Understanding sex differences in the cost of terrestrial locomotion

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Little is known regarding the physiological consequences of the behavioural and morphological differences that result from sexual selection in birds. Male and female Svalbard rock ptarmigans (Lagopus muta hyperborea) exhibit distinctive behavioural differences during the breeding season. In particular, males continuously compete for and defend territories in order to breed successfully, placing large demands on their locomotor system. Here, we demonstrate that male birds have improved locomotor performance compared with females, showing both a lower cost of locomotion (CoL) and a higher top speed. We propose that the observed sex differences in locomotor capability may be due to sexual selection for improved male performance. While the mechanisms underlying these energetic differences are unclear, future studies should be wary when pooling male and female data.

Keywords: sexual selection; sexual dimorphism; energetics; evolution; locomotion

1. INTRODUCTION

It is widely accepted that intra- and intersexual selection have led to the evolution of sexual dimorphism. Sexual dimorphism in birds can be striking: in some species, males are substantially larger than females [1]; however, reverse sexual dimorphism, where the female is larger, also occurs [2]. Sexual selection can also lead to differences in plumage; for example, male birds of paradise (family: Paradisaeidae) often have brightly coloured, ornate tail feathers in comparison with the more drab females [3]. The degree of sexual dimorphism is strongly influenced by the mating system and parental care [4]. Dimorphism mostly occurs in species in which females are the limiting resource on reproduction and provide parental care, while males must compete for the opportunity to mate with them [4]. Monogamous species, which exhibit bi-parental care, tend to exhibit little size dimorphism, although exceptions do occur [5,6].

Despite the extensive documentation on sexual dimorphism in birds and a relatively good understanding of its evolution, little is known about how dimorphism influences physiology. Energy used must be balanced by energy intake, and so knowledge of the energetic cost is critical in determining the time that can be apportioned to behaviours such as foraging patterns and parental investment, which ultimately influence fitness [7,8].

Given the large differences between male and female birds driven by sexual selection, it is perhaps surprising that many previous studies investigating avian energetics have not discriminated between male and female data [9–16]. Being metabolically costly, locomotion is a significant contributor to the energy balance of birds, and any change to the cost of locomotion (CoL, expressed as any measure of metabolic cost—i.e. $\dot{V}_O_2$ or $W$—per unit of body mass) will affect the energy available for other activities, and therefore the daily energy budget of the birds [17]. For example, in one detailed study, terrestrial locomotion alone accounted for around 60 per cent of daily energy expenditure [18]. Understanding the factors that influence the terrestrial CoL, such as body size [19,20], is important, as most birds spend some portion of their lives restricted to terrestrial locomotion, particularly during behaviours subject to sexual selection, such as lekking and caring for young. Although absolute energy expenditure increases with body mass, the mass-specific cost of transport (CoT, metabolic cost per unit of body mass per unit distance) decreases with size across a large range of bipedal and quadrupedal species [13,15,19,20]. While the exact nature of the relationship is contentious [21], body size profoundly influences energy expenditure during locomotion. The reduction in CoT with size is thought to be a result of the increased time available to generate force during the relatively longer strides of animals of increasing size, which allows more efficient, slow muscle fibres to be used [22]. Additional-ly, the more erect postures that are associated with increased size improve mechanical advantage of the limbs and may result in improved efficiency of locomotion [23].

Despite numerous investigations into avian terrestrial locomotor energetics [9,13,15,16,24–26], only one has focused on sex differences [27]. In this case, male and female domestic fowls exhibited the same mass-specific CoL, despite males being 56 per cent heavier than females. Females, however, were not able to achieve the maximum sustainable running speeds of males, in congruence with some data from humans [28–30] and other vertebrates [31–33]. Males are thought to run faster as they must actively search and compete for mates.

Svalbard rock ptarmigans (Lagopus muta hyperborea) are terrestrial phasianid birds found on the Arctic archipelago of Svalbard. Although capable of flight, these birds spend much of their time locomoting terrestrially. In particular, during the breeding season, males defend...
territories of up to 50 hectares from rival males throughout the 24 h period. Male ptarmigans have previously been shown to be excellent athletes and demonstrate an energetic saving upon the onset of aerial running [34]. Male birds also reduce the CoL (at the expense of speed) during winter fattening [35]. Male and female ptarmigans are similar in appearance and have similar body masses during summer [36]. Females are responsible for brooding, whereas parental care from males ranges from little to none, depending on the time of breeding [37]. In addition to ornamental cues (suprarbital comb), female ptarmigans may rely on other indicators of fitness such as motor skills in order to pick a mate [38].

Here, we investigate differences in the metabolic CoL in male and female Svalbard rock ptarmigans. We hypothesize that male ptarmigans have adaptations for efficient locomotion that manifest in differences in the energetic CoL when compared with female birds.

2. MATERIAL AND METHODS

(a) Animals

Adult male \((n = 6, \text{ mean body mass } \pm \text{s.e. } = 501.06 \pm 19.04 \text{ g})\) and female \((n = 5, \text{ mean body mass } = 476.7 \pm 19.9 \text{ g})\) Svalbard rock ptarmigans were housed at the Department of Arctic and Marine Biology, University of Tromsø, Norway (previously used by Nudds et al. [34]). Birds had ad libitum access to food and water, and were housed in wooden cages with wire mesh floors. Under these conditions, the birds undergo their natural seasonal physiological changes [39,40]. Experiments were conducted during July. Birds were not fasted prior to metabolic measurements and were trained to run on a treadmill for three months prior to data collection. The same females were used in both the summer and winter trials, to determine whether they also showed a seasonal difference in the CoL, as previously found in males [35].

(b) Energetics and kinematics

Rates of \(V_{\text{O}_2}\) consumption \((\dot{V}_{\text{O}_2}, \text{ ml min}^{-1} \text{ Kg}^{-1})\) and \(CO_2\) production \((\dot{V}_{\text{CO}_2}, \text{ ml min}^{-1} \text{ kg}^{-1})\) were measured using an open-flow respirometry system. The system consisted of a Perspex box \((30 \times 26 \times 61.7 \text{ cm})\) mounted onto a treadmill (Bremshey Trail Sport, Finland). Air was pulled through the box at flow rates \((\text{FRs})\) of 52 l min\(^{-1}\) (male summer and female winter trials) and 52.8 l min\(^{-1}\) (female summer trials). The flow was then sub-sampled into a carboy at 6 l min\(^{-1}\) (Bremshey Trail Sport, Finland). Air was pulled through the Perspex box (30 × 26 × 61.7 cm) mounted onto a treadmill (Bremshey Trail Sport, Finland). Air was pulled through the box at flow rates (FRs) of 52 l min\(^{-1}\) (male summer and female winter trials) and 52.8 l min\(^{-1}\) (female summer trials). The flow was then sub-sampled into a carboy at 6 l min\(^{-1}\) and further sub-sampled at 0.115 l min\(^{-1}\) for gas analysis. Water vapour pressure (WVP) and relative humidity measurements were recorded using an RH300 (Sable Systems International, Las Vegas, NV, USA). Water was then scrubbed using calcium chloride (2–6 mm granular; Merck, Darmstadt, Germany). Then the sample was drawn through the Foxbox-C (Sable Systems International). \(CO_2\) was recorded before being scrubbed using soda lime with indicator (2–5 mm granular; Sigma Aldrich, Steinheim, Germany) and finally \(O_2\) was measured. Prior to calculation of \(\dot{V}_{\text{O}_2}\) and \(\dot{V}_{\text{CO}_2}\), the primary FR of the system was converted to a corrected flow rate \((\text{FR}_c)\), taking into account measured barometric pressure (BP) and WVP values, using equation (2.1) (eqn 8.6 in [41]),

\[
\text{FR}_c = \frac{\text{FR} \times (\text{BP} - \text{WVP})}{\text{BP}},
\]

\((2.1)\)

Proc. R. Soc. B (2012) and \(\dot{V}_{\text{O}_2}\) and \(\dot{V}_{\text{CO}_2}\) were calculated using equations (2.2) and (2.3), respectively [41]:

\[
\dot{V}_{\text{O}_2} = \frac{\text{FR}_c(\Delta \dot{V}_{\text{O}_2})}{(1 - 0.2095)},
\]

\((2.2)\)

and

\[
\dot{V}_{\text{CO}_2} = \frac{\text{FR}_c(\Delta \dot{V}_{\text{CO}_2}) - (0.0004(\dot{V}_{\text{O}_2}))}{(1 - 0.0004)},
\]

\((2.3)\)

\(\Delta O_2\) and \(\Delta CO_2\) are the differences between excurrent and background \(O_2\) and \(CO_2\) concentrations, respectively. The respiratory quotients (RQs) of exercising birds were calculated from these values as \(\dot{V}_{\text{CO}_2}/\dot{V}_{\text{O}_2}\), and used to calculate the rate of energy metabolism \((W)\) [42]. These values were then converted to mass-specific metabolic power consumption \((P_{\text{met}}; \text{W Kg}^{-1})\), representing the CoL. The accuracy of the respirometry set-up \((\pm 2\% \text{ across all treadmill speeds})\) was validated using a \(N_2\) dilution test [34,43,44].

For the experiments, birds were exercised upon the treadmill at randomized speeds between 0.22 and 1.5 ms\(^{-1}\). The maximum speed attainable by females was 1.5 ms\(^{-1}\), although males were able to run up to 2.25 ms\(^{-1}\). Birds were kept in the respirometry chamber until a steady resting trace was obtained, defined by the \(O_2\) trace remaining at a plateau for at least 2 min. Data were then collected for each bird at a given speed until a stable gas reading was obtained. Kinematic data were obtained from high-speed video (Handycam HDR-XR520, Sony, Japan) at a frame rate of 100 Hz. Birds were filmed laterally over 5–10 strides and the footage was used to calculate duty factor \((DF)\), stride frequency \((f_{\text{stride}})\), stride length \((l_{\text{stride}})\), and the duration of the swing and stance phases \((t_{\text{swing}}; t_{\text{stance}}\) respectively) using TRACKER software v. 2.6 (Open Source Physics), in which the left foot was tracked over 5–10 strides at a stable speed. All birds were rested for 5–10 min between speeds within a trial, subjected to no more than four speeds per trial and given a rest day between trials.

(c) Statistical analyses

Potential differences in the metabolic cost of walking/running and kinematics between sexes across all speeds \((U)\) were investigated using ANCOVA. First, both the slopes and intercepts were tested for differences. If the interaction term \((\text{gender} \times U)\) was non-significant indicating similar slopes, it was removed from the ANCOVA and the ANCOVA was rerun assuming parallel lines (similar slopes), and hence testing for a difference only in the intercepts. All statistical analyses were conducted using the statistics toolbox in MATLAB R2010a (The MathWorks, Inc., Natick, MA, USA). Means for the energetics and leg length data are displayed as \(\pm\text{s.e.}\) and those for the kinematics as \(\pm\text{s.d.}\) because the standard errors are too small to be visible when graphed.

3. RESULTS

(a) Energetics

An ANCOVA showed that the slope of the relationship between \(\dot{V}_{\text{O}_2}\) and \(U\) was common \((14.542)\) for males and females \((\text{gender} \times U; F_{1,8} = 1.38, \text{ } p = 0.273)\). \(\dot{V}_{\text{O}_2}\) increased with increasing \(U\), but was 12.7 ml \text{min}^{-1}\text{kg}^{-1} higher across all speeds (figure 1a) in females \((\text{gender}; F_{1,0} = 24.29, r^2 = 0.42, \text{ } p < 0.001; U; F_{1,0} = 24.18, r^2 = 0.42, \text{ } p < 0.001)\). The CoL, in terms of \(P_{\text{met}}\) showed a similar pattern to \(\dot{V}_{\text{O}_2}\) across speeds. The incremental increase in \(P_{\text{met}}\) with increasing \(U\) was similar.
Figure 1. The mass-specific rate of oxygen consumption ($V_{O_2}$) and the mass-specific power consumption ($P_{net}$) plotted against speed for males (squares and black dashed lines) and females (circles and solid lines). The lines fitted through the data are derived from the ANCOVA output, and are ($a$) $V_{O_2} = 46.296 + 14.542U$ for males and $V_{O_2} = 58.959 + 14.542U$ for females, and ($b$) $P_{net} = 15.368 + 5.811U$ for males and $P_{net} = 20.514 + 5.811U$ for females.

The ANCOVA output was divided by (5.811) for both males and females (gender: $F_{1,8} = 2.02$, $p = 0.193$). $P_{net}$ increased with $Fr$, and was 4.09 W kg$^{-1}$ higher in females than males across all speeds (gender x $U$: $F_{1,8} = 18.66$, $r^2 = 0.31$, $p = 0.002$; $U$: $F_{1,9} = 31.69$, $r^2 = 0.53$, $p < 0.001$); the equations describing the relationship between $P_{net}$ and $Fr$ derived from the ANCOVA are $P_{net} = 5.464 + 18.032Fr$ for males and $P_{net} = 5.464 + 22.123Fr$ for females. Therefore, size differences in leg morphology did not appear to account for the disparity in the CoL.

To test whether female ptarmigans undergo the energetic savings observed in males during the winter [35], summer and winter female $P_{net}$ data were compared. The incremental increase in $P_{net}$ with $U$ was similar (common slope = 5.86) for both summer and winter females (season x $U$: $F_{1,8} = 0.14$, $p = 0.72$). Likewise, the cost of $P_{net}$ at any given speed did not differ between winter and summer birds, with $P_{net}$ increasing with increasing $U$ (season: $F_{1,9} = 0.82$, $r^2 = 0.024$, $p = 0.39$; $U$: $F_{1,9} = 23.72$, $r^2 = 0.71$, $p < 0.001$). Female birds do not show a reduced $P_{net}$ during the winter.

(b) Kinematics
DF decreased with $U$ (figure 2a) and the relationship between the two variables differed between sexes (gender: $F_{1,8} = 0.79$, $r^2 = 0.01$, $p = 0.400$; $U$: $F_{1,8} = 518.36$, $r^2 = 0.96$, $p < 0.001$; gender x $U$: $F_{1,8} = 11.38$, $r^2 = 0.02$, $p = 0.010$), with DF higher in males at slower $U$ (less than 1 ms$^{-1}$) and higher in females at faster $U$ (greater than 1 ms$^{-1}$).

A similar (common slope = 0.228) incremental increase in $f_{stance}$ with increasing $U$ (figure 2b) was found in both sexes (gender x $U$: $F_{1,8} = 0.45$, $r^2 < 0.01$, $p = 0.523$), but was 0.13 m longer in males than females across all speeds, and was positively correlated with $U$ (gender: $F_{1,8} = 10.98$, $r^2 = 0.02$, $p = 0.099$; $U$: $F_{1,8} = 437.71$, $r^2 = 0.96$, $p < 0.001$). Again, the slope of the relationship between $f_{stance}$ and $U$ was similar (1.444) for both sexes (gender x $U$: $F_{1,8} = 0.22$, $r^2 < 0.01$, $p = 0.654$). $f_{stance}$ increased linearly with $U$ (figure 2c) and was similar in males and females across all speeds (gender: $F_{1,8} = 16.90$, $r^2 = 0.04$, $p = 0.003$; $U$: $F_{1,9} = 404.97$, $r^2 = 0.94$, $p < 0.001$). $f_{stance}$ decreases curvilinearly with increasing $U$ and was similar for both sexes across all speeds (figure 2d). Previous work has indicated that $f_{swing}$ does not differ with speed in male Ptarmigan [34] and the data were similar here for both sexes. An ANOVA confirmed that $f_{swing}$ was of similar duration in females (0.143 ± 0.006 s) and males (0.152 ± 0.010 s) ($F_{1,10} = 3.46$, $r^2 = 0.26$, $p = 0.093$).
4. DISCUSSION

During the breeding season, to ensure their reproductive success, males defend territories of up to 50 hectares from rival males [37]. This involves undertaking energetically costly pursuits with other males to defend their territory and maximize breeding opportunities, while still maintaining foraging activity [37]. Males with improved locomotor performance may be at an advantage, being able to defend larger territories, potentially improving their reproductive success. Indeed, the very ability of males to persistently defend their territories may be a criterion by which they are selected by females [5,46]. The finding that males have a lower CoL compared with females is therefore consistent with the notion of sexual selection-driven locomotor dimorphism [47].

The present data are the first to reveal a sex difference in the metabolic cost of terrestrial locomotion in a bird, and the differences between the sexes in this study are pronounced. Female ptarmigans have a higher metabolic CoL than male birds. This elevated cost differs from findings in the only comparable avian study, in which the CoL was the same between the sexes, despite males being 56 per cent heavier than females [27]. Male ptarmigans have previously been shown to switch from compliant to aerial running between 1.5 and 1.67 m s$^{-1}$, and can reach speeds in excess of 2 m s$^{-1}$ [34]. In contrast, females are not capable of aerial running and have a maximum achievable speed of 1.5 m s$^{-1}$. Similar findings have been observed in domestic fowl; the maximum sustainable speed of males (2.7 m s$^{-1}$) was almost double that of females (1.4 m s$^{-1}$) [27]. In the study by Brackenbury & Elsayed [27], kinematics were not measured and no other data are available with regard to gender differences in kinematics in birds. Female junglefowl have a lower metabolic scope than males [48]. This may be because males are physiologically suited to improved locomotor performance, with 43 per cent larger hearts and lungs along with 29 per cent heavier leg muscles [49]. Conversely, females are more suited to energy acquisition, with larger intestines and livers [49]. It is unknown if the locomotor performance of female ptarmigans can be explained by these sorts of differences.

The CoL has previously been studied in a wide range of bird taxa with differing degrees of sexual dimorphism. These studies have either mixed female and male data [9–12] or not stated the genders of test species [13–16]. Our findings indicate that gender should be taken into account when presenting CoL data. Here, mixing the sexes would not have affected the estimate of the incremental cost (the slopes of the relationship between CoL and $U$ were similar; figure 1), but the absolute cost would change (the intercepts of the relationship between CoL and $U$ differed; figure 1) depending on which gender was used or whether genders were mixed.

Figure 2. Gait kinematics parameters plotted against forward speed ($U$) for males (black squares and dashed lines) and females (circles and solid lines). The lines fitted through the data are derived from the ANCOVA output, and are (a) duty factor = 0.841 – 0.247$U$ (males) and duty factor = 0.778 – 0.185$U$ (females), (b) stride length = 0.134 + 0.228$U$ (males) and stride length = 0.103 + 0.228$U$ (females), and (c) stride frequency = 1.176 + 1.444$U$ (males) and stride frequency = 1.432 + 1.444$U$ (females). (d) Lines have not been fitted to the stance phase data.
If, however, there were a systematic bias in the speeds over which the genders were tested, then the incremental cost would also be affected. For example, if only females were tested at low speeds and males at high speeds then the incremental cost estimate (slope) would be lower, and vice versa. Therefore, the outcome of comparisons of the CoL across species may potentially be affected by the relative contribution of the genders to the data. These complications may also extend to non-avian studies that mix data (e.g. [50–54]).

The cost of terrestrial locomotion is dictated by the generation of muscular force during each step and the time available to generate this force [22]. In the current study the incremental speed response and absolute gait kinematics values were similar in males and females. Despite this combining \( \dot{V}_O_2 \) with \( f_{stance} \) showed the metabolic cost per stride to be the same for males and females. This is surprising given female ptarmigan have a shorter total leg length than males. However, \( P_{net} \) when plotted against \( F_r \) was still lower in males suggesting that factors other than just skeletal size were driving gender differences in the CoL at a given speed. Few studies have collected kinematic data in tandem with energetics, but those that have show that different gaits in birds are closely associated with changes in the pattern of energy expenditure [34,55]. These data suggest that kinematic factors other than \( f_{stance} \) may dictate gender differences in the CoL. Indeed, it seems that in at least some species the CoL may be determined by \( f_{stance} \). A human study including kinematic and energetic data had similar findings [28].

Although our results indicate a selection for improved male performance, some degree of selection resulting in a reduction in female performance cannot be ruled out completely (e.g. perhaps a reduced ratio of skeletal muscle to body organ size, driven by the need for nutrient acquisition for egg production [49]). This seems unlikely, however, as male Svalbard ptarmigans exhibit exceptional locomotor ability, showing a reduced CoL during the winter, despite being almost twice their summer body mass [35]. The data from females suggest that they do not exhibit the same energetic savings and that the CoL is the same during both summer and winter. Together, these data indicate that the lower CoL in male Svalbard ptarmigans is a result of selection for improved male locomotor performance as opposed to factors resulting in reduced female performance. If the latter were the case, we would not expect to see such exceptional energetic savings in winter males when females do not require them for over-winter survival. Previous studies finding improved locomotor performance in males also tend to occur in species in which females are choosy and males must search and compete for mates [31,32,49,56]. These adaptations appear to be less important to the females for which (at least in terms of reproductive success) improved locomotor performance is not selected for. Research in junglefowl supports this, as the females suffer no loss of social rank in relation to aerobic performance [57]. One obvious factor that could affect only female birds is the requirement of egg laying, which is associated with altered pelvic anatomy [58]. A larger pelvis is a common female trait that has important consequences for locomotion [59,60]. Another consequence of producing eggs is a reduction in bone fracture resistance to provide calcium for egg formation [61–63]. Females in the present study were tested during the post-egg-laying period, in which bones, including those of the hind limbs, may have been weakened. Therefore, it is possible that the altered stride length observed in females is a mechanism for reducing the forces acting upon these weakened bones.

In summary, female and male Svalbard ptarmigans demonstrate differing locomotor performance both in terms of CoL and attainable top speed. There are also potential gender-based differences in kinematic parameters, driven by more than just size differences, which could influence the interpretation of results mixing data from both genders. The exact mechanisms underlying these differences and their ubiquity among both avian and non-avian species are currently unknown. However, in the Svalbard ptarmigan, it appears that the differences may result from improved male performance driven by sexual selection. A number of authors have looked into the kinematics of locomotion in birds; however, these have either pooled male and female data, or not stated the genders used for investigation [55,64–66]. More work is needed to assess the extent of intrasexual kinematic differences, potential underlying reasons for them and their effects upon locomotor performance. It would be interesting to determine, for example, the daily energy expenditure of male and female birds. It seems likely that differences in the cost of locomotion would manifest in differences in the time budget associated with these behaviours. It is clear that the potential for sex differences in locomotor performance should be considered in future studies.

NOTE ADDED IN PROOF
Due to a discrepancy with the imaging equipment, the frame rate during the experiment was 100 Hz, not 120 Hz as initially published. We have amended the methods and results with the correct frame rate. Neither the primary results, findings of the study or their significance are affected.

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