Energetics and kinematics of walking in the barnacle goose (*Branta leucopsis*)☆

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ABSTRACT

Barnacle geese were walked on a treadmill at speeds ranging from 0.25 to 1.25 m s^{-1}, which was their highest sustainable speed. No evidence for a gait change was found. The gait of a barnacle goose appears to conform to the classical pendulum mechanics based model of walking, with the kinetic energy of forward motion (horizontal kinetic energy, E_{kh}) out-of-phase with the sum of the gravitational potential (E_p), and vertical kinetic (E_{kv}) energies of the centre of mass at all speeds. Why barnacle geese are unable to aerial run when other 'waddling' species do show an aerial phase (e.g., mallard ducks) is unclear. Presumably, however, it is likely to relate to the amount of lateral kinetic energy generated, which is a feature of 'waddling'. We predict that lateral kinetic energy generated by barnacle geese and other waddling species that cannot aerial run, is higher than in those that can. Due to competing selection pressures for swimming and flight, barnacle geese are mechanically and energetically inefficient walkers relative to more specialist cursorial birds. Their upper walking speed, however, appears to be limited by morphology (via kinematics) and not metabolic capacity (energetics).

1. Introduction

The terrestrial locomotion of birds (and animals in general) is subject to both morphological (manifesting in kinematics) and physiological (primarily energetic) constraints. It is therefore important to simultaneously quantify the kinematics and energetics of animals during locomotion when trying to identify the constraints acting upon locomotor systems. Birds may be split into three categories based upon their dominant locomotor mode after flight: specialist walkers, divers and non-specialist birds (Tickle et al., 2007; Tickle et al., 2009). It should be noted that specialist walkers refers to birds adapted to a largely terrestrial life style that preferentially walk and/or run for transport (e.g., Paleognathes and Galiiformes). Most studies of terrestrial locomotion, particularly with reference to gaits and transitions between gaits (i.e., walking to running), have understandably focused on specialist walking species (Cavagna et al., 1977; Gatesy and Biewener, 1991; Rubenson et al., 2004). It is, however, important to give equal consideration to non-specialist walkers. Their potentially sub-optimal walking gaits, relative to specialist walkers, mean that they are likely to give different insights into the constraints acting upon the avian terrestrial locomotion system than finely tuned specialist walkers. Particularly, because, although there are broad kinematic and

energetic similarities in the terrestrial locomotion of birds and animals in general (Taylor et al., 1971; Taylor and Rowntree, 1973; Taylor et al., 1982; Gatesy and Biewener, 1991; Nolet et al., 1992; Roberts et al., 1998; Bruinzeel et al., 1999; Gatesy, 1999; Abourachid, 2000; Abourachid and Renous, 2000; Abourachid, 2001; White et al., 2008), previous work has implied that the relationships between kinematic parameters and forward velocity during avian terrestrial locomotion vary depending upon the posture (crouching or upright) (Gatesy and Middleton, 1997) or dominant locomotor mode used by the species (Abourachid, 2001). Furthermore, it has been shown previously that differences in the energetic cost of locomotion depend on both locomotor mode and ecological niche (Pinshow et al., 1977; Bruinzeel et al., 1999).

The top speed when walking is limited and therefore, to increase velocity further, bipedal animals must shift from a walking gait to a running gait (Cavagna et al., 1977). A change of gait may be identified in three ways. Running and walking gaits may be defined by the phasing between the kinetic energy of forward motion (horizontal kinetic energy, E_{kh}) and the sum of the gravitational potential (E_p) and vertical kinetic (E_{kv}) energies of the centre of mass, CoM (Cavagna et al., 1977). In walking, an out-of-phase exchange of these two energies occurs, whereas in running, E_{kh} and $E_p + E_{kv}$ are in-phase and additive (Cavagna et al., 1977). The transition between walking and running may also be defined more traditionally by duty factor, which is the proportion of a stride that the foot is in contact with the ground. A duty factor >0.5 indicates a walking gait and <0.5 a running gait (Hayes and Alexander, 1983) — i.e., running has an aerial phase, where both feet are of the ground, while walking does not. The final way a change of gait may be discerned is by the identification of a discontinuous change in the

relationship between kinematics variables and velocity (Alexander, 1989).

Unlike humans, gait changes in birds are not characterised by an abrupt discontinuous alteration from out-of-phase to in-phase E_{kh} and $E_p + E_{kv}$ (Heglund et al., 1982; Muir et al., 1996; Rubenson et al., 2004). Several studies, that have not calculated E_{kh}, E_p and E_{kv} (Gatesy and Biewener, 1991; Gatesy, 1999; White et al., 2008), have used discontinuities to indicate gait changes. The discontinuities took the form of a significant decrease (>50%) in the slope describing the relationship between stride frequency (f_{stride}) and velocity (U). These apparent gait changes, occurred at duty factors >0.5 indicating a switch to a running gait without an aerial phase: 'grounded' or 'groucho' running (Gatesy and Biewener, 1991; Gatesy, 1999; Rubenson et al., 2004). Therefore, it appears that birds go through a 'grounded' or 'groucho' running phase prior to reaching a full aerial phase (McMahon et al., 1987; Gatesy and Biewener, 1991; Gatesy, 1999; Rubenson et al., 2004).

Generally studies of avian terrestrial locomotion gaits have focused on specialist walking birds. Notable exceptions are a study of the cormorant (*Phalacrocorax carbo*), a diving species with a waddling gait (White et al., 2008) and two studies of ducks (Abourachid, 2001; Usherwood et al., 2008). The cormorant was shown to have a duty factor in excess of 0.7 at the highest speed it could attain upon a treadmill (White et al., 2008). An inflection in the stride frequency versus U plot suggested a gait transition at around 0.3 m s^{-1}, but again simultaneous measurements of energy fluctuations were not made. Nonetheless, the implication was that the highest walking speed (0.5 m s^{-1}) of the cormorants was achieved using a different gait from that used at lower speeds. It is possible then, that divers may change gait to a grounded run like specialist walkers and it was concluded that the pedestrian locomotion of cormorants is generally similar to that of cursorial birds at comparable speeds (White et al., 2008). In contrast, the Mallard (*Anas platyrhyncos*) and Indian runner duck both used an aerial phase at their highest speeds, but their running gaits are unlikely to be wholly comparable to that of cursorial bipeds (Usherwood et al., 2008). Interestingly, not all ducks are capable of aerial running (i.e., Aylesbury duck, Usherwood et al., 2008), which implies at least subtle variations in terrestrial gaits and walking performance among even closely related species. Hence, to fully understand the constraints operating on the avian terrestrial locomotor system requires expansion of the available data on walking biomechanics and energetics, particularly in generalist species.

The barnacle goose (*Branta leucopsis*) is a migratory waterfowl that is capable of flying, swimming and walking, and at various times during its annual cycle must perform each one of the three locomotor modes. During moult, barnacle geese shed their flight feathers and are rendered temporarily flightless (Owen and Ogilvie, 1979). As a consequence, escape from predators during moult can only occur by either walking or swimming away. Therefore, they represent an ideal bird for investigating terrestrial gaits in generalist species. Geese have a relatively high cost of locomotion among birds (Bruinzeel et al., 1999), which is attributed to their waddling (wide track-ways) gait also used by cormorants (White et al., 2008). Humans were shown to use 40% more metabolic energy when walking with a very wide track-way of 0.45 times leg length, than when using their preferred track-way width (Donelan et al., 2001). The energetics of terrestrial locomotion in the barnacle goose has already been investigated, but with reference to comparing methods for measuring energy expenditure (Nolet et al., 1992) and not focusing upon gait kinematics. Whether barnacle geese, arguably ecologically more terrestrial than mallards, are capable of changing gait to a grounded or aerial run is not yet known. Accordingly, here the kinematics of barnacle geese walking over a range of speeds up to their maximum was quantified. Evidence for a gait change was investigated using all three methods described above — energy phase, duty factor and discontinuity in the relationship between kinematics parameters and U. Energy expenditure was measured coincident with the kinematics data to determine whether changes in gait kinematics are linked to metabolic costs. The study set out to answer two questions. Firstly, do barnacle geese change gait and perform grounded running or running with an aerial phase? And secondly, is it energy expenditure or gait biomechanics that constrains the upper limits of terrestrial locomotion in the barnacle geese?

2. Materials and methods

2.1. Study species

Five barnacle geese eggs were incubated and the resulting goslings reared within the BSF Animal Unit at the University of Manchester. Geese were maintained on a 13:11 h light–dark cycle and housed within a 12 m^2 room furnished with an area of turf and a 30 cm deep raised pond and were given food (Poultry Grower Pellets, Small Holder Range, Norfolk, UK: fat 4.8%, protein 16%, carbohydrate 73.7%, and fibre 5.5%) and water *ad libitum*. The geese were not fasted prior to the respirometry experiments. Measurements were taken when the geese were 6 months old at which point their body masses (mean = 1.79 kg and range = 1.5–2.1 kg) had stabilised and were comparable to an older 17-month-old cohort (mean = 1.75 kg and range = 1.5–2.1 kg) reared under the same conditions. The geese were imprinted upon hatching and were trained regularly to locomote enclosed inside the respirometry chamber upon a treadmill (Tunturi T60, Turku, Finland) from the age of 3 months. All experimental procedures were approved by the University of Manchester Ethics Committee and conducted in accordance with the Animals (Scientific Procedures) Act (1986) under a UK Home Office Licence held by Dr Codd (40/3001).

2.2. Indirect calorimetry

A standard open-flow respirometry system was used to measure rates of O$_2$ ($\dot{V}_{CO_2}$) consumption and CO$_2$ ($\dot{V}_{CO_2}$) production (Withers, 2001; Lighton, 2008). The geese walked inside a Perspex® chamber with maximum internal dimensions of $66 \times 48.5 \times 46.5$ cm and a volume of 148 l. The chamber was sealed upon the treadmill, using rubber and brush seals. Air was pushed through the chamber using two vacuum pumps (Models: 2750CGH160 and 2688CHI44 — Thomas, Sheboygan, WI, USA) at 255 l min^{-1}. The high flow rate relative to the chamber size was desirable to ensure the measured gas volumes stabilised quickly, reducing the amount of time the geese had to walk. Excurrent air was sub-sampled at 0.110 l min^{-1} downstream of the chamber and passed through an RH300 (Sable Systems International, Las Vegas, NV, USA) for measurements of relative humidity and water vapour pressure. The air was then scrubbed of H$_2$O (using magnesium perchlorate) and passed through a CA-10A CO$_2$ analyzer (Sable Systems International, Las Vegas, NV, USA), then scrubbed of CO$_2$ (using Ascarite (II)®) prior to passing through a dual absolute and differential O$_2$ analyzer (Oxzilla II — Sable Systems International, Las Vegas, NV, USA). Hence, the air entering the O$_2$ analyzer was both CO$_2$ and H$_2$O free. The second channel in the O$_2$ analyzer continuously measured oxygen levels in ambient air. Prior to analysis in the second O$_2$ channel, Ascarite (II)® and magnesium perchlorate were used to scrub CO$_2$ and H$_2$O from the ambient air. The sub sampling pumps (TR-SS3 mass flow meters — Sable Systems International, Las Vegas, NV, USA) were downstream of the gas analyzers. All scrubbing chemicals were supplied by Acros organics, NJ, USA. Voltage outputs were recorded using a UI2 interface and ExpeData version 1.25 (both Sable Systems International, Las Vegas, NV, USA).

Water was scrubbed from the sub-sampled air stream prior to O$_2$ and CO$_2$ analysis and therefore the primary flow rate (FR) was adjusted to a dry-corrected flow rate (FR$_c$) using (Eq. 8.6 in Lighton, 2008)

$$FR_c = FR \cdot (BP - WVP) / BP \qquad (1)$$