



The relationship between energy expenditure and speed during pedestrian locomotion in birds: A morphological basis for the elevated y-intercept?



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ABSTRACT

The slope of the typically linear relationship between metabolic rate and walking speed represents the net cost of transport (NCOT). The extrapolated y-intercept is often greater than resting metabolic rate, thus representing a fixed cost associated with pedestrian transport including body maintenance costs. The full cause of the elevated y-intercept remains elusive and it could simply represent experimental stresses. The present literature-based study compares the mass-independent energetic cost of pedestrian locomotion in birds (excluding those with an upright posture, i.e. penguins), represented by the y-intercept, to a known predictor of cost of transport, hip height. Both phylogenetically informed and non-phylogenetically informed analyses were undertaken to determine if patterns of association between hip height, body mass, and the y-intercept are robust with respect to the method of analysis. Body mass and hip height were significant predictors of the y-intercept in the best phylogenetically-informed and non-phylogenetically informed models. Thus there is evidence that, in birds at least, the elevated y-intercept is a legitimate component of locomotion energy expenditure. Hip height is probably a good proxy of effective limb length and thus perhaps birds with greater hip heights have lower y-intercepts because their longer legs more efficiently accommodate body motion and/or because their limbs are more aligned with the ground reaction forces.

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1. Introduction

In many species that use pedestrian locomotion, rate of oxygen consumption (V_{O_2} , mL min^{-1}) is a linear function of speed (e.g. Schmidt-Nielsen, 1972a; Taylor et al., 1982). The slope of the linear regression between these two variables is a speed-independent quantity (the net cost of transport, NCOT; $\text{mL O}_2 \text{ m}^{-1}$) that is the amount of oxygen, above that represented by the extrapolated y-intercept, required by an animal to move a unit distance (Fig. 1A). The extrapolated y-intercept represents a fixed cost associated with pedestrian transport ($\text{mL O}_2 \text{ min}^{-1}$) and includes body maintenance costs. The y-intercept is often higher than V_{O_2} measured when the animal is naturally at rest (Taylor et al., 1970; White et al., 2008) and therefore may also include some costs specifically associated with walking, but which are not included in NCOT (e.g. the cost of maintaining the body in a locomotory posture (postural cost; Schmidt-Nielsen, 1972a), see also Ellerby et al. (2003)). While the costs of standing (e.g. activation of leg and trunk muscles for balance, posture and support; Weyand et al., 2009) are likely a part of the explanation for the elevated y-intercept (the difference between the y-intercept and resting metabolic rate), the full cause of the elevated y-intercept remains elusive and it may simply represent any of a number of experimental stresses (Fig. 1B).

If the elevated y-intercept represents a locomotory cost then presumably a reasonable possibility is that such costs are related to a morphological characteristic of locomotion. Thus, one way to determine whether the elevated y-intercept represents a legitimate locomotory cost is to test for an interspecific association between the elevated y-intercept and a relevant potential correlate. Pontzer (2007) showed that, having accounted for body mass, hip height is a predictor of cost of transport across species representing a broad range of taxa. Hip height is a characteristic length for calculation of Froude numbers in analyses invoking physical similarity (e.g. Alexander, 1976) and is relatively easy to measure. Therefore, in the present study, the energetic cost of pedestrian locomotion represented by the y-intercept is also compared to hip height, in birds. The y-intercept is used rather than the elevated y-intercept because resting metabolic rate varies temporally and between populations (Broggi et al., 2004; Portugal et al., 2007; McKechnie, 2008; Smit and McKechnie, 2010; White et al., 2011), and was often not reported in the papers from which the y-intercept was obtained and/or was not defined. The following question is addressed: Is the y-intercept, as a component of locomotory energy expenditure, related to hip height?

2. Materials and methods

Data for the y-intercept of the relationship between absolute V_{O_2} ($\text{mL O}_2 \text{ min}^{-1}$) and speed (m min^{-1}), not including values where speed = 0, were collated from the peer reviewed literature and

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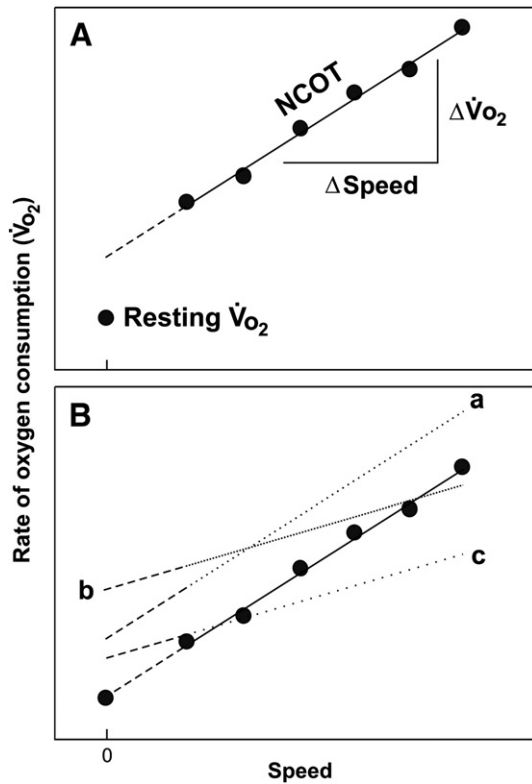


Fig. 1. Hypothetical relationships between rate of oxygen consumption (V_{O_2}) and speed. (A) Net cost of transport (NCOT) is calculated as the slope of the relationship relating V_{O_2} to speed for speeds greater than zero. (B) Potential influence of measurement errors on the intercept of the relationship relating V_{O_2} to speed for speeds greater than zero. Such errors include (a) experimental stress elevating V_{O_2} at all speeds, (b) irregular walking patterns at low speeds that elevate V_{O_2} at these speeds or (c) an increased anaerobic component to metabolism at fast speeds such that the increase in V_{O_2} is reduced at these speeds (Herreid and Full, 1984).

unpublished data (Table 1) during a data search on going between 2005 and 2012 inclusive. The y-intercept (V_{O_2}) was determined by extrapolating the regression slope to $x = 0$, where $x = \text{speed}$. When relationships were not provided (e.g. Bevan et al., 1994), figures were digitised (TechDig v2.0) and regressions calculated using ordinary least squares. Data for penguins were not included in the

analysis due to their unusual upright posture exhibited both at rest and during walking, and this may result in a different interplay between postural costs and hip height. Large ratites (emus, ostriches, rheas) were also excluded as they have recently been shown to exhibit a curved relationship between V_{O_2} and speed (Watson et al., 2011); such relationships appear to become apparent when data over a greater range of speeds and/or more data points are obtained. Data for Ruff Sandpipers were excluded because the birds were walked at an incline of 8° (Vaillancourt et al., 2005). For Marabou storks, data were included from walking trials at 0° because, although these data are arguably non-linear, the y-intercept reported (for a linear regression) is very similar to that for data obtained at inclines of 5° and 7° , where the relationship between V_{O_2} and speed was more clearly linear (Bamford and Maloiy, 1980). To avoid problems associated with potentially inaccurate O_2 energy equivalences (Walsberg and Hoffman, 2005), data are expressed in units of mL of O_2 . Where necessary, data were converted from units of rate of energy expenditure (e.g. W) using the energy equivalence of O_2 provided by the authors or 20.1 J mL^{-1} (Withers, 1992) if no energy equivalence was provided.

Measures of hip height were collated from Gatesy and Biewener (1991) or were measured either on live birds, taxidermy mounts of standing birds, or from side-on photographs of birds in a standing posture such that the position of the hip could be estimated from the location of external morphometric features in combination with information on species size. Hip height was measured from the protruding part of the proximal end of the femur to the ground while the (live) bird was placed in a standing posture that was as natural as possible based on visual comparison with photographs of the relevant species in the field. Where possible, hip heights were measured by two researchers independently and those values compared. They were always found to be very similar.

Data were analysed without phylogenetic information using ordinary least square in SPSS (v. 19, IBM Company). Data were analysed with phylogenetic information using phylogenetic generalised least squares (PGLS) (Grafen, 1989; Martins and Hansen, 1997; Garland and Ives, 2000) in the APE (Analysis of Phylogenetics and Evolution) package within R (Ihaka and Gentleman, 1996; Paradis et al., 2004) according to established procedures and using published code (Halsey et al., 2006; Duncan et al., 2007) and a phylogeny based on a published informal supertree (see White et al., 2008 and references therein). Because the branch lengths in the tree are unknown, a range of branch length transformations were compared: star (non-phylogenetic), punctuated (all branches set equal, and equal to 1), Grafen's (1989), Nee's

Table 1
Mass, elevated y-intercept values and hip heights of birds.

Common name	Latin name	Mass (g)	y-intercept (mL $O_2 \text{ min}^{-1}$)	Hip height (cm)	Reference
Australasian gannet	<i>Morus serrator</i>	2314	56.2 (9)	15	Aitken-Simpson, Green and Frappell unpublished, this study
Bantam chicken	<i>Gallus gallus</i>	780	14.4 (8)	20	Green et al., 2009, this study
Bar-headed goose	<i>Anser indicus</i>	2163	35.0 (3)	23	Ward et al., 2002, this study
Barnacle goose	<i>Branta leucopsis</i>	1885	32.5 (5, 4)	21	Nolet et al., 1992; Ward et al., 2002, this study
Black-browed albatross	<i>Thalassarche melanophrys</i>	3425	83.4 (11)	23	Bevan et al., 1994; Kabat et al., 2007, this study
Bobwhite quail	<i>Colinus virginianus</i>	194	4.5 (5)	10	Fedak, 1974; Gatesy and Biewener, 1991
Chukar partridge	<i>Alectoris chukar</i>	489	12.1 (3)	14	Fedak, 1974, this study
Eider duck	<i>Somateria mollissima</i>	1791	51.6 (1)	20	Hawkins et al., 2000, this study
Great cormorant	<i>Phalacrocorax carbo</i>	2295	68.6 (8)	17	White et al., 2008, this study
Greater road runner	<i>Geococcyx californianus</i>	285	10.6 (2)	16	Fedak and Seeherman, 1979, this study
Grey-headed albatross	<i>Thalassarche chrysostoma</i>	3240	55.2 (5)	25	Kabat et al., 2007, this study
Greylag goose	<i>Anser anser</i>	3913	41.6 (4, 2)	22	Fedak, 1974; Halsey et al., 2009, this study
Guinea fowl	<i>Numida meleagris</i>	1363	30.7 (5, 3)	20	Ellerby et al., 2003; Fedak, 1974; Gatesy and Biewener, 1991
Marabou stork	<i>Leptoptilos crumeniferus</i>	4500	41.0 (4)	60	Bamford and Maloiy, 1980, this study
Painted quail	<i>Excalfactoria albognata</i>	42	1.6 (5)	5	Fedak, 1974; Gatesy and Biewener, 1991
Tinamou	<i>Nothoprocta pentlandi</i>	310	3.6 (1)	23	Fedak, 1974, this study
Turkey	<i>Meleagris gallopavo</i>	4306	46.6 (2)	40	Fedak, 1974; Gatesy and Biewener, 1991
Wilson's plover	<i>Charadrius wilsonia</i>	18	0.7	13	Taylor et al., 1982, this study

Values in parentheses represent the number of individual birds per study to obtain the y-intercept presented, where available; this value of N is either known or otherwise assumed to be the number of birds reported to have been used in the original study.

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