running occurs approximately at *Fr* of 0.6 and at a relative l_{stride} (i.e. l_{stride} divided by hip height) of 2.0. His suggestions were based on a comparison of extant mammals under the principle of dynamic similarity. Our results partially agree with those intervals. By estimating relative l_{stride} using the mean hip height of 0.1727 m for a male ptarmigan as hip height doesn't change [19], our data suggest that ptarmigan shift from walking to grounded running at a maximum relative l_{stride} taken by a walking bird of 2.03 ($l_{\text{stride}} = 0.35$ m) (Fig. 1b). The fastest walking ptarmigan was recorded moving at a *Fr* of 0.5 ($U = 0.92\ \text{ms}^{-1}$) (Fig. 1b). These data support the widely accepted idea that animals shift from a pendular to a bouncing gait at similar relative speeds when moving in a dynamically similar fashion [11, 36]. Consequently, it is not surprising that our predictions for the walking gaits fall within these proposed boundaries. In a further attempt to distinguish between trotting and running gaits, Thulborn and Wade [23] extended the scope of the Alexander [10] method by incorporating the transition from trotting to running at a relative l_{stride} of 2.9 [23]. However, this conclusion was based on records of ungulates shifting from trotting to galloping/running [39] and therefore they may not be applicable to the bipedal gaits of birds. Indeed, differences in the leg kinematics of birds and mammals moving at similar Fr were shown by Lees et al. [62]. Our results suggest that ptarmigan shift from grounded to aerial running at a lower relative l_{stride} ranging from 1.93 to 2.57. Within the existing literature, however, there are conflicting results even among avian species. For example, a closer look at the relative l_{stride} vs. relative velocity plot in Gatesy and Biewener [11] shows similar values for ostriches (relative $l_{\mathrm{stride}} = 2.44$) and rhea (relative $l_{\mathrm{stride}} = 2.37$) at the point of change to aerial running. Abourachid and Renous [13] found that relative l_{stride} at the transition to aerial running is 2.02 and 1.76 for ostriches and emus, respectively. In contrast, turkeys and guinea fowls show a higher relative l_{stride} of 3.14 and 3.73 at the transition, respectively [11]. Such differences suggest that posture needs to be considered if a diagnosis of gait is to be made solely on the footprints of extant animals and casts doubt on using this approach for extinct animals.

Implication for trackways of extinct animals

Obtaining accurate information from trackways in relation to speed and gait choice is difficult even for extant animals for which morphological measurement, and matched field and laboratory treadmill data exist. However, meaningful data are only possible if researchers are able to measure locomotor kinematics and gait selection of the animal concomitant with analysis of the trackways. Therefore, in order to obtain accurate predictions of the biomechanics of locomotion from trackways this requires data from the animal themselves in order to ground truth the data. Unfortunately, the uncertainty about morphology of extinct bipeds lead to several assumptions that may compromise speed estimates derived from hip height when using Alexander [10] and Thulborn and Wade [23] methods, in particular if they are derived from trackways alone. When using trackways, posture is often estimated by deriving hip height as approximately four times foot length (e.g. [10, 23, 32–34, 63, 64]). However, such postural estimates can vary by a factor of 1.5 or more [59, 60], and might be further affected if the trackmakers moved over compliant substrates, such as sedimentary river banks or mud, creating mismatches between the “real” foot morphology of the trackmaker compared to the imprinted track that may be relatively smaller [49, 52]. These methodical limitations are often acknowledged in such studies and were recognized by Alexander himself [60, 61]. Numerous efforts to incorporate biomechanical principles to improve the predictive models have been done in regards to posture on specimens where fossilized skeletons are available ([10, 40–42], reviewed in [61, 65]). researchers have also recognized the sensitivity to assumptions on hindlimb anatomy [41, 65], including assumptions on muscular mass and power [66]. Hence, irrespective of the equation used, the reliability of estimates of speed are compromised by the lack of certainty in the foot length–hip height ratio of an extinct trackmaker [39–42, 59] and the use of stride l_{stride} boundaries that may not be compatible with bipedal gaits [39]. Trackways are therefore restricted in the information that they can provide as much of the information needed for accurate locomotion analysis, such as leg morphology and stride frequency, depends on data from the animal itself.

The lack of certainty on the morphology of the track maker raises the conundrum that if data from the animal is required when it is making the tracks to calculate speed and gait choice, why keep trying to get this information from the trackways alone? There is no doubt that tracks offer an unique record of behavioural and evolutionary aspects of extinct fauna, including discrete locomotor events like transition from slow to fast locomotion [34, 35, 67]. The caveat is that the trackways on their own cannot provide a complete and accurate quantification of the animals’ speed and gait [39, 60, 61]. For the ptarmigan 34% of tracks would have been unable to be classified into a given gait and speed based on the trackways l_{stride} alone because of the overlap when the birds were transitioning between either walking to grounded running or grounded running to aerial running gaits. It should be noted that we are only able to accurately assess the error in predicting just from tracks for the ptarmigan as it represents a ‘best case scenario’ where we have all possible information. Many birds and other animals use transitional gaits, suggesting this issue is likely widespread in extinct forms as well. Other unknowns, not quantified in the current study, but likely to further cloud the inferences from tracks in isolation are the influence of sex differences on the kinematics of locomotion [16, 68–70] and ontogenetic influences [21] all of which cannot be quantified in extinct animals. Inferences into the biology of extinct forms commonly suffers from large errors [60, 61, 71] and rely on numerous assumptions when extrapolating from extant to extinct forms [65, 72, 73].

Conclusion

Here we calculated the speed of locomotion of the Svalbard rock ptarmigan measured from video recordings of ptarmigan while moving over snow, and immediately after estimated using l_{stride} from trackways left by the birds, using one species specific model that accounted for body size and two more general models based on dynamic similarity of locomotion [10, 23]. After ground truthing the measured speed with estimated speeds with three models giving estimates with 30–35% of error, 55 and 55% error, for the species-specific model (our study), and the models of Alexander [10], and Thulborn and Wade [23], respectively. Similarly, more than one third of the tracks were not able to be assigned to a specific gait due to speed ranges overlapping between gaits. Our results suggest that speed and gait estimates are not reliable when they are only based on trackways. A better understanding of the interaction between tracks and locomotion is likely to be useful for future studies, in conjunction with biologging data on activity budgets, for examining how substrates influence the metabolic cost of locomotion. For example, to improve the predictive power of all models, in particular for transitional gaits, future analysis including a quantitative assessment of the hardness, density and roughness of the substrate immediately after the impression of trackways are made would be beneficial.

Methods

Animals and data collection

All data were collected in Adventdalen valley (78°13′18″ N, 15°38′30″E) and the surrounding side valleys in the Svalbard Archipelago, during Spring, 22nd April to 4th May 2017. At this time of year, the ground is covered by snow and daylight persists for 24 h per day. Svalbard ptarmigan were already at their summer weight [74]. Male birds were spotted with binoculars, identified by their distinctive calls and secondary sexual characteristics; red supraorbital combs and thick black eye stripes. Birds were generally close to the foothills or near clear patches were food is accessible. Sites where individual bird data were collected were GPS marked and used only once to minimise, as much as possible, any pseudo replication.

We recorded videos (25fps, SONY® Handycam, HDR-XR250, SONY® Corporation, Japan) with the camera parallel and at a fixed height and position relative to the birds ($n = 50$) moving across level ground covered in snow at self-selected U. After filming, when the bird had moved out of shot, the camera was left recording, kept in its position and a 1 m scale bar was then held above each track way so it was visible on the video recording to determine actual speed for comparison with that calculated from the trackways. Bird speeds were calculated by analysing the videos using the Tracker® v. 5.0.5 (Open Source Physics) program to calculate speed as the distance moved for a given time. Only recordings where the bird was moving steadily were included in the study. To facilitate prediction of self-selected speed (U) using stride length (l_{stride}), a photograph of each trackway was taken after filming from approximately 1.5 m directly above the tracks, individual strides were documented corresponding to the exact region of the track where the video recording was taken. Trackway photos were used for a direct comparison between speed from the video and trackway stride length (l_{stride}). The mean of l_{stride} was measured from 1 to 5 strides using Image J v.1.50i. Data from the current study were also previously used to examine the differences between the kinematics of locomotion for freely moving ptarmigan in the field and from laboratory treadmill studies (see [1]).

Data analyses

The relationship between leg kinematic parameters and U differs (i.e., the incremental change of y with x) depending on the gait used (e.g. [11, 13, 18, 75, 76]). Therefore, here, walking, grounded running and aerial running gaits were analysed separately. In a previous study [1] the relationship between l_{stride} and U was determined for free ranging male Svalbard ptarmigan. Here the same data were used, but this time U became the dependent variable and l_{stride} the independent variable to produce a gait specific predictive relationship (Fig. 1a). The sample sizes were $n = 48$ for walking, $n = 56$ for grounded running and $n = 61$ aerial running. Shapiro-Wilks tests were run on the residuals from the three regressions to ensure the data approximated a normal distribution, which they did in each case. To estimate speed using Alexander [10] and Thulborn and Wade [23] models, it is necessary to obtain hip height (h) for the ptarmigan. Unfortunately, we were not able to capture the birds, therefore we took the hip height estimate of 172.7 mm from literature [19]. To assess the accuracy of predictions of U derived from the three regression models for the 50 birds whose data were collected in this study, we estimated the percentage of error (Fig. 2) using the following:

$$\%\text{error} = \frac{\text{predicted } u - \text{measured } u}{\text{measured } u} \tag{4}$$

Where predicted U is the estimate derived from the line of best fit based on the data from Marmol-Guijarro, Nudds [1] and measured U refers to the speed derived from the 50 new video recordings. All analyses were done in R v. 3.5.2 "Eggshell Igloo" [77].

Abbreviations

Fr: Froude Number; l_{stride}: Stride Length; f_{stride}: Stride Frequency; t_{stance}: Stance Phase; t_{swing}: Swing Phase; *U*: Speed; *g*: Gravity; *h*: Functional Hip Height; SD: Standard Deviation

Acknowledgements

The authors would like to thank John Lees for his contribution to the research project collecting the ptarmigan laboratory dataset. John Marrin assisted in conducting field work. Logistical and field support was provided by the University of Tromsø. We would also like to thank the Governor of Svalbard's office (Sysselmannen) for permission to conduct these studies.

Authors' contributions

JC designed the study with assistance of AMG, RN and LF. JC, AMG, RN and LF all assisted in collection of field data, writing and approval of the final manuscript. AMG and RN analysed the data.

Funding

This research was supported by a BBSRC grant (BB/G011338/1) to JC and a Secretaría Nacional de Educación Superior Ciencia, Tecnología e Innovación del Ecuador (SENESCYT) award (ARQ2-000199-2016) to AMG and JC.

Availability of data and materials

The datasets generated and/or analysed during the current study are available in the supplementary files associated with this manuscript.

Ethics approval and consent to participate

This project was conducted under ethical approval from the University of Manchester Animal Ethics Committee and fieldwork permits through Research in Svalbard (RiS) Project Numbers 10,790, 11,034 and 11,248.

Competing interests

The authors declare that we have no competing interests.

Author details

[1]Faculty of Biology, Medicine & Health, University of Manchester, Manchester, UK. [2]Department of Arctic and Marine Biology, University of Tromsø - The Arctic University of Norway, Tromsø, Norway.

Received: 11 March 2020 Accepted: 20 May 2020

References

1. Marmol-Guijarro AC, Nudds RL, Marrin JC, Folkow LP, Codd JR. Terrestrial locomotion of the Svalbard rock ptarmigan: comparing field and laboratory treadmill studies. Sci Rep. 2019;9(1):11451.
2. Pagano AM, Durner GM, Rode KD, Atwood TC, Atkinson SN, Peacock E, Costa DP, Owen MA, Williams TM. High-energy, high-fat lifestyle challenges an Arctic apex predator, the polar bear. Science. 2018;359(6375):568.
3. Ratzlaff MH, Grant BD, Rathgeber-Lawrence R, Kunka KL. Stride rates of horses trotting and cantering on a treadmill. J Equine Vet Sci. 1995;15(6):279–83.
4. Williams TM, Ben-David M, Noren S, Rutishauser M, McDonald K, Heyward W. Running energetics of the north American river otter: do short legs necessarily reduce efficiency on land? Comp Biochem Physiol, Part A Mol Integr Physiol. 2002;133(2):203–12.
5. Brockway JM, Gessaman JA. The energy cost of locomotion on the level and on gradients for the red deer (*Cervus elaphus*). Q J Exp Physiol Cogn Med Sci. 1977;62(4):333–9.
6. Bélanger M, Drew T, Provencher J, Rossignol S. A comparison of treadmill locomotion in adult cats before and after spinal transection. J Neurophysiol. 1996;76(1):471–91.
7. Herbin M, Hackert R, Gasc J-P, Renous S. Gait parameters of treadmill versus overground locomotion in mouse. Behav Brain Res. 2007;181(2):173–9.
8. Herbin M, Hommet E, Hanotin-Dossot V, Perret M, Hackert R. Treadmill locomotion of the mouse lemur (*Microcebus murinus*); kinematic parameters during symmetrical and asymmetrical gaits. J Comp Physiol A. 2018;204(6):537–47.
9. Mori S, Miyashita E, Nakajima K, Asanome M. Quadrupedal locomotor movements in monkeys (*M. fuscata*) on a treadmill: kinematic analyses. Neuroreport. 1996;7(14):2277–86.
10. Alexander RM. Estimates of speeds of dinosaurs. Nature. 1976;261(5556):129–30.
11. Gatesy SM, Biewener AA. Bipedal locomotion: effects of speed, size and limb posture in birds and humans. J Zool. 1991;224:127–47.
12. Abourachid A. Kinematic parameters of terrestrial locomotion in cursorial (ratites), swimming (ducks), and striding birds (quail and Guinea fowl). Comp Biochem Physiol, Part A Mol Integr Physiol. 2001;131(1):113–9.
13. Abourachid A, Renous S. Bipedal locomotion in ratites (Paleognatiform) examples of cursorial birds. Ibis. 2000;142:538–49.
14. Daley MA, Channon AJ, Nolan GS, Hall J. Preferred gait and walk–run transition speeds in ostriches measured using GPS-IMU sensors. J Exp Biol. 2016;219(20):3301–8.
15. Nudds RL, Gardiner JD, Tickle PG, Codd JR. Energetics and kinematics of walking in the barnacle goose (*Branta leucopsis*). Comp Biochem Physiol, Part A Mol Integr Physiol. 2010;156:318–24.
16. Rose KA, Codd JR, Nudds RL. Differential sex-specific walking kinematics in leghorn chickens (*Gallus Gallus domesticus*) selectively bred for different body size. J Exp Biol. 2016;44:jeb.139709.
17. Watson RR, Rubenson J, Coder L, Hoyt DF, Propert MWG, Marsh RL. Gait-specific energetics contributes to economical walking and running in emus and ostriches. Proc R Soc B. 2011;278(1714):2040–6.
18. Nudds RL, Folkow LP, Lees JJ, Tickle PG, Stokkan KA, Codd JR. Evidence for energy savings from aerial running in the Svalbard rock ptarmigan (*Lagopus muta hyperborea*). Proc R Soc B. 2011;278(1718):2654–61.
19. Lees JJ, Nudds RL, Folkow LP, Stokkan KA, Codd JR. Understanding sex differences in the cost of terrestrial locomotion. Proc R Soc B. 2012;279(1729):826–32.
20. Lees JJ, 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. 2010;5:e15490.
21. Lees JJ, Stokkan K-A, Folkow LP, Codd JR. Locomotor development in the Svalbard rock ptarmigan (*Lagopus muta hyperborea*). Polar Biol. 2012;35:867–74.
22. Lee Y-N. Bird and dinosaur footprints in the woodbine formation (Cenomanian). Texas Cretac Res. 1997;18(6):849–64.
23. Thulborn RA, Wade M. Dinosaur trackways in the Winton formation (mid-Createaceous) of Queensland. Mem Queensl Mus. 1984;21(2):413–517.
24. McKeever PJ. The behavioral and biostratigraphical significance and origin of vertebrate trackways from the Permian of Scotland. Palaios. 1994;9(5):477–87.
25. Currie PJ, Eberth DA. On gregarious behavior in *Albertosaurus*. Can J Earth Sci. 2010;47(9):1277–89.
26. Lockley MG, Nadon G, Currie PJ. A diverse dinosaur-bird footprint assemblage from the lance formation, upper cretaceous, Eastern Wyoming: Implications for ichnotaxonomy. Ichnos. 2004;11(3–4):229–49.
27. Warren JW, Wakefield NA. Trackways of tetrapod vertebrates from the upper Devonian of Victoria, Australia. Nature. 1972;238(5365):469–70.
28. Clack JA. Devonian tetrapod trackways and trackmakers; a review of the fossils and footprints. Palaeogeogr Palaeoclimatol Palaeoecol. 1997;130(1):227–50.
29. Crompton RH, Pataky TC, Savage R, D'Août K, Bennett MR, Day MH, Bates K, Morse S, Sellers WI. Human-like external function of the foot, and fully upright gait, confirmed in the 3.66 million year old Laetoli hominin footprints by topographic statistics, experimental footprint-formation and computer simulation. Interface Focus. 2012;9(69):707–19.
30. Raichlen DA, Pontzer H, Sockol MD. The Laetoli footprints and early hominin locomotor kinematics. J Hum Evol. 2008;54(1):112–7.
31. Raichlen DA, Gordon AD, Harcourt-Smith WEH, Foster AD, Haas WR Jr. Laetoli footprints preserve earliest direct evidence of human-like bipedal biomechanics. PLoS One. 2010;5(3):e9769.
32. McCrea RT, Buckley LG, Farlow JO, Lockley MG, Currie PJ, Matthews NA, Pemberton SG. A 'terror of tyrannosaurs': the first trackways of Tyrannosaurids and evidence of gregariousness and pathology in Tyrannosauridae. PLoS One. 2014;9(7):e103613.
33. González Riga BJ. Speeds and stance of titanosaur sauropods: analysis of *Titanopodus* tracks from the late cretaceous of Mendoza, Argentina. An Acad Bras Cienc. 2011;83:279–90.
34. Farlow JO. Estimates of dinosaur speeds from a new trackway site in Texas. Nature. 1981;294(5843):747–8.
35. Day JJ, Norman DB, Upchurch P, Powell HP. Dinosaur locomotion from a new trackway. Nature. 2002;415:494.
36. Alexander RM, Jayes AS. A dynamic similarity hypothesis for the gaits of quadrupedal mammals. J Zool. 1983;201:135–52.
37. Thulborn RA. Preferred gaits of bipedal dinosaurs. Alcheringa. 1984;8(3):243–52.
38. Alexander RM, Langman VA, Jayes AS. Fast locomotion of some African ungulates. J Zool. 1977;183(3):291–300.
39. Hutchinson JR, Allen V. The evolutionary continuum of limb function from early theropods to birds. Naturwissenschaften. 2009;96(4):423–48.
40. Henderson D. Footprints, trackways, and hip heights of bipedal dinosaurs—testing hip height predictions with computer models. Ichnos. 2003;10(2–4):99–114.

41. Gatesy SM, Bäker M, Hutchinson JR. Constraint-based exclusion of limb poses for reconstructing theropod dinosaur locomotion. J Vert Paleontol. 2009;29(2):535–44.
42. Henderson DM. Simulated weathering of dinosaur tracks and the implications for their characterization. Can J Earth Sci. 2006;43(6):691–704.
43. Daley MA, Usherwood JR, Felix G, Biewener AA. Running over rough terrain: Guinea fowl maintain dynamic stability despite a large unexpected change in substrate height. J Exp Biol. 2006;209(1):171.
44. Daley MA, Biewener AA. Running over rough terrain reveals limb control for intrinsic stability. Proc Natl Acad Sci U S A. 2006;103(42):15681.
45. Daley MA, Usherwood JR. Two explanations for the compliant running paradox: reduced work of bouncing viscera and increased stability in uneven terrain. Biol Lett. 2010;6(3):418–21.
46. Parker KL, Robbins CT, Hanley TA. Energy expenditures for locomotion by mule deer and elk. J Wildl Manag. 1984;48(2):474–88.
47. Fancy SG, White RG. Energy expenditures for locomotion by barren-ground caribou. Can J Zool. 1987;65(1):122–8.
48. Droghini A, Boutin S. The calm during the storm: snowfall events decrease the movement rates of grey wolves (*Canis lupus*). PLoS One. 2018;13(10): e0205742.
49. Falkingham PL, Gatesy SM. The birth of a dinosaur footprint: subsurface 3D motion reconstruction and discrete element simulation reveal track ontogeny. Proc Natl Acad Sci U S A. 2014;111(51):18279.
50. Sollas WJ. On some three-toed footprints from the Triassic conglomerate of South Wales. Quart J Geol Soc London. 1879;35(1–4):511.
51. Padian K, Olsen PE. Ratite footprints and the stance and gait of Mesozoic theropords. In: Gillete DD, Lockley MG, editors. Dinosaur tracks and traces. Cambride: Cambridge University Press; 1989. p. 231–41.
52. Gatesy SM, Middleton KM, Jenkins FA Jr, Shubin NH. Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. Nature. 1999;399(6732):141–4.
53. Milàn J. Variations in the morphology of emu (*Dromaius novaehollandiae*) tracks reflecting differences in walking pattern and substrate consistency: ichnotaxonomic implications. Palaeontology. 2006;49(2):405–20.
54. Qiao M, Hughes M, Jindrich DL. Response to medio-lateral perturbations of human walking and running. Gainsville: American Society of Biomechanics Annual Meeting; 2012.
55. Qiao M, Jindrich DL. Compensations during unsteady locomotion. Integr Comp Biol. 2014;54(6):1109–21.
56. 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. 2013;335:97–107.
57. Cham R, Redfern MS. Changes in gait when anticipating slippery floors. Gait Posture. 2002;15(2):159–71.
58. Cappellini G, Ivanenko YP, Dominici N, Poppele RE, Lacquaniti F. Motor patterns during walking on a slippery walkway. J Neurophysiol. 2010;103(2): 746–60.
59. Rainforth EC, Mazella M. Estimating speeds of dinosaurs from trackways: a re-evaluation of assumptions. In: Rainforth EC, editor. Contributions to the Paleontology of New Jersey (II)–Field and Guide Proceedings. Pennsylvania: Geological Association of New Jersey, XXIV Annual Conference and Field Trip; East Stroudsburg University, East Stroudsburg; 2007. p. 41–8.
60. Alexander RM. Doubts and assumptions in dinosaur mechanics. Interdiscipl Sci Rev. 1991;16(2):175–81.
61. Alexander RM. Dinosaur biomechanics. Proc Biol Sci. 2006;273(1596):1849–55.
62. Lees JJ, Gardiner J, Usherwood J, Nudds R. Locomotor preferences in terrestrial vertebrates: an online crowdsourcing approach to data collection. Sci Rep. 2016;6:28825.
63. Paik IS, Huh M, Park KH, Hwang KG, Kim KS, Kim HJ. Yeosu dinosaur track sites of Korea: the youngest dinosaur track records in Asia. J Asian Earth Sci. 2006;28(4):457–68.
64. Abrahams M, Bordy EM, Sciscio L, Knoll F. Scampering, trotting, walking tridactyl bipedal dinosaurs in southern Africa: ichnological account of a lower Jurassic palaeosurface (upper Elliot formation, Roma Valley) in Lesotho. Hist Biol. 2017;29(7):958–75.
65. Carrano MT, Biewener AA. Experimental alteration of limb posture in the chicken (*Gallus gallus*) and its bearing on the use of birds as analogs for dinosaur locomotion. J Morphol. 1999;240(3):237–49.
66. Sellers WI, Manning PL. Estimating dinosaur maximum running speeds using evolutionary robotics. Proc R Soc B. 2007;274(1626):2711–6.
67. Day JJ, Norman DB, Gale AS, Upchurch P, Powell HP. A middle Jurassic dinosaur trackway site from Oxfordshire, UK. Palaeontology. 2004;47(2):319–48.
68. Rose KA, Tickle PG, Lees JJ, Stokkan K-A, Codd JR. Neither season nor sex affects the cost of terrestrial locomotion in a circumpolar diving duck: the common eider (*Somateria mollissima*). Polar Biol. 2014;37(6):879–89.
69. Rose KA, Nudds RL, Butler PJ, Codd JR. Sex differences in gait utilization and energy metabolism during terrestrial locomotion in two varieties of chicken (*Gallus gallus domesticus*) selected for different body size. Biol Open. 2015;4: 1306–15.
70. Rose KA, Bates KT, Nudds RL, Codd JR. Ontogeny of sex differences in the energetics and kinematics of terrestrial locomotion in leghorn chickens (*Gallus gallus domesticus*). Sci Rep. 2016;6:1–11.
71. Hutchinson JR. Biomechanical modeling and sensitivity analysis of bipedal running ability. II Extinct taxa J Morphol. 2004;262(1):441–61.
72. Nudds RL, Dyke GJ. Narrow primary feather rachises in *Confuciusornis* and *Archaeopteryx* suggest poor flight ability. Science. 2010;328(5980):887.
73. Lees J, Garner T, Cooper G, Nudds R. Rachis morphology cannot accurately predict the mechanical performance of primary feathers in extant (and therefore fossil) feathered flyers. R Soc Open Sci. 2017;4(2):160927.
74. Mortensen A, Unander S, Kolstad M, Blix AS. Seasonal changes in body composition and crop content of Spitzbergen ptarmigan *Lagopus mutus hyperboreus*. Ornis Scand. 1983;14:144–8.
75. Rubenson J, Heliams DB, Lloyd DG, Fournier PA. Gait selection in the ostrich: mechanical and metabolic characteristics of walking and running with and without an aerial phase. Proc Biol Sci. 2004;271(1543):1091–9.
76. Hancock JA, Stevens NJ, Biknevicius AR. Whole-body mechanics and kinematics of terrestrial locomotion in the elegant-crested Tinamou *Eudromia elegans*. Ibis. 2007;149(3):605–14.
77. R Core Team. R: A Language and Environment for Statistical Computing. R version 3.5.2 ed. Vienna: R Foundation for Statistical Computing; 2018.

Publisher's Note

Chapter 6

General discussion

6. Discussion

Studies into the locomotion of terrestrial species are often performed under strict laboratory conditions controlling for environmental confounding factors like thermoneutral metabolic temperatures, wind, light, and substrate; all of them potentially impacting on the kinematics of locomotion of all animals. These studies have been most valuable to gain insights into the drivers behind the locomotor performance in many species and several rules have been obtained through these studies that are applicable to a large number of species representing many of the major taxa in the animal kingdom. Despite these efforts, there are still many unknowns regarding the ubiquity of these findings, in particular when extrapolations are made to animals moving on more natural environments. Prior to the onset of my PhD, little work had focused on the effects of the substrate on which animals often move in the wild. Thus, the ultimate aim of my PhD was to extend the knowledge of a high Arctic species, the Svalbard rock ptarmigan. Animals from the polar regions are confronted to a wide spectrum of substrates including snow. In contrast to other less variable substrates (i.e. rocks, sand, grass, etc.), snow is extremely variable, as it rapidly changes at a temporal and spatial scale depending of the environmental conditions that ultimately have profound effects on the energy expenditure of the species moving over it. Only by understanding how animals move on their own environment, it is possible to better understand the mechanisms by which species prevent any energetic imbalance and structural safety that are key for survival. In the case of the Svalbard rock ptarmigan, and for other high Arctic species, this is particularly relevant given the alarming current trend of global warming, which is strongly warming the Arctic region at a higher rate compared to other regions.

6.1. Summary of findings

The principal aim of this thesis was to examine how comparable treadmill-based approaches to study animal locomotion are to estimates for animals moving on their natural environment, in order to determine how representative are these results to wild populations of the species in question. The Svalbard ptarmigan were used as a model because the changes in terrestrial locomotion kinematics with increasing speed have been extensively studied under laboratory-treadmill conditions. Furthermore, these studies have sought to find how seasonal changes in body mass, sex and age may influence how the individuals of this species move. The principal findings in each of the chapters are as follows:

The objective of **Chapter 2** was to compare the locomotor kinematics at self-selected speeds of the wild Svalbard rock ptarmigan males moving on their natural environment compared to the kinematics of this species moving on treadmills at varying speeds finding that:

1) The wild Svalbard rock ptarmigan males moving in their natural environment are capable of the three terrestrial gaits previously reported in treadmill-based studies.
2) The kinematics of locomotion of wild Svalbard rock ptarmigan are comparable to those observed in captive individuals exercising on treadmills and are conserved for the waking and the aerial running gaits.
3) Grounded running kinematics differ between both groups when all types of substrates (i.e. soft and hard snow) are included. These differences, however, become less evident when only ptarmigan trials moving over very hard substrates are considered, confirming the effects that substrate has on the locomotor kinematics of the ptarmigan.

In **chapter 3**, the main objective was to determine the effects of substrate upon wild female Svalbard rock ptarmigan locomotion kinematics moving *in situ* by comparing them to the kinematics of captive females moving on treadmills. Furthermore, the analyses are extended to incorporate the sex effects upon locomotor kinematics of wild Svalbard rock ptarmigan when moving in the wild, to assess if substrate affects males and females in a similar way, which is interesting because males are larger than females. I found that:

1) Locomotion kinematics are remarkably conserved between the wild female Svalbard rock ptarmigan and females moving on treadmills, irrespective of the gait used, indicating that females may be less susceptible to substrate effects when compared to males.
2) Sex dimorphism in body size explained the differences observed between male and female wild Svalbard rock ptarmigan locomotion kinematics of walking gait.
3) Differences in the grounded running kinematics, on the other hand, could not be explained by the differences in body size between sexes, and a more crouched limb posture in the females relative to males could alternatively explain such differences.

The objective of **chapter 4** followed the results from **chapter 2** and **3** and are to ascertain the effects that snow supportiveness and footprint sinking depth into snow have upon ptarmigan locomotion speed, stride length (as a proxy of speed), which ultimately could lead to route choice in the Svalbard rock ptarmigan. I concluded that:

1) Footprint depth and snow supportiveness are poor predictors of stride length and speed of locomotion in the Svalbard rock ptarmigan.

2) The Svalbard rock ptarmigan footprint depth did not exceed the intertarsal joint in all the trials analysed, suggesting that the birds may be choosing the routes that minimize the effects of snow upon locomotion.
3) Foot subsurface rotation increases in deeper footprints, indicating that the birds may exploit the compressive nature of the uppermost snow layer to generate enough thrust during stance.

The aim of **chapter 5** was to develop a species-specific model to predict the gait and speed preferences only from stride lengths obtained from the Svalbard rock ptarmigan footprints. The findings in this chapter concluded:

1) Predictions on speed of locomotion using stride length as the only predictor, even when derived from a Svalbard rock ptarmigan species specific model involve large estimation errors, making them problematic
2) Although gait transition from walking and running could be predicted from trackways, transitions from grounded running to aerial running could not be precisely identified.

6.2. The walking gait: an ecological perspective

Animal locomotion is intimately linked to critical biological processes including food acquisition, predator avoidance and reproduction. The bouncing gaits and fast speed of locomotion are the result of strong selective pressures upon the locomotor system in order to allow species to avoid being catch by predators (Husak and Fox 2006; Irschick et al. 2005; Wilson et al. 2015). Sexual selection through reproductive success has also led to the evolution of improved locomotor performance in species where intrasexual competition is strong (Husak et al. 2006; Peterson and Husak 2006). In addition, fast speeds usually require less energy for a given distance travelled (Dawson and Taylor 1973; Fish et al. 2001; Maloiy et al. 2009; Nudds et al. 2011; Nudds et al. 2010; Rubenson et al.

2004; Watson et al. 2011). Slow speeds related to walking gaits, on the other hand, are more costly and therefore it should be expected to observe such speeds in nature with less frequency, at least if energetic economy is the main driver for speed and gait selection. In the following paragraphs I will argue the relevance of the walking speeds for the ptarmigan in an ecological and biomechanical context in an attempt to explain the great portion of walking trials recorded while the birds move on snow. In our dataset 32 % of the trials fell into the walking gait. Of particular interest is the fact that in ptarmigan males and females, the walking kinematics remain highly conserved across all walking speeds when comparing locomotion on snow compared to treadmill, despite the obvious differences between both substrates.

Studies on self-selected speeds of locomotion of animals moving in the wild are scarce. However, the few studies into this topic have shown that species often use self-selected speeds that are only a fraction of the maximum speed recorded for such species, suggesting that energy economy is not the only factor determining speed choice. A key task for the ptarmigan is to find enough food for reproduction in summer and to build up enough body fat reserves upon the onset of winter (Stokkan et al. 1986), aside from conserving basic metabolic and physiological functions such as growth and maintenance. Furthermore, in winter the ptarmigan still need to continuously find the sparce sources of food available (Stokkan et al. 1986), as their fat reserves are only capable to last for shorts periods of starvation before they are depleted – usually no more than 18 days (Grammeltvedt and Steen 1978). It is here where competing interests exist between the energy intake by means of food acquisition and the energy cost of moving to find the food; hence, the ptarmigan must undergo a decision-making process to evaluating where and how to move, and for how long keep foraging on a path of food in order to maximise fitness via energy expenditure optimisations in the cost of locomotion (per unit time) or the cost transport (per unit distance) (Wilson et al. 2015). By using slow walking speeds while foraging, the energy intake may offset the elevated costs of locomotion in the Svalbard ptarmigan. Walking slowly would enable ptarmigan to locate and peck for the nutritious buds from which they feed upon that are often found underneath snow, including the bulbils of *Saxifraga oppositifolia*, *Saxifraga cespitosa*, *Salix polaris* and *Polygonum viviparum* (Pedersen et al. 2005). Nonetheless, faster, more economical speeds and gaits may be preferred when the Svalbard rock ptarmigan commutes between food patches. This foraging strategy is consistent to what has been previously reported for other herbivore birds (Ebbinge et al. 1975; Zhang and Lu 1999) and mammals (Mace et al. 1983), where slow speeds of locomotion are used for feeding. This also aligns with the slow-speed foraging strategy reported for grizzly bears that are restricted to a mostly herbivore diet (Edwards et al. 2011). Further, such a foraging strategy would be in line with the decrease in locomotor activity of the ptarmigan from August until the end of winter to reduce the associated energy expenditure of moving (Lees et al. 2010; Stokkan et al. 1986).

Similar to the trade-off between food acquisition and the cost of transport, the relatively higher energetic costs of walking at less efficient low speeds may be preferable than moving cheaply but faster, as it might be on detriment of antipredator response. By choosing slower speeds, animals commuting through snow patches are expected to detect and react faster to sudden predation threats. For example, a study in juvenile convict cichlids (*Amantitlania nigrofasciata*) suggests that fish exploring a new enclosure took longer to trigger anti predatory responses when swimming faster compared to slower fish (Jones and Godin 2010). Antipredator responses, however, are also driven by habitat cover (i.e. open areas or areas with hiding places), interaction with conspecifics and other species, and predation intensity. Often species moving within covered habitats may show longer times to react in the presence of predators (Vásquez et al. 2002). Similarly, a species may trigger a faster antipredator response, if it associates with another species with better detection abilities (Fitzgibbon 1990). For instance, if two species of different heights are foraging together on a patch of tall grassland, the smaller species may benefit of an earlier antipredator response simply because the taller species would have a high sight, hence improved ability for predator detection. In species under constant predation pressures, paying an extra cost by moving at slowly offsets the gains of moving at more economical speed, as better detectability and faster antipredatory responses attainable at slow locomotor speeds may be prime to avoid being catch (Fu et al. 2015). In Svalbard, the ptarmigan are often found in open areas looking for the sparse patches of available food. Being the only herbivore, aside from the Svalbard reindeer, it is unlikely that these birds are seeking any association with other species to enhance an antipredator response. Yet, the ptarmigan are still predated by Arctic foxes (*Alopes lagopus*), glaucous gulls (*Larus hyperboreus*), the Arctic skua (*Stercorarius parasiticus*) (Pedersen et al. 2005) and presumably the snowy owl (*Nyctea scandiaca*) (Steen and Unander 1985). If the predation intensity upon the ptarmigan is relatively high, then moving slowly while foraging or exploring may help the ptarmigan to avoid predation, regardless the increased energetic cost of moving slow. However, this idea requires further investigation as predation intensity upon the Svalbard ptarmigan and how this affects males, females and juveniles remains unknown. There are only two direct observations reporting predation of the Svalbard ptarmigan and it appears that most of the predation occurs on eggs (Steen and Unander 1985).

A quantitative analysis of the speed preferences in the Svalbard ptarmigan moving in the wild was not made given that birds were encouraged to move by an investigator moving towards the bird to make them move past the camera to obtain the video recordings. Whilst this does not represent a totally natural situation the birds are still self selecting the speeds to move when ushered. Such stimulus could trigger a bird reaction that resembles more to an antipredatory response, making it difficult to interpret the recorded speed ranges as the preferred ones by the ptarmigan. It could also bias the results towards faster speeds, although I did not see evidence of this. A speed frequency distribution plot built upon the speed recorded in wild male ptarmigan (Chapter 2, figure S1) showed that all data points (*n* = 165) were evenly distributed across the entire speed range. This may imply that even with the stimulus, we could speculate on the decision making process linking speed of locomotion and energetics. Nonetheless, acknowledging this problem, interpretation of this data is only applicable to the ptarmigan analysed in this thesis, while data on daily activity patterns that effectively show speed preferences are still needed. Future work using remote biologging tags could help to build a complete picture of speed and gait selection in wild birds.

From a biomechanical perspective, a walking gait may contribute to maintain dynamic stability during locomotion, meaning that animals would be less prone to fall and injury, therefore increasing the probability of survival (therefore fitness). It has been suggested that a walking gait is robust to external perturbations, including the ones caused by the substrate. A study, where mediolateral perturbations are applied to human subjects, suggests that the displacements of the COM are comparatively lower within the walking gait compared to running (Qiao and Jindrich 2014). This works in conjunction with faster compensatory mechanisms for stability because it involves longer stance periods and extended double support that allows the system recovery in fewer subsequent steps than in running (Qiao et al. 2012; Qiao and Jindrich 2014). Further, by allowing longer periods of time to visually detect physical perturbations, slow walking speeds enable earlier anticipatory responses (Gordon et al. 2015). Thus, the dynamic stability and the improved visual response found in the walking gaits provide a biomechanical explanation to the higher proportion of walking trials observed in the male and female ptarmigan in this thesis.

It is intriguing, however, that walking kinematics in the wild Svalbard ptarmigan on snow paralleled those reported for individuals exercising on treadmills, regardless of sex. Changes in the physical properties of the substrate, namely when comparing compliant to firm substrate or by selecting substrates of low friction coefficients with the limb, often result in shorter but faster strides (Cappellini et al. 2010; Cham and Redfern 2002; Clark and Higham 2011; Lejeune et al. 1998). Although, most of the empirical evidence regarding kinematic adjustments with varying substrates comes from humans (Cappellini et al. 2010; Cham and Redfern 2002; Lejeune et al. 1998) making comparisons with birds complicated. Snow, in particular, may show extremely high spatial variation in terms of compliance and slipperiness, and the only study on the effects of slippery substrates in the locomotion of a bird used substrate with a very low friction coefficient with the feet (Clark and Higham 2011), which represent only a fraction of the snowy substrates that the ptarmigan may find in the wild. One possible explanation for the lack of kinematic adjust seen in the ptarmigan walking over snow and on the treadmill may be linked to their ancestry. The ptarmigan avian limb allows for greater flexibility for limb adjustments, where effective leg length can be shortened or lengthened to a greater extend, in contrast to the already extended leg in human, making the ptarmigan limb more robust to the foot sinking in the snow (analogous to a sudden drop) (Blum et al. 2011), although I can not test this idea with my datasets. Alternatively, it might be that snow on which wild ptarmigan walk exert only minor disturbances that require little kinematic adjustment to deal with, thus making walking kinematics on snow highly similar to those used on the treadmill. This second idea is supported by the results reported in **chapter 4**, suggesting that the ptarmigan may be selecting for optimal routes on which to move that do not impede locomotion.

6.3. The ecological relevance of grounded running

It has previously been challenged the ecological relevance of the grounded running gaits for species moving in their natural environment (Nudds et al. 2011). The increased leg compliance associated to the grounded running gait coupled with the lack of aerial phases are thought to improve stability compared to aerial running as altogether they reduce the GRF acting upon the limb (Gatesy and Biewener 1991). Additionally, grounded running gait attenuates the forces transmitted to the head via trunk thus stabilising vision (Andrada et al. 2013b; Hancock et al. 2007; McMahon et al. 1987), and reduces negative work done by the bouncing viscera (Daley and Usherwood 2010). Although this gait has been widely reported among literature in avian and human locomotion, the majority of these studies have manipulated the speeds at which birds move using treadmills (Abourachid 2001; Abourachid and Renous 2000; Andrada et al. 2015; Gatesy and Biewener 1991; Lees et al. 2010; Nudds et al. 2011; Rose et al. 2015b; Rubenson et al. 2004; Watson et al. 2011). Thus, this led to researchers to challenge the existence of the grounded running gait as part of the normal gait repertoire in species moving in the wild (Nudds et al. 2011). Yet, the evidence found in the ptarmigan suggest that the gait enables to move faster than with a walking gait without compromising the stability of locomotion and therefore minimizing the risk of fall.

The results in **chapter 2**, **3** and **4**, provides evidence of the use of the grounded running gait in male and female ptarmigan while moving on snow. In the males, the grounded running gait is viewed as a mechanism to move faster while keeping locomotion dynamically stable. On treadmills and in the wild l_{stride} and f_{stride} increased linearly with increasing speed within grounded running. However, there are differences in the rates at which both parameters increase. In the wild, speed increases are mainly achieved by faster strides, whilst on the treadmill longer strides are contributing the most to increase speed. In other words, wild ptarmigan moving over snow take shorter but faster strides at a given grounded running speed. Such differences, however, disappear when trials when the snow was hard and supportive were included into the analyses, providing evidence of substrate effects on the kinematics of locomotion in the grounded running gait. The kinematic disparities found in wild ptarmigan grounded running over snow may be the result of modifications in the effective leg length, leg stiffness and the leg angle of contact with ground at the end of the swing phase, just before stance begin (Birn-Jeffery et al. 2014; Blum et al. 2011; Daley and Biewener 2006; Daley and Birn-Jeffery 2018; Daley and Usherwood 2010; Daley et al. 2006; Seyfarth et al. 2003). With more compliant limbs rotating at an appropriate angular velocity for an earlier limb retraction, it is possible to reduce loadings acting on the limb without missing stance phase ensuring that the COM passes over the supporting limb. This might be key for dealing with unsupportive snow emulating sudden drops (Birn-Jeffery and Daley 2012; Blum et al. 2014; Daley and Usherwood 2010; Daley et al. 2006; Seyfarth et al. 2003) or simply when snow is too slippery and GRF must be maximized (Clark and Higham 2011). Moving with a more compliant limb usually requires shorter and faster strides (Gatesy and Biewener 1991).

An intriguing result is that the grounded running kinematics of the wild Svalbard ptarmigan females paralleled the kinematics reported of those running on treadmill (results **chapter 3**). There is no reason to think that stability is not prime for the Svalbard ptarmigan females; therefore, the lack of kinematic tunning (i.e. earlier limb retraction) may suggest different intrinsic limb compliances between sexes, with females having a more compliant limb posture overall. By making pair-comparison using size-corrected kinematic parameters and relative speed ($\widehat{U} = U/(gh)^{0.5}$) between males and females, it is possible to see evidence of non-dynamically similar grounded running gait, thereby providing suggesting a more crouched posture in the females. For a given grounded running $\widehat{U}$, wild females showed lower $\hat{f}_{\text{stride}}$ but higher $\hat{l}_{\text{stride}}$, compared to the males. This is consistent with the kinematics reported for crouched-limb posture species, as the females appear to undergo greater limb excursions of the limb (Gatesy and Biewener 1991). Similarly, the females showed longer $\hat{t}_{\text{stance}}$, which result in higher DF, which could be associated to the greater stability to the females (Gatesy and Biewener 1991). The anatomical basis for such postural differences is unclear, however, it is likely that them are a direct result of sexual dimorphism.

A first indicator of sexual dimorphism in limb anatomy in the Svalbard rock ptarmigan is related to the relatively longer swing periods of females, which can be associated to the moments of inertia acting upon the limb joints (Kilbourne et al. 2016; Tickle et al. 2010). If the inertial moments were greater in the female ptarmigan compared to the males, it would be expected to see larger muscle masses on each limb segment in the females. However, this seems unlikely given than males, on average, have greater body masses and longer limbs compared to the females (Steen and Unander 1985). Alternatively, it is possible that the ptarmigan females have proportionally smaller muscles in the proximal limb segment than males, thus making it more difficult for females to decelerate the swinging limb. Similarly, the relatively longer stance phases may be viewed as a mechanism by which females compensate for the lower capacity of the proximal muscles to generate forces. A detailed anatomical description of limb musculoskeletal anatomy would provide useful information about the morphological constraints dictating the sex-specific strategies by which ptarmigan keep dynamic stability.

Metabolically speaking, the grounded running gait offers more economical speeds of locomotion compared to the slower walking gait. Flightless birds including ostriches (*Struthio camelus*) (Daley and Birn-Jeffery 2018; Rubenson et al. 2004; Watson et al. 2011), rhea (*rhea americana*) (Roberts et al. 1998; Watson et al. 2011) and emus (*Dromaius novahollandiae*) (Watson et al. 2011) all experience an abrupt drop in the cost of transport at the walking-grounded running gait transition. Other ground dwellers also show more economical grounded running gaits, although with a more continuous transition including the chicken (*Gallus gallus*) (Rose et al. 2015b). The Svalbard ptarmigan are no exception. At the grounded running speed range – from 1 to 1.5 ms^{-1} – the ptarmigan males use ~33% less energy on average, compared to the fastest walking speed before the transition (Nudds et al. 2011). Therefore, if the only consideration for gait selection is dictated by energy optimisation, animals should always prefer grounded running gaits rather than the more metabolically costly walking gaits. Results from **chapter 2** and **3** may be aligned with the idea of locomotor economy. From all the Svalbard ptarmigan data approximately 40% of all trials recorded, including males (*n*= 56) and females (*n*= 32), fell into the grounded running gait. It is possible, however, that the energy savings from using a more economical grounded running gait compensate for the costs lifting the feet from snow in particular when snow is unsupportive (Heinonen et al. 1959; Parker et al. 1984; Ramaswamy et al. 1966) in particular in winter when snow influence may be more pronounced. Yet, evidence of the latter in the wild ptarmigan remains to be found.

6.4. The aerial running as a result of sexual dimorphism

Aerial running is thought to be the result of sexual selection upon improved locomotor performance of the males (Lees et al. 2012a), as they compete with other males to defend their breeding territories during the reproductive season (Steen and Unander 1985; Unander and Steen 1985). On the other hand, females achieve top speed ranges restricted to the grounded running gait compared to males (Lees et al. 2012a). In line with evidence obtained in the lab, aerial running gaits were only recorded for wild ptarmigan males (**chapter 2**). They accounted for ~36 % of the 165 trials recorded in males. The maximum self-selected speed for wild male ptarmigan was 2.72 ms^{-1}, a 1.36-fold increase compared to the maximum sustainable speed reported on treadmills (Nudds et al. 2011); a common finding among studies where animals are not restricted to aerobically sustainable speeds (e.g. Daley et al. 2016). Nevertheless, wild female ptarmigan do not show such an increase; they only attain speeds 8% higher than from treadmill studies within the grounded running gait (**chapter 3**) (Lees et al. 2012a). This difference may again be the result of divergent limb anatomies, in particular muscles. Faster speeds within the aerial gait require of muscle physiologically capable to generate large forces acting on ground concomitantly with stiffer legs (Andrada et al. 2013a). Thus, it might be that the absence of aerial running gait in the females is related to smaller physiological cross-sectional area (PCSA) of the muscles in charged to do work against the ground. Proportionally longer stances may also compensate the reduced force capacity of the muscles by providing longer times to develop enough force for thrust, consistent with a more crouched limb posture as discussed in the previous section.

Similar to a walking gait, aerial running kinematics were highly conserved when comparing males on treadmills vs. males running on snow. Although fine adjustments for stable locomotion cannot be ruled out as compensatory mechanisms for stability, it is possible that aerial running stability is directly correlated to the high f_{stride}, thereby allowing for rapid recoveries when ground perturbations are found (Qiao and Jindrich 2014), which might explain the similarities between both approaches. Furthermore, aerial running only occurred over firm terrain where snow offered enough support for optimal energy recovery through recoil of the elastic elements without high energy losses to the substrate (Lejeune et al. 1998). This also might explain the lack of kinematic differences when our data is compared to Svalbard ptarmigan using aerial running over treadmills. The fact that no aerial running gaits were found when ptarmigan moved over softer snow is in line with the narrower speed ranges reported for other species moving in unsupportive snow (Crête and Larivière 2003; Droghini 2016; Whiteman and Buskirk 2013).

Activities involving fast running speeds with aerial phases are thought to be mostly attained under extreme circumstances, either to escape from predators, to chase a prey or to engage in combat with other conspecifics of the same sex (Reilly et al. 2007). These activities, however, are very infrequent compared to the whole activity landscape of species (e.g. Williams et al. 2014; Wilson et al. 2013) as they are often strenuous and demands extremely high locomotor costs (i.e. J kg^{-1} s^{-1}). In the Svalbard rock ptarmigan, intraspecific male combat only occurs during the breeding season, between April and June (Steen and Unander 1985; Unander and Steen 1985), thus the chances of spotting fast aerial running speeds may increase during this time. Despite this, the accounts regarding activity patterns of territorial ptarmigan males are anecdotic, and time-based characterization of them are solely inexistent. A similar situation relates to escaping behaviour, where no detailed account has been made for the Svalbard rock ptarmigan. It would be interesting to see which is the escaping strategy (i.e. top speed or agile turns) most frequently used by the ptarmigan under a predatory stimulus. It has been widely reported for many species that they rarely use they maximum sprinting in the wild, even under the presence of predators, which might indicate that more manoeuvrable and agile speeds of locomotion may be more relevant for escaping from predators (Irschick et al. 2005; Reilly et al. 2007; Wilson et al. 2018). More interesting would be to find that aerial running gaits in other activities apart from the ones previously discussed. There would be clear energetic benefits if ptarmigan use aerial running gaits simply for travel.

6.5. Challenges of studying the Svalbard rock ptarmigan in the field

One of the main objectives of my PhD was to tend the links between the locomotor biomechanics of the Svalbard rock ptarmigan and with ecologically relevant aspects of their life history. It is often the case that what has been reported from studies into the locomotor performance of diverse taxa are difficult to interpret under an ecological context due to fundamental aspects of laboratory-based approaches used by researchers. Laboratory-based approaches are intended to provide greater control over the experimental design so the data could be fitted into a simpler model due to a reduced number of confounding variables coupled with a number of replicates per experiment. This has allowed researchers to tackle questions on the effects of specific morphological (e.g. limb posture, body size), physiological (i.e. sex, age, seasonal) and external (i.e. locomotion on inclines or uneven substrate, temperature, etc.) factors acting upon locomotion, although in nature all these factors interact between each other in intricate ways. Moreover, the inherent nature of field research makes it challenging to obtain adequate sample sizes that may be affected by unpredictable changes in weather conditions, and increased model complexity due to additional environmental cofounding factors that are not necessarily under scrutiny coupled with higher risk of pseudo-replicates. Some of these problems can be mitigated by planning the fieldwork before hand, but others might be more difficult to circumvent. In the following section I discuss on the challenges of studying the Svalbard rock ptarmigan *in situ*.

Typically, getting an appropriate sample size in the field demands great effort from the researcher first to visually detect individuals of the species of interest, and second to obtain the data of interest from individuals. By the time when fieldwork was conducted – at the beginning of the Spring – both male and female Svalbard rock ptarmigan are in their winter plumage and snow cover is still present, meaning that the birds easily blend with the white snowy landscape (Unander and Steen 1985). Moreover, the Svalbard rock ptarmigan population density is relatively low, with individuals ranging from 2.7 to 4.9 individuals per kilometre square (Pedersen et al. 2005). These make it an extremely difficult task for the observer to spot the birds even at short distances. Once a bird was spotted, the risk of failure was still present given that some birds would take-off before obtaining suitable video-recordings for speed and gait kinematic analysis, which make up for a large portion of the data measured in the field. The latter besides the known tameness of the Svalbard rock ptarmigan compared to other ptarmigan species in lower latitudes (Unander et al. 2016). These caveats, however, are minor and were controlled by increasing the time spent looking for individuals while covering as much area where ptarmigan are known to be found as possible.

A major factor affecting sampling relates to the number of days of with extreme weather events that drastically change the physical properties of the snowpack. In years with more events of rain on snow and overall warmer temperatures, the snowpack suffers a defrost-refreeze cycle that promotes the formation of icy crusts and the decrease of the snowpack (Cohen et al. 2015). These brings two consequences affecting our sampling. First, a smaller snowpack means that snow will retreat earlier in the following Spring (Cohen et al. 2015), therefore, most of the sampling sites that were accessed only by snow scooter become inaccessible. Indeed, during the last fieldwork season – in early spring of 2019 – snow began melting earlier restricting the sampling sites adjacent to the main road. Second, rain on snow can also restrict food access to the Svalbard rock ptarmigan and other high-Arctic herbivores due to the formation of ice layers covering the plants on which these species feed on, resulting in a reduction of the population in all these species (Hansen et al. 2011; Hansen et al. 2013; Yoccoz and Ims 1999). Although I do not have evidence for the latter being the case, the fall in the number of birds spotted in 2019 to a ~30% of the numbers recorded in 2017 (87 birds) and 2018 (84 birds) can be explained by our limited capacity to cover greater areas, as the earlier retreat of snow cover in the Spring of 2019 restricted us only to places accessible by walking.

Finally, to counter to some extent the low number of birds spotted in 2019 repeated measures of footprint depths were taken for a number of tracks left by all the bird included into the analysis in **chapter 4**. If repeated measurements in the dataset are mistakenly considered independent, any statistical inference on the effects of snow over speed becomes misleading due to overestimated degrees of freedom that may give spurious significant trends (Crawley 2013; Steel et al. 2013). This problem is often referred as pseudoreplication (Hurlbert 1984). A proper analysis of the data required the use of linear mixed models, where the individual contribution of each Svalbard rock ptarmigan to the model (i.e. the repeated measures of each bird) is considered, resulting in an adequate estimation of the degrees of freedom for statistical inference (Bolker et al. 2009; Hurlbert 1984). As a result, the linear mixed models describing the data in **chapter 4** are comparatively more complex than the linear regressions used in **chapter 2** and **3** where no repeated measures were taken.

Other challenges inherent to field research are associated to a higher complexity in the logistics required to visit remote places like Svalbard, where local permits to conduct research must be obtained, accommodation may be expensive and data collection relies on the proper function of equipment. These challenges may discourage researchers to do fieldwork. Moreover, the relatively smaller funding available for field research coupled with a reduced scope of high-profile journals where to publish their work may induce researchers to opt for other approaches including laboratory and model-based studies (Ríos-Saldaña et al. 2018). Clearly, huge progress has been made in the field of animal physiology and biomechanics thanks to these two approaches. Specifically for animal locomotion, laboratory based approaches have been key to understand the links between physiology and performance (Gatesy and Biewener 1991; Irschick et al. 2005; Lees et al. 2012a; Nudds et al. 2011), favouring energy optimisation (Hoyt and Kenagy 1988; Hoyt and Taylor 1981; Rubenson et al. 2004; Watson et al. 2011) while keeping the structural safety of the locomotor system (Daley and Usherwood 2010), whereas modelling studies have enabled us to gain insights on the general locomotor dynamics (Blickhan 1989; Pontzer 2007; Seyfarth et al. 2003) of extant (Birn-Jeffery et al. 2014;

Clark and Higham 2011) and extinct organisms (Alexander 1976; Sellers and Manning 2007; Sellers William et al. 2005). However, field work is also crucial to integrate the results obtained for species studied in lab with the data on natural behaviour of the species while interacting with its habitat. This allows us to gain insights into the ecological and evolutionary constrains dictating how animal locomotion (**chapter 2**). Likewise, mathematical models explaining a phenomenon of interest, for example predicting speeds and gaits from trackways of elusive or extinct species (as shown with the Svalbard rock ptarmigan in **chapter 5**), would benefit from further refinement by ground truthing predictions with data through direct observation of animals moving in the wild. Hence, both approaches, laboratory-based studies and field research, should be taken as complementary.

6.6. Future directions

The data presented in this thesis have shed new light on the constraints on the biomechanics of locomotion of the Svalbard rock ptarmigan, in particular when birds move over snow. However, this thesis constitutes only the beginning of a series of studies linking ptarmigan locomotion into ecological and evolutionary contexts. Thus, new avenues of research are warrant.

6.6.1. Mechanism for stability while moving on snow

The data presented in this thesis suggest that snow, particularly when it is soft and unsupportive, lead to the adjustment of the basic kinematics of grounded running in males. Such changes are translated into faster f_{stride} and shorter $l_{\mathrm{stride}}$with increasing U. Despite this result parallels those found in laboratory studies testing for a specific neuromechanical response to a given external perturbance (i.e. obstacles, drops, slippery or compliant substrates) in human (Cappellini et al. 2010; Clark and Higham 2011) and birds (Birn-Jeffery et al. 2014; Daley et al. 2006), I could not identify if the kinematic adjustments obey to the same mechanism reported in those studies with my data. It was impossible to detect precisely the time when foot contacts the ground and to track the limb joints to measure the orientation of the limb segments to each other, to the trunk and to the ground. Optimised swing leg control (i.e. leg retraction) prior stance phase and leg actuation at foot-ground contact are key to stabilise the mechanical energy of the COM, while keeping the structural safety of the leg (Blum et al. 2014). Perhaps this mechanism explains the decrease in l_{stride} and the increase in f_{stride}, if the leg of the ptarmigan male is retracting relatively faster, leading to a more crouched posture and a lower vertical peak in the GRF. Evidence of this could be obtained by making trials where the ptarmigan males run over a force platform covered by a layer of snow of a given depth and supportiveness to compare if the GRF patterns coincide with those reported by for other species (Birn-Jeffery et al. 2014; Blum et al. 2014; Daley et al. 2006). Such an experiment would parallel the kinematic response and recovery of a sudden drop and would allow to track limb segment trajectories. Alternatively, by using a triaxial accelerometer sensor directly attached to the limb segments of wild Svalbard rock ptarmigan males moving *in situ*, it could be possible to quantify the maximum force applied by the bird at the beginning of stance which reciprocates GRF and overall limb dynamics, aside from other basic gait parameters such as stance and swing phase, step velocity and stride length. This technique has been previously applied on walking male turkeys (*Meleagris gallopavo*) (Stevenson et al. 2019). Either way, a study examining in more detailed the effects of snow on limb dynamics remains to be done. Such data could also be representative for avian species that often experience foot sinking while moving on mud or sand.

6.6.2. Sex dimorphism on limb architecture in the Svalbard ptarmigan

Our results also suggest a strong sex component affecting the kinematic adjustments to negotiate with snowy substrates in the Svalbard rock ptarmigan. Sexual dimorphism is widespread among birds, and it has been recently that such differences have been reported in the avian locomotor system in species including the jungle fowl (Hammond et al. 2000), the leghorn (Rose et al. 2016a; Rose et al. 2016b) and in the locomotion energetics and performance in the Svalbard rock ptarmigan moving on treadmills (Lees et al. 2012a). Contrary to the males, female ptarmigan appear to be more robust to the effects of snow, which is reflected in the indistinguishable kinematic adjustments while moving on snow. Our data suggest that this may be the result of a more crouched posture given the morphological constrains of sex; although again, it was impossible to directly measure posture due to the inability to track limb joints and limb segments from our recordings. A similar approach using accelerometers directly attached to the female's limb could provide valuable information on the dynamic changes in limb posture at ground contact (Heebner et al. 2015; Takeda et al. 2009). However, this technique requires a larger number of sensors attached to the upper limb, knee and ankle (Takeda et al. 2009), which might affect normal locomotion of the females due to the added weight (Tickle et al. 2010). If such is the case, more traditional approaches using reflective marking to visually detect the motion of each limb joint, may also preferred.

Moreover, up to date, there is no detail anatomical account on the limb muscle physiology of the adult Svalbard rock ptarmigan of both sexes. Based on our results, we would expect to see comparatively smaller muscle masses in the thigh of the females, which would be consistent with the proportionally longer t_{swing} required to counter the moments of inertia acting on the limb joints, as seen in **chapter 3**. This would also make more challenging for the females to provide enough power for fast gaits, which is also consistent with the lack of high speeds at aerial running gaits observed in **chapter 3** and a previous report (Lees et al. 2012a). Such data would be valuable not only to gain insight into the mechanisms behind the greater intrinsic stability of the females to moving on snow, but also to understand the physiological basis dictating the more expensive locomotion seen in females compared to males.

6.6.3. Ubiquity of findings - Understanding the energy landscape of the Svalbard rock ptarmigan

A central idea to understand whether or not the movement patterns of animals are highly influenced by external environmental factors that vary over time and space is that organisms must aim to optimise their energy costs by modulating a set of behavioural responses to save energy (Shepard et al. 2013; Wilson et al. 2012). The integration of the environmental variability of habitat of a species to the effects it has on the energetic costs is known as the energetic landscape (Shepard et al. 2013; Wilson et al. 2012). Eliciting the energy landscape of a species may provide valuable information on the routes the species take that implies the less energy costs (Wall et al. 2006), on the animal's energy budget ascribed to daily activity patterns (Williams et al. 2014; Wilson et al. 2013), and if individuals move at speeds and gaits favouring energy economy under a given environmental constraint like substrate (e.g. Droghini and Boutin 2018a; Fancy and White 1987) and water currents (e.g. Wilson et al. 2012).

This thesis may be viewed as a first attempt to examine how environmental factors constraining locomotion in the Svalbard rock ptarmigan while moving in their natural habitat. In Svalbard, there is a number of environmental factors that are likely to increase the locomotor costs. These factors could change seasonally – e.g., snow cover, vegetation cover – while other may drastically change in days or in hours – e.g., wind speed, temperature, sun. Other factors, such as topography, may be regarded as immutable as they remain consistent over millennia. In this thesis, however, the analysis was restricted to the effects of snow upon locomotion of individual birds: during fieldwork, good trials were considered only the ones were the birds were moving on level ground, while the effects of wind, temperature and precipitation were assumed to be negligible, as data was taken mostly when weather conditions were favourable.

The results in **chapter 4** may suggest that the Svalbard rock ptarmigan are deliberately selecting routes with snow patches where foot sinking do not exceed the intertarsal joint in order to avoid excessive increases in the costs of locomotion associated to move over deep, unsupportive snow. However, confirmation of such behaviour occurring in the field is still required. Moreover, one of the motivations to conduct the study in **chapter 5** was to develop an alternative economic model to predict the use of self-selected speeds and gaits by the ptarmigan in the wild solely from footprints; however, the large errors associated to the speed predictions coupled with the inability to identify the gait transition between grounded and aerial running ruled out this possibility. Thus, future studies could be focused to build the snow-related energy landscape of the Svalbard rock ptarmigan, by overlaying the movement patterns of these birds onto the seasonal variation in snow cover changes occurring throughout a year in Svalbard. With the advent of a new generation of smaller bio-loggers capable to record multiple biologically relevant aspects of the bird life history, including location and the body dynamics state, it is possible to analyse *in vivo* activities that are ecologically relevant for the ptarmigan. GPS tracking, for example, would enable us to determine if an individual moves stochastically around its habitat or if its movement follow a specific pattern – e.g. to avoid steep terrain (Wall et al. 2006). Measuring the external accelerations acting on the body of an individual via triaxial accelerometers (i.e. body dynamics) can be used to identify specific activities, including if the birds is foraging, traveling or resting; and for how long these activities endure. Moreover, triaxial accelerometry can be used to estimate energy expenditures proxies ascribed to a particular locomotor activity (Green et al. 2009; Wilson et al. 2006). Such technique has been already applied in several birds and mammals including the imperial cormorant *Phalacrocorax atriceps* (Wilson et al. 2012), the common chicken *Gallus gallus* (Green et al. 2009), the little penguin *Eudyptula minor* (Carroll et al. 2014), the Magellanic penguin *Spheniscus magellanicus* (Wilson et al. 2008), the cheetah *Acinonyx jubatus* (Wilson et al. 2013), the puma *Puma concolor* (Williams et al. 2014) and the polar bear *Ursus maritimus* (Pagano et al. 2018). On the other hand, fine timescale geographically referenced information on the variation of several environmental factors measured over decades, including snow cover, are available as GIS maps for the entire Svalbard Archipelago, and have been already used to model suitable breeding habitats for the Svalbard rock ptarmigan (Pedersen et al. 2017; Pedersen et al. 2007). The integration of such information into the energy landscape of the Svalbard rock ptarmigan will be useful to validate the results reported in **chapter 4**. Moreover, the development of the Svalbard rock ptarmigan energy landscape may help to gain insight into the life history of the species during winter regarding habitat preferences and locomotor activities during winter, when many physiological changes affecting locomotion occur and that have remained elusive to researchers.

More broadly, with the addition of other relevant environmental factors like vegetation cover, terrain slopes (Pedersen et al. 2017) and intraspecific and interspecific competition (Henden et al. 2017) to the energy landscape of the Svalbard rock ptarmigan, it would be possible to better understand how individuals partition their energy and time for specific activities and behaviours linked energy optimisation and fitness, which are paramount to develop conservation and management strategies for the Svalbard rock ptarmigan in a rapidly changing Arctic environment. Although, the Svalbard rock ptarmigan may be regarded as an ideal model to build a broad energy landscape, given that these birds are embedded in a much simpler trophic chain compared to other ptarmigan across the circumpolar region (Henden et al. 2017), the information provided by such model could found resonance in the conservation efforts of other ptarmigan populations, including the willow and the rock ptarmigan inhabiting the low-Arctic and high alpine regions of Europe, Asia, North America and Japan, as well as other high-artic populations from Iceland and Greenland, which are likely to be affected by climate change.

Concluding remarks

Selective pressures act upon whole-organism performance on ecologically relevant activities, including animal locomotion. Locomotion requires precise kinematic tunning, that may largely depend on the morphological and physiological traits of individuals, to move over complex environments. On the other hand, energy optimisation while moving would largely depend on the decision-making processes dictated by environmental constrains – biotic or abiotic – that may change in a daily or seasonal basis. By integrating the internal (organismal) and external (environmental) factors into broad scale studies will provide insights into the animal adaptations to live in their environment environments, and how changes in these environments, in particular those created by human activity, may affect the species survival. While more efforts should be devoted to study animal locomotion *in situ* powered by sustained advances in technological tools that allow us to quantitatively analyse relevant physiological aspects of individuals in the wild, this thesis highlights the importance of laboratory-based studies as baselines to interpret the results obtained in the field. Only by combining both approaches, it is possible gain insight into the internal (organismal) and external (environmental) factors behind animal adaptations to succeed in their habitat, and how changes in these environments, in particular those created by human activity, may affect the species survival.

References

Aaslund MK, Moe-Nilssen R (2008) Treadmill walking with body weight support: Effect of treadmill, harness and body weight support systems. Gait and Posture 28:303-308 doi:https://doi.org/10.1016/j.gaitpost.2008.01.011

Abourachid A (2001) Kinematic parameters of terrestrial locomotion in cursorial (ratites), swimming (ducks), and striding birds (quail and guinea fowl). Comparative Biochemistry and Physiology, Part A: Molecular & Integrative Physiology 131:113-119 doi:http://dx.doi.org/10.1016/S1095-6433(01)00471-8

Abourachid A, Renous S (2000) Bipedal locomotion in ratites (Paleognatiform) examples of cursorial birds. Ibis 142:538-549 doi:https://doi.org/10.1111/j.1474-919X.2000.tb04455.x

Aerts P (1998) Vertical jumping in Galago senegalensis: the quest for an obligate mechanical power amplifier. Philosophical Transactions of the Royal Society B: Biological Sciences 353:1607-1620 doi:10.1098/rstb.1998.0313

Alexander RM (1976) Estimates of speeds of dinosaurs. Nature 261:129-130 doi:10.1038/261129a0

Alexander RM (1989) Optimization and gaits in the locomotion of vertebrates. Physiological Reviews 69:1199-1227 doi:10.1152/physrev.1989.69.4.1199

Alexander RM (2000) Walking and running strategies for humans and other mammals. In: Blake PW, Domenici P (eds) Biomechanics in Animal Behaviour. BIOS Scientific Publishers, Oxford, pp 49-58

Alexander RM (2003a) The best way to travel. In: Principles of Animal Locomotion. STU - Student edition edn. Princeton University Press, pp 1-14

Alexander RM (2003b) Principles of Animal Locomotion.371

Alexander RM (2004) Bipedal animals, and their differences from humans. Journal of Anatomy 204:321-330 doi:10.1111/j.0021-8782.2004.00289.x

Alexander RM (2005) Models and the scaling of energy costs for locomotion. Journal of Experimental Biology 208:1645 doi:10.1242/jeb.01484

Alexander RM, Jayes AS (1983) A dynamic similarity hypothesis for the gaits of quadrupedal mammals. Journal of Zoology 201:135-152 doi:https://doi.org/10.1111/j.1469-7998.1983.tb04266.x

Anderson RA (1993) Analysis of foraging in the lizard *Cnemidophorus tigris*. In: Wright J, Vitt LJ (eds) Biology of *Cnemidophorus*. University of Oklahoma Press, Norman, pp 83-116

Anderson RA, Karasov WH (1981) Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. Oecologia 49:67-72 doi:10.1007/BF00376899

Andrada E et al. (2015) Mixed gaits in small avian terrestrial locomotion. Scientific Reports 5:13636 doi:10.1038/srep13636

Andrada E, Nyakatura JA, Bergmann F, Blickhan R (2013a) Adjustments of global and local hindlimb properties during terrestrial locomotion of the common quail (*Coturnix coturnix*). The Journal of Experimental Biology 216:3906 doi:10.1242/jeb.085399

Andrada E, Rode C, Blickhan R (2013b) Grounded running in quails: Simulations indicate benefits of observed fixed aperture angle between legs before touch-down. Journal of Theoretical Biology 335:97-107 doi:https://doi.org/10.1016/j.jtbi.2013.06.031

Bateman AJ (1948) Intra-sexual selection in Drosophila. Heredity 2:349-368 doi:10.1038/hdy.1948.21

Bennett MB, Stafford Ja (1988) Tensile properties of calcified and uncalcified avian tendons. Journal of Zoology 214:343-351 doi:10.1111/j.1469-7998.1988.tb04727.x

Biewener AA (1989) Scaling body support in mammals: limb posture and muscle mechanics. Science 245:45-48 doi:https://doi.org/10.1126/science.2740914

Biewener AA (1990) Biomechanics of mammalian terrestrial locomotion. Science (New York, NY) 250:1097-1103 doi:10.1126/science.2251499

Biewener AA (1991) Musculoskeletal design in relation to body size. Journal of Biomechanics 24:19-29 doi:10.1016/0021-9290(91)90374-V

Biewener AA (2005) Biomechanical consequences of scaling. Journal of Experimental Biology 208:1665 doi:10.1242/jeb.01520

Biewener AA, Patek S (2018) Animal Locomotion. second edition edn. Oxford University Press, Oxford, United Kingdom

Birn-Jeffery AV, Daley MA (2012) Birds achieve high robustness in uneven terrain through active control of landing conditions. The Journal of Experimental Biology 215:2117 doi:https://doi.org/10.1242/jeb.065557

Birn-Jeffery AV, Hubicki CM, Blum Y, Renjewski D, Hurst JW, Daley MA (2014) Don't break a leg: running birds from quail to ostrich prioritise leg safety and economy on uneven terrain. The Journal of Experimental Biology 217:3786 doi:https://doi.org/10.1242/jeb.102640

Blaszczyk J, Loeb GE (1993) Why cats pace on the treadmill. Physiology and Behavior 53:501-507 doi:https://doi.org/10.1016/0031-9384(93)90144-5

Blickhan R (1989) The spring-mass model for running and hopping. Journal of Biomechanics 22:1217-1227 doi:https://doi.org/10.1016/0021-9290(89)90224-8

Blix AS (2005) Arctic animals and their adaptations to life on the edge.296

Blum Y, Birn-Jeffery A, Daley MA, Seyfarth A (2011) Does a crouched leg posture enhance running stability and robustness? Journal of Theoretical Biology 281:97-106 doi:https://doi.org/10.1016/j.jtbi.2011.04.029

Blum Y, Vejdani HR, Birn-Jeffery AV, Hubicki CM, Hurst JW, Daley MA (2014) Swing-leg trajectory of tunning Guinea fowl suggests task-level priority of force regulation rather than disturbance rejection. PloS One 9:e100399 doi:10.1371/journal.pone.0100399

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127-135 doi:https://doi.org/10.1016/j.tree.2008.10.008

Booth FW, Ruegsegger GN, Toedebusch RG, Yan Z (2015) Chapter Six - Endurance exercise and the regulation of skeletal muscle metabolism. In: Bouchard C (ed) Progress in Molecular Biology and Translational Science, vol 135. Academic Press, pp 129-151. doi:https://doi.org/10.1016/bs.pmbts.2015.07.016

Bruland O, Liston GE, Vonk J, Sand K, Killingtveit Å (2004) Modelling the snow distribution at two high arctic sites at Svalbard, Norway, and at an alpine site in central Norway. Hydrology Research 35:191-208 doi:10.2166/nh.2004.0014

Buchner HHF, Savelberg HHCM, Schamhardt HC, Merkens HW, Barneveld A (1994) Kinematics of treadmill versus overground locomotion in horses. Veterinary Quarterly 16:87-90 doi:https://doi.org/10.1080/01652176.1994.9694509

Cappellini G, Ivanenko YP, Dominici N, Poppele RE, Lacquaniti F (2010) Motor patterns during walking on a slippery walkway. Journal of Neurophysiology 103:746-760 doi:https://doi.org/10.1152/jn.00499.2009

Carroll G, Slip D, Jonsen I, Harcourt R (2014) Supervised accelerometry analysis can identify prey capture by penguins at sea. The Journal of Experimental Biology 217:4295 doi:10.1242/jeb.113076

Cavagna GA, Heglund NC, Taylor CR (1977) Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. American Journal of Physiology: Regulatory, Integrative and Comparative Physiology 233:R243-R261 doi:https://doi.org/10.1152/ajpregu.1977.233.5.R243

Cham R, Redfern MS (2002) Changes in gait when anticipating slippery floors. Gait and Posture 15:159-171 doi:https://doi.org/10.1016/S0966-6362(01)00150-3

Clark AJ, Higham TE (2011) Slipping, sliding and stability: locomotor strategies for overcoming low-friction surfaces. The Journal of Experimental Biology 214:1369 doi:https://doi.org/10.1242/jeb.051136

Cohen J, Ye H, Jones J (2015) Trends and variability in rain-on-snow events. Geophysical Research Letters 42:7115-7122 doi:https://doi.org/10.1002/2015GL065320

Crawley MJ (2013) The R book. Second edition. Chichester, West Sussex, United Kingdom : Wiley, 2013.,

Crête M, Larivière S (2003) Estimating the costs of locomotion in snow for coyotes. Canadian Journal of Zoology 81:1808-1814 doi:10.1139/z03-182

Currey JD (1984) Effects of differences in mineralization on the mechanical properties of bone. Philosophical Transactions of the Royal Society B: Biological Sciences 304:509-518 doi:DOI: 10.1098/rstb.1984.0042

Daley MA (2018) Understanding the agility of running birds: sensorimotor and mechanical factors in avian bipedal locomotion. Integrative and Comparative Biology 58:884-893 doi:10.1093/icb/icy058

Daley MA, Biewener AA (2003) Muscle force-length dynamics during level versus incline locomotion: a comparison of in vivo performance of two guinea fowl ankle extensors. The Journal of Experimental Biology 206:2941-2958 doi:10.1242/jeb.00503

Daley MA, Biewener AA (2006) Running over rough terrain reveals limb control for intrinsic stability. Proceedings of the National Academy of Sciences of the United States of America 103:15681 doi:https://doi.org/10.1073/pnas.0601473103

Daley MA, Biewener AA (2011) Leg muscles that mediate stability: mechanics and control of two distal extensor muscles during obstacle negotiation in the guinea fowl. Philosophical Transactions of the Royal Society of London Series B: Biological Sciences 366:1580-1591 doi:https://doi.org/10.1098/rstb.2010.0338

Daley MA, Birn-Jeffery A (2018) Scaling of avian bipedal locomotion reveals independent effects of body mass and leg posture on gait. The Journal of Experimental Biology 221:jeb152538 doi:10.1242/jeb.152538

Daley MA, Channon AJ, Nolan GS, Hall J (2016) Preferred gait and walk–run transition speeds in ostriches measured using GPS-IMU sensors. The Journal of Experimental Biology 219:3301-3308 doi:https://doi.org/10.1242/jeb.142588

Daley MA, Felix G, Biewener AA (2007) Running stability is enhanced by a proximo-distal gradient in joint neuromechanical control. The Journal of Experimental Biology 210:383 doi:https://doi.org/10.1242/jeb.02668

Daley MA, Usherwood JR (2010) Two explanations for the compliant running paradox: reduced work of bouncing viscera and increased stability in uneven terrain. Biology Letters 6:418-421 doi:https://10.1098/rsbl.2010.0175

Daley MA, Usherwood JR, Felix G, Biewener AA (2006) Running over rough terrain: guinea fowl maintain dynamic stability despite a large unexpected change in substrate height. The Journal of Experimental Biology 209:171 doi:https://doi.org/10.1242/jeb.01986

Daley MA, Voloshina A, Biewener AA (2009) The role of intrinsic muscle mechanics in the neuromuscular control of stable running in the guinea fowl. The Journal of Physiology 587:2693-2707 doi:10.1113/jphysiol.2009.171017

Daniels F, Vanderbie JH, Winsman FR (1953) Energy cost of treadmill walking compared to road walking. US Office of the Quatermaster General, Lawrence, Massachusetts

Dawson TJ, Taylor CR (1973) Energetic cost of locomotion in kangaroos. Nature 246:313-314

Droghini A (2016) Snowfall, travel speed, and seismic lines: The effects of snow conditions on wolf movement paths in boreal Alberta. University of Alberta

Droghini A, Boutin S (2018a) The calm during the storm: Snowfall events decrease the movement rates of grey wolves (*Canis lupus*). PloS One 13:e0205742 doi:https://10.1371/journal.pone.0205742

Droghini A, Boutin S (2018b) Snow conditions influence grey wolf (*Canis lupus*) travel paths: the effect of human-created linear features. Canadian Journal of Zoology 96:39-47 doi:10.1139/cjz-2017-0041

Dunn PO, Whittingham LA, Pitcher TE (2001) Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. Evolution 55:161-175 doi:10.1111/j.0014-3820.2001.tb01281.x

Dyck J (1979) Winter plumage of the rock ptarmigan: structure of the air-filled barbules and function of the white colour. Danks Ornithologisk Forenings Tidsskrift 73:41-58

Ebbinge B, Canters K, Drent R (1975) Foraging routines and estimated daily food intake in Barnacle Geese wintering in the northern Netherlands. Wildfowl 26:5-19

Edwards MA, Derocher AE, Hobson KA, Branigan M, Nagy JA (2011) Fast carnivores and slow herbivores: differential foraging strategies among grizzly bears in the Canadian Arctic. Oecologia 165:877-889 doi:10.1007/s00442-010-1869-9

Ellerby DJ, Henry HT, Carr JA, Buchanan CI, Marsh RL (2005) Blood flow in Guinea fowl *Numida meleagris* as an indicator of energy expenditure by individual muscles during walking and running. Journal of Physiology 564:631-648 doi:https://doi.org/10.1113/jphysiol.2005.082974

Elliott BC, Blanksby BA (1976) A cinematographic analysis of overground and treadmill running by males and females. Medicine and Science in Sports 8:84-87

Falkingham PL, Gatesy SM (2014) The birth of a dinosaur footprint: Subsurface 3D motion reconstruction and discrete element simulation reveal track ontogeny. Proceedings of the National Academy of Sciences of the United States of America 111:18279 doi:10.1073/pnas.1416252111

Fan DM, Yang YP (2009) Altitudinal variations in flower and bulbil production of an alpine perennial, *Polygonum viviparum* L. (Polygonaceae). Plant Biology 11:493-497 doi:https://doi.org/10.1111/j.1438-8677.2008.00188.x

Fancy SG, White RG (1987) Energy expenditures for locomotion by barren-ground caribou. Canadian Journal of Zoology 65:122-128 doi:https://doi.org/10.1139/z87-018

Farley CT, Glasheen J, McMahon TA (1993) Running springs: speed and animal size. Journal of Experimental Biology 185:71

Fish FE, Frappell PB, Baudinette RV, MacFarlane PM (2001) Energetics of terrestrial locomotion of the platypus *Ornithorhynchus anatinus*. Journal of Experimental Biology 204:797

Fitzgibbon CD (1990) Mixed-species grouping in Thomson's and Grant's gazelles: the antipredator benefits. Animal Behaviour 39:1116-1126 doi:https://doi.org/10.1016/S0003-3472(05)80784-5

Fu C, Fu S-J, Yuan X-Z, Cao Z-D (2015) Predator-driven intra-species variation in locomotion, metabolism and water velocity preference in pale chub (*Zacco platypus*) along a river. The Journal of Experimental Biology 218:255 doi:10.1242/jeb.109561

Full RJ (1987) Locomotion Energetics of the Ghost Crab: I. Metabolic Cost and Endurance. Journal of Experimental Biology 130:137

Full RJ, Tu MS (1991) Mechanics of a rapid running insect: two-, four- and six-legged locomotion. Journal of Experimental Biology 156:215

Gatesy SM, Biewener AA (1991) Bipedal locomotion: effects of speed, size and limb posture in birds and humans. Journal of Zoology 224:127-147 doi:https://doi.org/10.1111/j.1469-7998.1991.tb04794.x

Gatesy SM, Falkingham PL (2017) Neither bones nor feet: track morphological variation and 'preservation quality'. Journal of Vertebrate Paleontology 37:e1314298 doi:10.1080/02724634.2017.1314298

Geyer H, Seyfarth A, Blickhan R (2006) Compliant leg behaviour explains basic dynamics of walking and running. Proceedings of the Royal Society B: Biological Sciences 273:2861-2867 doi:10.1098/rspb.2006.3637

Gordon AM, Huxley AF, Julian FJ (1966) The variation in isometric tension with sarcomere length in vertebrate muscle fibres. The Journal of Physiology 184:170-192 doi:5921536

Gordon JC, Rankin JW, Daley MA (2015) How do treadmill speed and terrain visibility influence neuromuscular control of guinea fowl locomotion? The Journal of Experimental Biology 218:3010 doi:10.1242/jeb.104646

Grammeltvedt R, Steen JB (1978) Fat Deposition in Spitzbergen Ptarmigan (*Lagopus mutus hyperboreus*). Arctic 31:496-498

Green JA, Halsey LG, Wilson RP, Frappell PB (2009) Estimating energy expenditure of animals using the accelerometry technique: activity, inactivity and comparison with the heart-rate technique. Journal of Experimental Biology 212:471-482 doi:10.1242/jeb.026377

Hagenmuller P, Chambon G, Flin F, Morin S, Naaim M (2014) Snow as a granular material: assessment of a new grain segmentation algorithm. Granular Matter 16:421-432 doi:10.1007/s10035-014-0503-7

Hammond KA, Chappell MA, Cardullo RA, Lin R, Johnsen TS (2000) The mechanistic basis of aerobic performance variation in red junglefowl. Journal of Experimental Biology 203:2053

Hancock JA, Stevens NJ, Biknevicius AR (2007) Whole-body mechanics and kinematics of terrestrial locomotion in the Elegant-crested Tinamou *Eudromia elegans*. Ibis 149:605-614 doi:https://doi.org/10.1111/j.1474-919X.2007.00688.x

Hansen BB, Aanes R, Herfindal I, Kohler J, Sæther B-E (2011) Climate, icing, and wild arctic reindeer: past relationships and future prospects. Ecology 92:1917-1923 doi:https://doi.org/10.1890/11-0095.1

Hansen BB et al. (2013) Climate events synchronize the dynamics of a resident vertebrate community in the high Arctic. Science 339:313 doi:10.1126/science.1226766

Heebner NR, Akins JS, Lephart SM, Sell TC (2015) Reliability and validity of an accelerometry based measure of static and dynamic postural stability in healthy and active individuals. Gait and Posture 41:535-539 doi:https://doi.org/10.1016/j.gaitpost.2014.12.009

Heglund NC, Cavagna GA, Taylor CR (1982a) 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. Journal of Experimental Biology 97:41-56

Heglund NC, Fedak MA, Taylor CR, Cavagna GA (1982b) Energetics and mechanics of terrestrial locomotion. IV. Total mechanical energy changes as a function of speed and body size in birds and mammals. Journal of Experimental Biology 97:57

Heinonen AO, Karvones MJ, Ruosteenoja R (1959) The energy expenditure of walking on snow at various depths. Ergonomics 2:389-394 doi:https://doi.org/10.1080/00140135908930455

Henden J-A, Ims RA, Fuglei E, Pedersen ÅØ (2017) Changed Arctic-alpine food web interactions under rapid climate warming: implication for ptarmigan research. Wildlife Biology 2017 doi:10.2981/wlb.00240

Herbin M, Hackert R, Gasc J-P, Renous S (2007) Gait parameters of treadmill versus overground locomotion in mouse. Behavioural Brain Research 181:173-179 doi:https://doi.org/10.1016/j.bbr.2007.04.001

Hill AV (1938) The heat of shortening and the dynamic constants of muscle. Proceedings of the Royal Society of London Series B - Biological Sciences 126:136-195 doi:10.1098/rspb.1938.0050

Höst P (1942) Effect of Light on the Moults and Sequences of Plumage in the Willow Ptarmigan. The Auk 59:388-403 doi:10.2307/4079208

Hoyt DF, Kenagy GJ (1988) Energy Costs of Walking and Running Gaits and Their Aerobic Limits in Golden-Mantled Ground Squirrels. Physiological Zoology 61:34-40 doi:10.1086/physzool.61.1.30163734

Hoyt DF, Taylor RC (1981) Gait and the energetics of locomotion in horses. Nature 292:239-240

Hurlbert SH (1984) Pseudoreplication and the Design of Ecological Field Experiments. Ecological Monographs 54:187-211 doi:10.2307/1942661

Husak JF (2006) Do female collared lizards change field use of maximal sprint speed capacity when gravid? Oecologia 150:339-343 doi:10.1007/s00442-006-0513-1

Husak JF, Fox SF (2006) Field use of maximal sprint speed by collared lizards (*Crotaphytus collaris*): compensation and sexual selection. Evolution 60:1888-1895

Husak JF, Fox SF, Lovern MB, Bussche RAVD (2006) Faster lizards sire more offspring: sexual selection on whole-namial performance. Evolution 60:2122-2130 doi:10.1111/j.0014-3820.2006.tb01849.x

Hutchinson JR, Schwerda D, Famini DJ, Dale RHI, Fischer MS, Kram R (2006) The locomotor kinematics of Asian and African elephants: changes with speed and size. Journal of Experimental Biology 209:3812 doi:10.1242/jeb.02443

Huxley HE (1963) Electron microscope studies on the structure of natural and synthetic protein filaments from striated muscle. Journal of Molecular Biology 7:281-IN230 doi:https://doi.org/10.1016/S0022-2836(63)80008-X

Huxley HE (1969) The mechanism of muscular contraction. Science 164:1356-1366

Irschick DJ, Herrel A, Vanhooydonck B, Huyghe K, Damme Rv (2005) 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 doi:https://doi.org/10.1111/j.0014-3820.2005.tb01807.x

Irschick DJ, Jayne BC (1999) Comparative three-dimensional kinematics of the hindlimb for high-speed bipedal and quadrupedal locomotion of lizards. Journal of Experimental Biology 202:1047-1065

Jansen E et al. (2020) Past perspectives on the present era of abrupt Arctic climate change. Nature Climate Change 10:714-721 doi:10.1038/s41558-020-0860-7

Jenkins FA (1971) Limb posture and locomotion in the Virginia opossum (*Didelphis marsupialis*) and in other non-cursorial mammals. Journal of Zoology 165:303-315 doi:https://doi.org/10.1111/j.1469-7998.1971.tb02189.x

Jindrich DL, Full RJ (2002) Dynamic stabilization of rapid hexapedal locomotion. The Journal of Experimental Biology 205:2803-2823

Jones KA, Godin J-GJ (2010) Are fast explorers slow reactors? Linking personality type and anti-predator behaviour. Proceedings of the Royal Society B: Biological Sciences 277:625-632 doi:10.1098/rspb.2009.1607

Kerdok AE, Biewener AA, McMahon TA, Weyand PG, Herr HM (2002) Energetics and mechanics of human running on surfaces of different stiffnesses. Journal of Applied Physiology 92:469-478 doi:10.1152/japplphysiol.01164.2000

Kilbourne BM, Andrada E, Fischer MS, Nyakatura JA (2016) Morphology and motion: hindlimb proportions and swing phase kinematics in terrestrially locomoting charadriiform birds. The Journal of Experimental Biology 219:1405-1416 doi:https://doi.org/10.1242/jeb.124081

Konow N, Azizi E, Roberts TJ (2012) Muscle power attenuation by tendon during energy dissipation. Proceedings of the Royal Society B: Biological Sciences 279:1108-1113 doi:10.1098/rspb.2011.1435

Kram R, Taylor CR (1990) Energetics of running: a new perspective. Nature 346:265-267 doi:https://doi.org/10.1038/346265a0

Lailvaux SP, Husak JF (2014) The life history of whole-organism performance. The Quarterly Review of Biology 89:285-318 doi:10.1086/678567

Landis WJ, Librizzi JJ, Dunn MG, Silver FH (1995) A study of the relationship between mineral content and mechanical properties of turkey gastrocnemius tendon. Journal of bone and mineral research : the official journal of the American Society for Bone and Mineral Research 10:859-867 doi:10.1002/jbmr.5650100606

Langman VA et al. (1995) Moving cheaply: energetics of walking in the African elephant. The Journal of Experimental Biology 198:629

Langman VA, Rowe MF, Roberts TJ, Langman NV, Taylor CR (2012) Minimum cost of transport in Asian elephants: do we really need a bigger elephant? The Journal of Experimental Biology 215:1509

Lees J, Folkow L, Stokkan KA, Codd J (2013) The metabolic cost of incline locomotion in the Svalbard rock ptarmigan (*Lagopus muta hyperborea*): the effects of incline grade and seasonal fluctuations in body mass. The Journal of Experimental Biology 216:1355-1363 doi:10.1242/jeb.078709

Lees JJ, Folkow LP, Codd JR, Nudds RL (2014a) Seasonal differences in jump performance in the Svalbard rock ptarmigan (*Lagopus muta hyperborea*). Biology Open 3

Lees JJ, Folkow LP, Nudds RL, Codd JR (2014b) The effects of season and sex upon the morphology and material properties of keratin in the Svalbard rock ptarmigan (*Lagopus muta hyperborea*). Journal of Thermal Biology 44:126-130 doi:10.1016/j.jtherbio.2014.01.002

Lees JJ, Nudds R, Stokkan K-A, Folkow L, Codd J (2010) Reduced metabolic cost of locomotion in Svalbard rock ptarmigan (*Lagopus muta hyperborea*) during winter. PloS One 5:e15490 doi:https://doi.org/10.1371/journal.pone.0015490

Lees JJ, Nudds RL, Folkow LP, Stokkan KA, Codd JR (2012a) Understanding sex differences in the cost of terrestrial locomotion. Proceedings of the Royal Society B: Biological Sciences 279:826-832 doi:https://doi.org/10.1098/rspb.2011.1334

Lees JJ, Stokkan K-A, Folkow LP, Codd JR (2012b) Locomotor development in the Svalbard rock ptarmigan (*Lagopus muta hyperborea*). Polar Biology 35:867-874 doi:https://doi.org/10.1007/s00300-011-1131-x

Lejeune TM, Willems PA, Heglund NC (1998) Mechanics and energetics of human locomotion on sand. The Journal of Experimental Biology 201:2071-2080

Li C, Hsieh ST, Goldman DI (2012) Multi-functional foot use during running in the zebra-tailed lizard (*Callisaurus draconoides*). The Journal of Experimental Biology 215:3293 doi:10.1242/jeb.061937

Li C, Zhang T, Goldman DI (2013) A terradynamics of legged locomotion on granular media. Science 339:1408 doi:10.1126/science.1229163

Mace GM, Harvey PH, Clutton-Brock TH, Swingland IR, Greenwood PJ (1983) Vertebrate home-range size and energetics requirements. In: Swingland IR, Greenwood PJ (eds) The ecology of animal movement. Oxford University Press, New York,

Maloiy GMO, Rugangazi BM, Rowe MF (2009) Energy expenditure during level locomotion in large desert ungulates: the one-humped camel and the domestic donkey. Journal of Zoology 277:248-255 doi:10.1111/j.1469-7998.2008.00535.x

Maresh JL et al. (2015) Summing the strokes: energy economy in northern elephant seals during large-scale foraging migrations. Movement Ecology 3:22 doi:10.1186/s40462-015-0049-2

Marmol-Guijarro AC, Nudds RL, Marrin JC, Folkow LP, Codd JR (2019) Terrestrial locomotion of the Svalbard rock ptarmigan: comparing field and laboratory treadmill studies. Scientific Reports 9:11451 doi:https://doi.org/10.1038/s41598-019-47989-6

Marsh RL, Ellerby DJ, Carr JA, Henry HT, Buchanan CI (2004) Partitioning the energetics of walking and running: Swinging the limbs is expensive. Science 303:80

Marsh RL, Ellerby DJ, Henry HT, Rubenson J (2006) The energetic costs of trunk and distal-limb loading during walking and running in guinea fowl *Numida meleagris*: I. Organismal metabolism and biomechanics. The Journal of Experimental Biology 209:2050-2063 doi:10.1242/jeb.02226

Matson A, Konow N, Miller S, Konow PP, Roberts TJ (2012) Tendon material properties vary and are interdependent among turkey hindlimb muscles. Journal of Experimental Biology 215

Mattfeld GF (1974) The energetics of winter foraging by white-tailed deer: A perspective on winter concentration. State university of New York

Mazouchova N, Umbanhowar PB, Goldman DI (2013) Flipper-driven terrestrial locomotion of a sea turtle-inspired robot. Bioinspiration & Biomimetics 8:026007 doi:10.1088/1748-3182/8/2/026007

McMahon TA, Cheng GC (1990) The mechanics of running: How does stiffness couple with speed? Journal of Biomechanics 23:65-78 doi:https://doi.org/10.1016/0021-9290(90)90042-2

McMahon TA, Greene PR (1979) The influence of track compliance on running. Journal of Biomechanics 12:893-904 doi:https://doi.org/10.1016/0021-9290(79)90057-5

McMahon TA, Valiant G, Frederick EC (1987) Groucho running. Journal of Applied Physiology 62:2326

Mochon S, McMahon TA (1980) Ballistic walking: an improved model. Mathematical Biosciences 52:241-260 doi:https://doi.org/10.1016/0025-5564(80)90070-X

Mortensen A, Blix AS (1985) Seasonal changes in the effects of starvation on metabolic rate and regulation of body weight in Svalbard rock ptarmigan. Ornis Scandinavica 16:20-24

Mortensen A, Unander S, Kolstad M, Blix AS (1983) Seasonal changes in body composition and crop content of Spitzbergen ptarmigan *Lagopus mutus hyperboreus*. Ornis Scandinavica 14:144-148 doi:https://doi.org/10.2307/3676018

Murray DL, Boutin S (1991) The influence of snow on lynx and coyote movements: does morphology affect behavior? Oecologia 88:463-469 doi:https://doi.org/10.1007/bf00317707

Nelson RC, Dillman CJ, Lagasse P, Bickett P (1972) Biomechanics of overground versus treadmill running. Medicine and Science in Sports 4:232-240

Nicot F (2004) Constitutive modelling of snow as a cohesive-granular material. Granular Matter 6:47-60 doi:10.1007/s10035-004-0159-9

Nudds RL, Folkow LP, Lees JJ, Tickle PG, Stokkan KA, Codd JR (2011) Evidence for energy savings from aerial running in the Svalbard rock ptarmigan (*Lagopus muta hyperborea*). Proceedings of the Royal Society B: Biological Sciences 278:2654-2661 doi:https://doi.org/10.1098/rspb.2010.2742

Nudds RL, Gardiner JD, Tickle PG, Codd JR (2010) Energetics and kinematics of walking in the barnacle goose (*Branta leucopsis*). Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology 156:318-324 doi:https://doi.org/10.1016/j.cbpa.2010.01.023

Owens IPF, Hartley IR (1998) Sexual dimorphism in birds: why are there so many different forms of dimorphism? Proceedings of the Royal Society of London Series B: Biological Sciences 265:397-407 doi:10.1098/rspb.1998.0308

Pagano AM et al. (2018) High-energy, high-fat lifestyle challenges an Arctic apex predator, the polar bear. Science 359:568

Pandolf KB, Haisman MF, Goldman RF (1976) Metabolic Energy Expenditure and Terrain Coefficients for Walking on Snow. Ergonomics 19:683-690 doi:https://doi.org/10.1080/00140137608931583

Parker KL, Robbins CT, Hanley TA (1984) Energy expenditures for locomotion by mule deer and elk. Journal of Wildlife Management 48:474-488 doi:https://doi.org/10.2307/3801180

Pedersen ÅØ, Fuglei E, Hörnell-Willebrand M, Biuw M, Jepsen JU (2017) Spatial distribution of Svalbard rock ptarmigan based on a predictive multi-scale habitat model. Wildlife Biology 2017 doi:10.2981/wlb.00239

Pedersen ÅØ, Jepsen JU, Yoccoz NG, Fuglei E (2007) Ecological correlates of the distribution of territorial Svalbard rock ptarmigan (*Lagopus muta hyperborea*). Canadian Journal of Zoology 85:122-132 doi:10.1139/z06-197

Pedersen ÅØ, Overrein Ø, Unander S, Fuglei E (2005) Svalbard Rock Ptarmigan (*Lagopus mutus hyperboreus*) – a status report. Norsk Polarinsitutt 125

Peter JB, Barnard RJ, Edgerton VR, Gillespie CA, Stempel KE (1972) Metabolic profiles of three fiber types of skeletal muscle in guinea pigs and rabbits. Biochemistry 11:2627-2633

Peterson CC, Husak JF (2006) Locomotor performance and sexual selection: individual variation in sprint speed of collared LIzards (*Crotaphytus collaris*). Copeia 2006:216-224 doi:10.1643/0045-8511(2006)6[216:LPASSI]2.0.CO;2

Pollock CM, Shadwick RE (1994) Relationship between body mass and biomechanical properties of limb tendons in adult mammals. The American Journal of Physiology 266:R1016-R1021

Pontzer H (2007) Predicting the energy cost of terrestrial locomotion: a test of the LiMb model in humans and quadrupeds. The Journal of Experimental Biology 210:484 doi:10.1242/jeb.02662

Pontzer H (2016) A unified theory for the energy cost of legged locomotion. Biology Letters 12:20150935 doi:10.1098/rsbl.2015.0935

Pozzanghera CB, Sivy KJ, Lindberg MS, Prugh LR (2016) Variable effects of snow conditions across boreal mesocarnivore species. Canadian Journal of Zoology 94:697-705 doi:10.1139/cjz-2016-0050

Qiao M, Hughes M, Jindrich DL (2012) Response to medio-lateral perturbations of human walking and running. Paper presented at the American Society of Biomechanics Annual Meeting, Gainsville, Florida,

Qiao M, Jindrich DL (2014) Compensations during unsteady locomotion. Integrative and Comparative Biology 54:1109-1121 doi:https://doi.org/10.1093/icb/icu058

Ramaswamy SS, Dua GL, Raizada GP, Dimri GP, Viswanathan KR, Madhaviah J, Srivastava TN (1966) Effects of looseness of snow on energy expenditure in marching on snow-covered ground. Journal of Applied Physiology 21:1747-1749

Redfern MS et al. (2001) Biomechanics of slips. Ergonomics 44:1138-1166 doi:10.1080/00140130110085547

Reierth E, Van't Hof TJ, Stokkan KA (1999) Seasonal and daily variations in plasma melatonin in the high-arctic Svalbard ptarmigan (*Lagopus mutus hyperboreus*). Journal of Biological Rhythms 14:314-319 doi:10.1177/074873099129000731

Reilly SM, McElroy EJ, Biknevicius AR (2007) Posture, gait and the ecological relevance of locomotor costs and energy-saving mechanisms in tetrapods. Zoology 110:271-289 doi:https://doi.org/10.1016/j.zool.2007.01.003

Reinhardt L, Weihmann T, Blickhan R (2009) Dynamics and kinematics of ant locomotion: do wood ants climb on level surfaces? The Journal of Experimental Biology 212:2426 doi:10.1242/jeb.026880

Riley PO, Dicharry JAY, Franz J, Croce UD, Wilder RP, Kerrigan DC (2008) A kinematics and kinetic comparison of overground and treadmill running. Medicine and Science in Sports and Exercise 40:1093-1100 doi:https://doi.org/10.1249/mss.0b013e3181677530

Riley PO, Paolini G, Della Croce U, Paylo KW, Kerrigan DC (2007) A kinematic and kinetic comparison of overground and treadmill walking in healthy subjects. Gait and Posture 26:17-24 doi:https://doi.org/10.1016/j.gaitpost.2006.07.003

Ríos-Saldaña CA, Delibes-Mateos M, Ferreira CC (2018) Are fieldwork studies being relegated to second place in conservation science? Global Ecology and Conservation 14:e00389 doi:https://doi.org/10.1016/j.gecco.2018.e00389

Roberts TJ (2016) Contribution of elastic tissues to the mechanics and energetics of muscle function during movement. The Journal of Experimental Biology 219:266-275 doi:10.1242/jeb.124446

Roberts TJ, Azizi E (2010) The series-elastic shock absorber: tendons attenuate muscle power during eccentric actions. Journal of applied physiology (Bethesda, Md : 1985) 109:396-404 doi:10.1152/japplphysiol.01272.2009

Roberts TJ, Kram R, Weyand PG, Taylor CR (1998) Energetics of bipedal running. I. Metabolic cost of generating force. Journal of Experimental Biology 201:2745

Roberts TJ, Marsh RL, Weyand PG, Taylor RC (1997) Muscular force in running turkeys: The economy of minimizing work. Science 275:1113-1115 doi:10.1126/science.275.5303.1113

Roberts TJ, Scales Ja (2002) Mechanical power output during running accelerations in wild turkeys. The Journal of Experimental Biology 205:1485-1494

Rose KA, Codd JR, Nudds RL (2016a) Differential sex-specific walking kinematics in leghorn chickens (*Gallus gallus domesticus*) selectively bred for different body size. The Journal of Experimental Biology 44:jeb.139709 doi:https://doi.org/10.1242/jeb.139709

Rose KA, Nudds RL, Butler PJ, Codd JR (2015a) Sex differences in gait utilization and energy metabolism during terrestrial locomotion in two varieties of chicken (*Gallus gallus domesticus*) selected for different body size. Biology Open:1-10 doi:https://doi.org/10.1242/bio.013094

Rose KA, Nudds RL, Codd JR (2015b) Intraspecific scaling of the minimum metabolic cost of transport in leghorn chickens (Gallus gallus domesticus): links with limb kinematics, morphometrics and posture. The Journal of Experimental Biology 218:1028-1034 doi:10.1242/jeb.111393

Rose KA, Nudds RL, Codd JR (2016b) Variety, sex and ontogenetic differences in the pelvic limb muscle architectural properties of leghorn chickens (*Gallus gallus domesticus*) and their links with locomotor performance. Journal of Anatomy 228:952-964 doi:https://doi.org/10.1111/joa.12460

Rose KA, Tickle PG, Lees JJ, Stokkan K-A, Codd JR (2014) Neither season nor sex affects the cost of terrestrial locomotion in a circumpolar diving duck: the common eider (*Somateria mollissima*). Polar Biology 37:879-889 doi:10.1007/s00300-014-1488-8

Rubenson J, Heliams DB, Lloyd DG, Fournier PA (2004) Gait selection in the ostrich: mechanical and metabolic characteristics of walking and running with and without an aerial phase. Proceedings of the Royal Society of London Series B: Biological Sciences 271:1091-1099 doi:https://doi.org/10.1098/rspb.2004.2702

Sapir N, Wikelski M, McCue MD, Pinshow B, Nathan R (2010) Flight modes in migrating european bee-eaters: heart rate may indicate low metabolic rate during soaring and gliding. PloS One 5:e13956 doi:10.1371/journal.pone.0013956

Sawicki GS, Sheppard P, Roberts TJ (2015) Power amplification in an isolated muscle-tendon is load dependent. The Journal of Experimental Biology 218:3700-3709 doi:10.1242/jeb.126235

Schiller L, Seibel A, Schlattmann J (2019) Toward a gecko-inspired, climbing soft robot. Frontiers in Neurorobotics 13:106

Sellers WI, Manning PL (2007) Estimating dinosaur maximum running speeds using evolutionary robotics. Proceedings of the Royal Society B: Biological Sciences 274:2711-2716 doi:10.1098/rspb.2007.0846

Sellers William I, Cain Gemma M, Wang W, Crompton Robin H (2005) Stride lengths, speed and energy costs in walking of *Australopithecus afarensis*: using evolutionary robotics to predict locomotion of early human ancestors. Journal of The Royal Society Interface 2:431-441 doi:10.1098/rsif.2005.0060

Seyfarth A, Geyer H, Herr H (2003) Swing-leg retraction: a simple control model for stable running. The Journal of Experimental Biology 206:2547-2555 doi:https://doi.org/10.1242/jeb.00463.

Shepard ELC, Wilson RP, Rees WG, Grundy E, Lambertucci SA, Vosper SB (2013) Energy landscapes shape animal movement ecology. The American Naturalist 182:298-312 doi:10.1086/671257

Silver FH, Christiansen D, Snowhill PB, Chen Y, Landis WJ (2000) The role of mineral in the storage of elastic energy in turkey tendons. Biomacromolecules 1:180-185 doi:10.1021/bm9900139

Steel EA, Kennedy MC, Cunningham PG, Stanovick JS (2013) Applied statistics in ecology: common pitfalls and simple solutions. Ecosphere 4:art115 doi:https://doi.org/10.1890/ES13-00160.1

Steen JB, Unander S (1985) Breeding biology of the Svalbard rock ptarmigan *Lagopus mutus hyperboreus*. Ornis Scandinavica 16:191-197 doi:https://doi.org/10.2307/3676630

Stevenson R, Dalton HA, Erasmus M (2019) Validity of micro-data loggers to determine walking activity of turkeys and effects on turkey gait. Frontiers in Veterinary Science 5:319

Stokkan K-A (1979) Testosterone and daylength-dependent development of comb size and breeding plumage of male willow ptarmigan (*Lagopus lagopus lagopus*). The Auk 96:106-115 doi:10.1093/auk/96.1.106

Stokkan KA, Mortensen A, Blix AS (1986) Food intake, feeding rhythm, and body mass regulation in Svalbard rock ptarmigan. The American Journal of Physiology 251:R264-R267

Switalski TA (2003) Coyote foraging ecology and vigilance in response to gray wolf reintroduction in Yellowstone National Park. Canadian Journal of Zoology 81:985-993 doi:10.1139/z03-080

Takeda R, Tadano S, Natorigawa A, Todoh M, Yoshinari S (2009) Gait posture estimation using wearable acceleration and gyro sensors. Journal of Biomechanics 42:2486-2494 doi:https://doi.org/10.1016/j.jbiomech.2009.07.016

Taylor CR, Heglund NC, McMahon TA, Looney TR (1980) Energetic cost of generating muscular force during running: a comparison of large and small animals. Journal of Experimental Biology 86:9-18

Telfer ES, Kelsall JP (1984) Adaptation of some large North American mammals for survival in snow. Ecology 65:1828-1834 doi:10.2307/1937779

Thelen DG, Chumanov ES, Best TM, Swanson SC, Heiderscheit BC (2005) Simulation of biceps femoris musculotendon mechanics during the swing phase of sprinting. Medicine and Science in Sports and Exercise 37:1931-1938 doi:10.1249/01.mss.0000176674.42929.de

Thulborn RA (1984) Preferred gaits of bipedal dinosaurs. Alcheringa: An Australasian Journal of Palaeontology 8:243-252 doi:10.1080/03115518408618947

Tickle PG, Lean SC, Rose KA, Wadugodapitiya AP, Codd JR (2013) The influence of load carrying on the energetics and kinematics of terrestrial locomotion in a diving bird. Biol Open 2:1239-1244 doi:10.1242/bio.20135538

Tickle PG, Richardson MF, Codd JR (2010) Load carrying during locomotion in the barnacle goose (*Branta leucopsis*): The effect of load placement and size. Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology 156:309-317 doi:https://doi.org/10.1016/j.cbpa.2010.01.022

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the Descent of Man. Aldine, Chicago, pp 136-179

Turner ML, Falkingham PL, Gatesy SM (2020) It's in the loop: shared sub-surface foot kinematics in birds and other dinosaurs shed light on a new dimension of fossil track diversity. Biology Letters 16:20200309 doi:10.1098/rsbl.2020.0309

Unander S, Pedersen ÅØ, Soininen EM, Descamps S, Hörnell-Willebrand M, Fuglei E (2016) Populations on the limits: survival of Svalbard rock ptarmigan. Journal of Ornithology 157:407-418 doi:10.1007/s10336-015-1282-6

Unander S, Steen JB (1985) Behaviour and Social Structure in Svalbard Rock Ptarmigan *Lagopus mutus hyperboreus*. Ornis Scandinavica (Scandinavian Journal of Ornithology) 16:198-204 doi:https://doi.org/10.2307/3676631

Usherwood JR (2013) Constraints on muscle performance provide a novel explanation for the scaling of posture in terrestrial animals. Biology Letters 9:20130414 doi:https://doi.org/10.1098/rsbl.2013.0414

Van Ingen Schenau GJ (1980) Some fundamental aspects of the biomechanics of overground versus treadmill locomotion. Medicine and Science in Sports and Exercise 12

Vásquez RA, Ebensperger LA, Bozinovic F (2002) The influence of habitat on travel speed, intermittent locomotion, and vigilance in a diurnal rodent. Behavioral Ecology 13:182-187 doi:10.1093/beheco/13.2.182

Wall J, Douglas-Hamilton I, Vollrath F (2006) Elephants avoid costly mountaineering. Current Biology 16:R527-R529 doi:10.1016/j.cub.2006.06.049

Wank V, Frick U, Schmidtbleicher D (1998) Kinematics and electromyography of lower limb muscles in overground and treadmill running. International Journal of Sports Medicine 19:455-461 doi:https://doi.org/10.1055/s-2007-971944

Watson RR, Rubenson J, Coder L, Hoyt DF, Propert MWG, Marsh RL (2011) Gait-specific energetics contributes to economical walking and running in emus and ostriches. Proceedings of the Royal Society B: Biological Sciences 278:2040-2046 doi:https://doi.org/10.1098/rspb.2010.2022

Whitehead CC (2004) Overview of bone biology in the egg-laying hen. Poultry Science 83:193-199 doi:https://doi.org/10.1093/ps/83.2.193

Whiteman JP, Buskirk SW (2013) Footload influences wildlife use of compacted trails in the snow. Wildlife Biology 19:156-164 doi:https://doi.org/10.2981/12-112

Williams TM, Dobson GP, Mathieu-Costello O, Morsbach D, Worley MB, Phillips JA (1997) Skeletal muscle histology and biochemistry of an elite sprinter, the African cheetah. Journal of Comparative Physiology B 167:527-535 doi:10.1007/s003600050105

Williams TM et al. (2014) Instantaneous energetics of puma kills reveal advantage of felid sneak attacks. Science 346:81 doi:10.1126/science.1254885

Wilson AM et al. (2018) Biomechanics of predator–prey arms race in lion, zebra, cheetah and impala. Nature 554:183 doi:10.1038/nature25479
https://www.nature.com/articles/nature25479#supplementary-information

Wilson AM, Lowe JC, Roskilly K, Hudson PE, Golabek KA, McNutt JW (2013) Locomotion dynamics of hunting in wild cheetahs. Nature 498:185-189 doi:https://doi.org/10.1038/nature12295

Wilson RP, Quintana F, Hobson VJ (2012) Construction of energy landscapes can clarify the movement and distribution of foraging animals. Proceedings of the Royal Society B: Biological Sciences 279:975-980 doi:10.1098/rspb.2011.1544

Wilson RP, Shepard ELC, Liebsch N (2008) Prying into the intimate details of animal lives: use of a daily diary on animals. Endangered Species Research 4:123-137

Wilson RP, White CR, Quintana F, Halsey LG, Liebsch N, Martin GR, Butler PJ (2006) Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. Journal of Animal Ecology 75:1081-1090 doi:10.1111/j.1365-2656.2006.01127.x

Wilson RS, Husak JF, Halsey LG, Clemente CJ (2015) Predicting the movement speeds of animals in natural environments. Integrative and Comparative Biology 55:1125-1141 doi:10.1093/icb/icv106

Yoccoz NG, Ims RA (1999) Demography of small mammals in cold regions: the importance of environmental variability. Ecological Bulletins:137-144

Zamparo P, Perini R, Orizio C, Sacher M, Ferretti G (1992) The energy cost of walking or running on sand. European Journal of Applied Physiology and Occupational Physiology 65:183-187 doi:10.1007/BF00705078

Zhang J-X, Lu J-J (1999) Feeding ecology of two wintering geese species at Poyang lake, China. Journal of Freshwater Ecology 14:439-445 doi:10.1080/02705060.1999.9663702

Zhang R et al. (2017) Plantar pressure distribution of ostrich during locomotion on loose sand and solid ground. PeerJ 5:e3613 doi:10.7717/peerj.3613