

Differences in metabolic costs of terrestrial mobility in two closely related species of albatross

Alexander P. Kabat^{1,*}, Richard A. Phillips², John P. Croxall^{2,†} and Patrick J. Butler¹

¹Centre for Ornithology, School of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK and

²British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

*Author for correspondence (e-mail: Alexander.kabat@gmail.com)

†Present address: BirdLife International, Wellbrook Court, Girton Road, Cambridge CB3 0NA, UK

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Summary

Black-browed albatrosses *Thalassarche melanophrys* typically colonise steeper habitats than grey-headed albatrosses *T. chrysostoma*. The present study investigated the effect of colony philopatry on terrestrial locomotory ability in these two species, to determine: (1) if there is a difference in terrestrial locomotory ability between these two closely related species, and (2) what physiological or behavioural adaptations may account for any differences identified. We examined the metabolic cost, mechanical efficiency on an incline, and gait characteristics of terrestrial locomotion of these two species on both level and inclined planes. *T. chrysostoma* were able to perform at a significantly greater speed than *T. melanophrys* without reaching a significantly different maximal rate of oxygen consumption (\dot{V}_{O_2}). Conversely, *T. melanophrys* were able to

move up a significantly steeper incline than *T. chrysostoma* while maintaining a similar maximal \dot{V}_{O_2} . Each species demonstrates stride length, force production (behavioural) and leg length (morphological) adaptations that minimise the cost of traversing their chosen colonies, indicating a clear relationship between terrestrial performance and local topography. However, it is not possible to determine if the difference in locomotory ability results from differences in colony topography, or if choice of colony site is dictated by the ability of the species to traverse different terrain.

Key words: *Thalassarche melanophrys*, *Thalassarche chrysostoma*, cost of locomotion, metabolic rate, procellariiform, energetics, gait analysis.

Introduction

The present study investigated the metabolic cost, mechanical efficiency and gait characteristics of terrestrial movement in two closely related species of albatrosses, the black-browed albatross (BBA), *Thalassarche melanophrys*, and the grey-headed albatross (GHA), *T. chrysostoma*. Both BBA and GHA are pelagic, remaining at sea for 5–6 years after fledging but spending some months on land during each breeding season (Weimerskirch et al., 1985; Prince et al., 1994). Breeding site fidelity is high for both species, with movements of established breeders between adjacent colonies, even those separated by a few hundred metres, being rare (Prince et al., 1994). Both species nest on mounds of soil and vegetation, with BBA tending to favour steeper slopes than GHA (Tickell and Pinder, 1975). Although BBA will sometimes nest alongside GHA in relatively flat colonies, it is atypical to find GHA in the steeper colonies inhabited by BBA (Carboneras, 1992), thus suggesting one or more factors limit where GHA nest.

Once birds have taken flight, they can clear the topography of the land making the metabolic cost of movement independent of slope, terrain and other terrestrial obstacles. However, when on land albatrosses must cope with variations in topography, which may induce varying metabolic costs. In addition, many

birds must walk or run in order to become airborne. Relative colony slope may have an important influence on nest site selection and, given the high degree of nest site fidelity, it could be hypothesized that BBA possess greater locomotory efficiency during locomotion up an incline compared to GHA. Conversely, it could be hypothesized that GHA are better adapted for level terrestrial locomotion, thus minimizing metabolic costs compared to BBA.

In most animals, the rate of oxygen consumption (\dot{V}_{O_2}) is a linear function of speed during terrestrial locomotion in a horizontal plane (e.g. Schmidt-Nielsen, 1972; Taylor, 1985; Taylor, 1994; Taylor et al., 1982; Butler, 1991). The extrapolated y-intercept of this line is often higher than the \dot{V}_{O_2} measured when the animal is naturally at rest (Taylor et al., 1970). The difference between the y-intercept and resting \dot{V}_{O_2} has been termed the ‘postural’ effect (Schmidt-Nielsen, 1972), suggesting that it represents the energetic cost of maintaining the body in a locomotory posture.

The total metabolic cost of locomotion can be calculated as the sum of maintenance metabolic costs (equal to resting \dot{V}_{O_2}), postural costs, and the cost of moving an animal’s mass for a particular duration and distance. These costs are increased when the animal is moving on an incline, as the force of gravity is acting

against the mass of the animal as it moves upwards. Net mechanical efficiency on an incline is defined as the work done against gravity divided by the additional metabolic energy expended to accomplish this work. As efficient locomotion could be vital for maintaining an animal in a positive energy balance, maximising mechanical efficiency can be a substantial evolutionary pressure.

Interspecific comparisons across a range of animal sizes suggest that the mass-specific volume of muscle fibres activated to support body mass during locomotion is independent of body size (Taylor et al., 1980; Biewener, 1989; Kram and Taylor, 1990). It has also been suggested that there is a relationship between rate of metabolic energy expenditure and the rate of muscular force generation. The rate of force generation shows a linear relationship with running speed in both birds and mammals (Roberts et al., 1998; Kram and Taylor, 1990). Thus, the rate of energy expenditure during locomotion can be predicted by knowing an animal's body mass (proportional to the volume of active muscle used to generate force against the ground) and the foot-ground contact duration (t_c), which is inversely proportional to the rate of force generation ($1/t_c$) (Kram and Taylor, 1990; Roberts et al., 1998). By using this approach, the rate of energy expenditure during locomotion can be predicted without including any major complexities of muscle physiology (Kram and Taylor, 1990).

The present study investigated the metabolic cost, mechanical efficiency on an incline and gait characteristics of terrestrial walking in BBA and GHA in order to determine: (1) if there are any differences in terrestrial locomotory ability and (2) what behavioural or physiological adaptations might account for any observed differences.

Materials and methods

We followed the Scientific Procedures requirements for animal research as set forth by the United Kingdom Home Office in the Official Guidance on the Operation of the Animal Act of 1986. Our procedures also conformed to the Code of Ethics of Animal Experimentation in Antarctica.

Animal handling

The study was carried out on 11 black-browed albatross *Thalassarche melanophrys* Nunn 1998 and five grey-headed

albatross *T. chrysostoma* Brooke 2004 from two colonies on Bird Island, South Georgia (54°00'S, 38°03'W), in January of the 2005/2006 austral summer. In order to minimise potential impacts, only non-breeders of either sex were tested. These birds were mainly failed breeders or GHA in their 'sabbatical' year (Ryan et al., 2007). The nests that the birds were defending at the time of capture were used for the collection of topographical data (as below). It was not possible to obtain higher numbers of GHA, as this species spends little time at the colony during their 'sabbatical' year or following reproductive failure.

Nest site topography

The slope (θ) of the adjacent 1.0 m of ground surrounding each nest (Fig. 1A) was measured with a protractor (to 0.5°) in degrees from the horizontal (Fig. 1B,C), as determined by a spirit level. The angle facing directly down the slope was defined as the 0° position and the 90°, 180° and 270° measurements were taken in a clockwise pattern from this position (Fig. 1B). The mean θ of each nest was defined as the 'mean nest θ ' and is the mean of the absolutes of all angles (Fig. 1B). However, as it is likely that the bird will try to use the 'path of least resistance', the least steep slope for each nest was extracted (hereafter called the 'minimum approach θ ').

Metabolic rate

Rate of oxygen consumption (\dot{V}_{O_2}) of the 11 BBA and five GHA were measured both at rest and during treadmill exercise using standard open-flow respirometry (Bevan et al., 1994; Withers, 2001). A 246 l clear Perspex™ respirometer enclosed the bird while on a variable-gradient, variable-speed treadmill (model EG10, Powerjog Sports Engineering Ltd, Birmingham, West Midlands, UK). The respirometer was placed securely on a wooden frame that was permanently attached to the treadmill and rubber seals ensured an airtight fit between the respirometer and the frame. Brush-style draught excluders ensured a good seal between the wooden frame and the treadmill belt. Adequate gas mixing within the chamber was assured by the inclusion of two 12×12 cm, 12 V fans. Three B105 Charles Austen air pumps (Byfleet, Surrey, UK) pumped ambient air through the chamber at 110 l min⁻¹, measured using an electronic flow meter (100 Flo-Sen, McMillan Co., Georgetown, TX, USA), which was calibrated at the beginning, middle and end of the

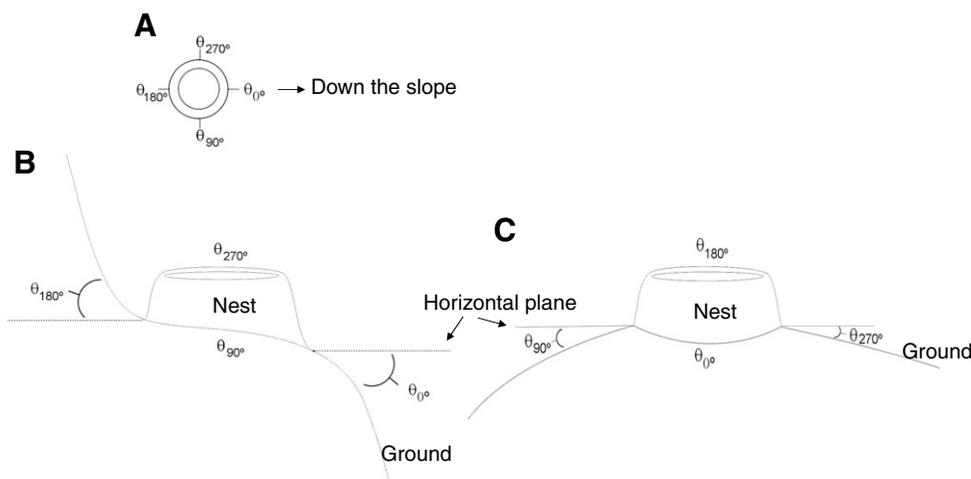


Fig. 1. (A) Top view of nest, showing the positions (0, 90, 180, 270°) at the bottom of the nest from which each measurement of slope angle (θ) was taken. (B) Side view of the nests showing the positions from which each measurement of slope θ is taken where θ_0° is the nest facing directly down slope, θ_{180° is the nest facing directly up slope, θ_{90° and θ_{270° are taken along the sides of the nest. Slope angle was measured from to the ground to the horizontal plane (dotted lines). (C) Front view schematic of same nest measurements.

experiment using a 150 l min⁻¹ mechanical flow meter (KDG, 2000, KDG Instruments, Crawley, Sussex, UK). Relative humidity, barometric pressure and temperature were recorded using a Honeywell HHH-3610 sensor (Farnell, UK). Water vapour was mathematically scrubbed by numerical integration of the product of the gas flow and fractions of partial pressures (see Fellows and Macdonald, 1985) to provide a flow rate corrected to standard temperature (273 K) and pressure (101.3 kPa) dry (STPD). The chamber temperature was maintained between 12 and 14°C. A sub-sample of excurrent air was drawn off downstream of the respirometer and passed through a column of self-indicating Drierite™ (Hammond Drierite Co., Xenia, OH, USA) and scrubbed for carbon dioxide before being sent to a Servomex 570A O₂ analyser (Crowborough, East Sussex, UK). The system was calibrated with gas mixtures of atmospheric air and nitrogen (Fedak et al., 1981) controlled by a Wösthoff gas mixing pump (2M301/a-F, Bochum, Germany). Nitrogen dilution tests (Fedak et al., 1981) showed that the accuracy of the system was within 2%, and the 99% wash-out time was calculated to be 10.4 min using the formula described by Lasiewski et al. (Lasiewski et al., 1966).

The output signals from the O₂ analyser, humidity and temperature sensors, and barometer were passed to a purpose-built interface box that amplified the signals to a standard range of -10 V to +10 V. The amplified output voltages were passed to a laptop computer (Dell LT316) fitted with a digital signal acquisition PCMCIA card (DAQCard-500 National Instruments, Newbury, UK). The computer sampled outputs at 1000 Hz, took a running mean and saved these values every 3 s throughout the experiment *via* a program developed using LabView v5.11 (National Instruments, Austin, TX, USA). Partial pressures of ambient O₂ were recorded for 3 min every 20 min, as an automated baseline check *via* a solenoid valve (SMC EVT307, Radio Spares, Corby, UK) controlled by the interface box and LabView software. Rate of oxygen consumption was calculated as ml min⁻¹ STPD for each animal.

Resting rates of oxygen consumption

Resting \dot{V}_{O_2} was measured from birds sitting quietly within the darkened respirometer while on the treadmill prior to each exercise session. Standing-at-rest \dot{V}_{O_2} was recorded for a minimum of 15 min or until a stable baseline was achieved. Birds of either species would consistently stand whenever the researchers approached and remained standing and alert if the researchers were within visual range. Previous studies have shown that although psychological stressors may cause an increase in heart rate, they are unlikely to result in a measurable difference in metabolic rate (Blix et al., 1974) and thus this is a suitable measure of standing-at-rest \dot{V}_{O_2} .

Exercise protocol

One to two training sessions were conducted at least 24 h prior to experimentation. Training consisted of placing a bird within the experimental chamber and walking it at 0.1–0.2 km h⁻¹ for 5–15 min depending on its willingness and ability to adapt to the treadmill. For experimental testing, birds were placed in the respirometer at least 4 h prior to the beginning of experimentation to allow acclimation. To determine maximum speed and rate of oxygen consumption at

maximal speed ($\dot{V}_{O_{2max, speed}}$), birds were randomly exercised at seven speeds (0.2–1.27 km h⁻¹). Each trial began with a 2–3 min warm-up at 0.1–0.2 km h⁻¹. Thereafter, the speed was increased in 0.2 km h⁻¹ increments every 2 min until the designated test speed was reached. Not all birds would walk at the higher speeds. Each experimental speed was maintained for a sufficient length of time to enable acclimation of the animal and equilibration of oxygen levels (minimum 20 min). A 5 min mean of the rate of oxygen consumption recorded during the prescribed experimental speed was used as the recorded \dot{V}_{O_2} for that trial. At sub-maximal speeds, animals were required to perform for a minimum of 45 min (including warm up). Experiments were terminated when an animal could not sustain the prescribed speed or would not walk consistently. At the completion of an exercise trial, the bird was allowed to recover while remaining within the respirometer until its \dot{V}_{O_2} returned to its resting level, at which point the bird was given at least an additional 30 min recovery time before the next exercise trial commenced.

The speed used in the incline experiments was the minimum speed at which all animals could sustain horizontal exercise for at least 25 min. At this speed (0.6 km h⁻¹ and hereafter called the 'cruising' speed), \dot{V}_{O_2} was 40–60% of the maximum recorded. This speed was chosen in order to induce a large increase in metabolic rate within the birds' aerobic scope (Ellerby et al., 2003), and at a speed that is above their walk–run transition speed (Gatesy, 1991; Gatesy, 1999). The walk–run transition speed was defined as the speed at which the body posture of the albatross changes, with the head, neck and torso becoming more parallel to the horizontal plane (regardless of treadmill angle). Animals were exercised at six different inclines (2–12%) in random order at the cruising speed in order to determine maximum incline and rate of oxygen consumption at maximal incline ($\dot{V}_{O_{2max, incline}}$). Each trial began with a 2–3 min warm up at 0.1–0.2 km h⁻¹ at 0% incline and the speed was then increased to 0.6 km h⁻¹ for an additional 2 min. At the completion of this warm-up, the incline was increased in 2% increments every 2 min until the designated test incline was reached. Each experiment was maintained for a sufficient length of time to enable acclimation of the animal and equilibration of oxygen levels (minimum 25 min). Longer acclimation and sampling times were required during the incline experiments, as both species took longer to settle into a rhythmic walking pattern. A 10 min mean of the oxygen consumption rate recorded during the prescribed experimental incline was used as the recorded \dot{V}_{O_2} for that trial. At the completion of the exercise, trial birds were allowed to recover as above.

Mechanical work efficiency

Vertical mechanical work was calculated using the formula corrected for the angle of the treadmill:

$$W = MgU\{\sin[\arctan(\psi/100)]\}, \quad (1)$$

where W is vertical mechanical work rate in joules, ψ is the percentage treadmill incline (as displayed by the treadmill), M is mass in kg, g is the force of gravity, and U is velocity. The factor $\sin[\arctan(\psi/100)]$ is the conversion factor from percentage incline to degrees incline of the treadmill. The net vertical efficiency (NVE) was then calculated as the vertical

mechanical work rate divided by the vertical metabolic power (incline metabolic rate – speed-matched level metabolic rate) multiplied by 100 (Full and Tullis, 1990) using the formula:

$$\text{NVE} = \frac{MgU\{\sin[\arctan(\psi/100)]\}}{(\dot{V}_{O_2\text{incline}} - \dot{V}_{O_2\text{cruising}})} \times 100, \quad (2)$$

where $\dot{V}_{O_2\text{incline}}$ is the rate of oxygen consumption during treadmill exercise at 0.6 km h⁻¹ and at the prescribed incline and $\dot{V}_{O_2\text{cruising}}$ is the rate of oxygen consumption during treadmill exercise at the cruising speed of 0.6 km h⁻¹ at 0% incline.

Video recording

Recordings were taken of each species while walking on the treadmill during both the speed and incline exercise trials using a Sony colour digital video camera (model DCV-HC40E) at 60 interlaced frames s⁻¹. File footage was downloaded into a Toshiba Tectra laptop computer for frame-by-frame analysis using Adobe Premiere 6.5 software. The position of the wooden frame used to secure the respirometer to the treadmill made it impossible to have a parallel view of the bird's feet, thus the camera position was elevated to 30° but remained perpendicular to the animal. Ten strides per speed per trial for each bird were analysed and stride length (L_s), and foot contact time (t_c) were determined from recorded trials. The inverse of foot-ground contact time was used to evaluate the rate of force generation as a predictor of differences in metabolic rate across speed in these two species (Kram and Taylor, 1990; Roberts et al., 1998).

To obtain morphological measurements, birds were anaesthetised using 3% isoflurane with O₂-enriched air. Leg length (L_1) was measured to the nearest 0.5 mm while in a natural

gait orientation. Natural gait was determined by matching limb position to digital photographs of undisturbed animals walking on relatively flat ground within their perspective colonies. L_1 was measured from the greater trochanter of the femur to the flexor tuberculum of the tarsometatarsal on both legs of each bird. Measurements were taken in replicates of five, and the means were used in further analysis.

Analysis

All statistical analyses were performed using 'R' v 2.3.1. Data are presented as means ± s.e.m. Slopes and intercepts of fitted relationships (including total body mass as a covariate when appropriate) were tested for difference from equality using Welch two-sample *t*-tests or analysis of covariance (ANCOVA) (Zar, 1998). For all tests, *P* was set at 0.05.

Maximum speeds, maximum inclines achieved, $\dot{V}_{O_2\text{max, speed}}$, and $\dot{V}_{O_2\text{max, incline}}$, were compared between species using nested repeated-measures (RM) ANCOVAs. Analysis was performed with species as the fixed factors and individual × species as the random factors. Prior to this, homogeneity of regression of the slopes was checked with a nested repeated-measures (RM) ANCOVA species × speed interaction and species × incline interaction in a model that included the following fixed factors: species + speed + species × speed, or species + incline + species × incline and the random factors: individual nested with species.

For exercising birds, \dot{V}_{O_2} and $1/t_c$, were compared using nested RM-ANCOVA with the following fixed factors: species + speed and a random factor: individual nested with species. Prior to this, homogeneity of regression slopes was checked with a nested RM ANOVA species × speed interaction, in a model that included the following fixed factors:

Table 1. The inter- and intra-species leg length, stride length at maximal speed and maximal incline, rate of force production, net vertical efficiency for black-browed albatross and grey-headed albatross

Comparisons	BBA	GHA	<i>F</i>	<i>P</i>
Morphological measurements				
Inter-species				
Mass (kg)	3.54±0.35	3.24±0.45	4.46 _{1,14}	0.894
L_1 (cm)	23.00±0.21	24.95±0.28	17.29 _{1,14}	0.004
$L_{s,\text{max, speed}}$ (cm)	15.80±0.27	15.74±0.35	0.01 _{1,14}	0.497
$L_{s,\text{max, incline}}$ (cm)	3.90±0.13	5.96±0.10	30.07 _{1,14}	0.000
Max. $1/t_{c,\text{incline}}$	3.09±0.16	2.60±0.07	42.46 _{1,14}	0.005
Max. $1/t_{c,\text{speed}}$	2.49±0.08	2.76±0.20	11.45 _{1,14}	0.049
Min. NVE	25.02±15.89	47.09±25.48	27.52 _{1,14}	0.000
Max. NVE	17.29±5.28	16.74±8.86	0.02 _{1,14}	0.878
Regression slope of mean NVE vs % incline	-0.69	-3.29	18.57 _{1,14}	0.019
	BBA		GHA	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Intra-species				
$L_{s,\text{max, speed}}$ vs $L_{s,\text{max, incline}}$	29.03 _{1,10}	0.001	31.65 _{1,4}	0.003
NVE _{incline} min. vs max.	0.33 _{1,10}	0.999	38.15 _{1,4}	0.000
$1/t_{c,\text{speed}}$ min. vs max.	46.46 _{1,10}	0.000	33.42 _{1,4}	0.000
$1/t_{c,\text{incline}}$ min. vs max.	19.33 _{1,10}	0.000	37.15 _{1,4}	0.011

BBA, black-browed albatross; GHA, grey-headed albatross; L_1 , leg length; L_s , stride length (at maximal speed and maximal incline); $1/t_c$, rate of force production; NVE, net vertical efficiency.

Values are means ± s.e.m. ($N=11$ BBA, 5 GHA), as tested by RM-ANCOVA or GLM.

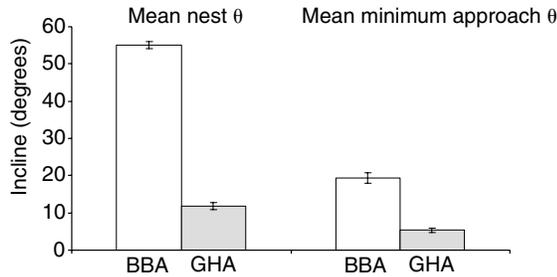


Fig. 2. Minimum approach angle (θ ; t -test: $t=16.7428$, $P=0.015$) and nest angle (θ ; t -test: $t=2.8339$, $P<0.000$) in degrees from horizontal of the ground surrounding the nest (see Fig. 1). Values are means \pm s.e.m. for 11 black-browed albatrosses (BBA; open columns) and 5 grey-headed albatrosses (GHA; filled columns).

species+speed+species \times speed or species+incline+species \times incline and a random factor: individual nested with species.

Results

There was no significant difference in mean mass between the two species (Table 1). There were significant differences between the two species in both mean nest θ and minimum approach θ (Fig. 2). The mean nest θ was $55.01\pm 0.89^\circ$ for the black-browed albatross and $11.70\pm 0.94^\circ$ for the grey-headed albatross, and the minimum approach θ were $19.40\pm 1.42^\circ$ and $5.30\pm 0.69^\circ$, respectively.

Mean maximal speeds differed significantly between the two species (Fig. 3A; Table 2). When performing on the flat, GHA were able to walk approximately 12% faster than BBA.

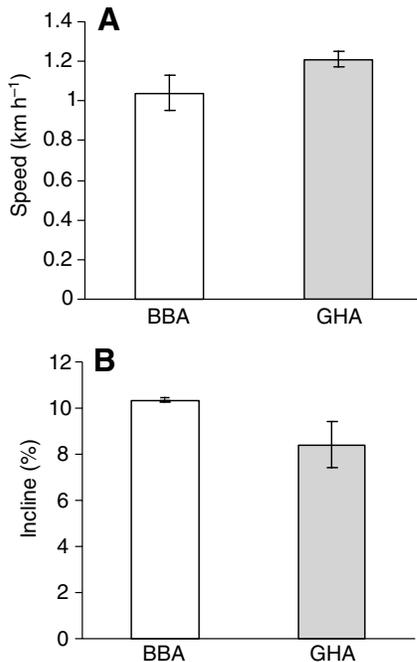


Fig. 3. (A) Mean (\pm s.e.m.) maximal speeds (km h⁻¹) achieved by 11 black-browed albatross (BBA; open columns) and 5 grey-headed albatross (GHA; filled columns), when walking on the treadmill with a 0% incline. (B) The mean maximal percent incline achieved by GHA and BBA, when walking on the treadmill at a speed of 0.6 km h⁻¹.

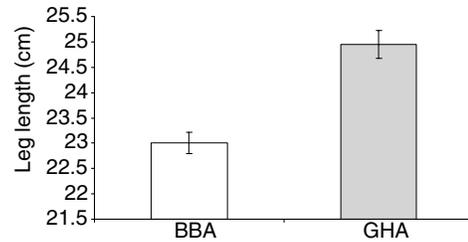


Fig. 4. Leg length (mean \pm s.e.m.) of the 11 black-browed albatross (BBA) and 5 grey-headed albatross (GHA). There is a significant difference between the species ($P=0.004$).

Whereas, BBA could walk at a significantly greater mean maximal incline at 0.6 km h⁻¹ than the GHA (Fig. 3B; Table 2).

ANCOVA indicated that mean L_1 was significantly shorter in BBA than in GHA (Fig. 4; Table 1). When on the flat, mean $L_{s,max, speed}$ of BBA was not significantly different from that of GHA (RM-ANCOVA; Table 1). There was, however, a significant difference in mean $L_{s,max, incline}$ between the BBA and GHA (Fig. 5A; Table 1). Intra-species analysis indicated that in both species, mean L_s was significantly shorter during maximal incline exercise than during maximal speed exercise (Fig. 5A,B; Table 1).

There was no significant difference in \dot{V}_{O_2} while standing between the BBA and the GHA (Table 3, Fig. 6A). Both BBA and GHA were able to walk at a ‘cruising’ speed of 0.6 ± 0.03 km h⁻¹ at 0% incline for more than 60 min, including the 3–5 min warm up. No significant difference was seen between species in mean \dot{V}_{O_2} at the cruising speed and 0% incline (Fig. 6B; Table 3). There was also no significant difference between species in mean $\dot{V}_{O_{2max, speed}}$ on the flat (Fig. 6C), and between species in mean $\dot{V}_{O_{2max, incline}}$ (Fig. 6D). Intra-species analysis showed no significant difference between mean $\dot{V}_{O_{2max, speed}}$ and mean $\dot{V}_{O_{2max, incline}}$ (Fig. 6C/D; Table 3).

RM-ANCOVA has shown that there were significant differences (Fig. 7; Table 1) in the rates of force generation

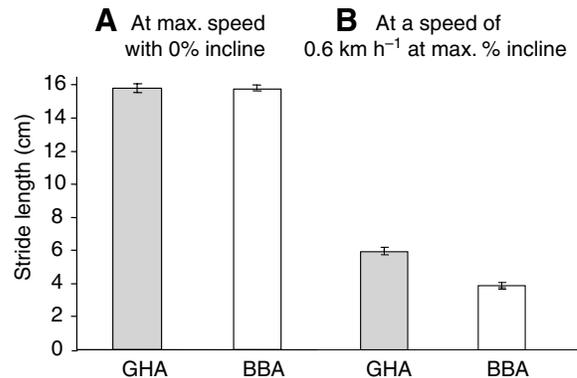


Fig. 5. (A) Stride length (L_s) (mean \pm s.e.m.) achieved by five grey-headed albatross (GHA) and 11 black-browed albatross (BBA), when walking on the treadmill at maximal speed with 0% incline ($P=0.497$). (B) Mean (\pm s.e.m.) L_s , when walking on the treadmill at a speed of 0.6 km h⁻¹ at maximal % incline. Significant differences can be seen between species ($P=0.000$). There is also a significant difference ($P=0.003$) in both BBA and GHA between L_s when performing on the flat (A) and on the incline (B).

Table 2. Maximal speed at 0% incline and mean maximal incline (%) at 0.6 km h⁻¹ for the treadmill exercise trials for black-browed albatross and grey-headed albatross

Trial	BBA	GHA	F	P
Max. speed (km h ⁻¹) at 0% incline	1.04±0.09	1.21±0.04	11.82 _{1,14}	0.004
Max. incline (%) at 0.6 km h ⁻¹ speed	10.30±0.51	8.40±1.00	14.76 _{1,14}	0.002

BBA, black-browed albatross; GHA, grey-headed albatross.

Values are means ± s.e.m. (N=11 BBA, 5 GHA), as tested by RM-ANCOVA.

Table 3. Inter- and intra species mean rates of oxygen consumption for the treadmill exercise trials for black-browed albatross and grey-headed albatross

Trial	Rate of oxygen consumption (ml min ⁻¹)		F	P
	BBA	GHA		
Inter-species				
Standing	47.20±2.60	45.90±3.93	0.89 _{1,14}	0.999
Cruising speed of 0.6 km h ⁻¹ at 0% incline	126.60±10.85	137.40±11.99	1.24 _{1,14}	0.393
Max. speed at 0% incline	220.25±8.29	233.34±12.29	0.38 _{1,14}	0.653
Max. incline at 0.6 km h ⁻¹	231.50±11.99	240.30±10.85	0.98 _{1,14}	0.985
	BBA		GHA	
	F	P	F	P
Intra-species				
Max. speed at 0% incline vs max. incline at 0.6 km h ⁻¹	0.87 _{1,10}	0.825	0.12 _{1,4}	0.999

BBA, black-browed albatross; GHA, grey-headed albatross.

Values are means ± s.e.m. (N=11 BBA, 5 GHA), as tested by RM-ANCOVA.

(1/*t_c*) between these species during both maximal speed and maximal incline exercise. Intra-species comparisons showed that for both the BBA and GHA, the 1/*t_c* produced were significantly greater at maximal speed than those at minimum speed and at maximal incline compared to those at minimum incline (Fig. 7; Table 1).

Inter-species RM-ANCOVA (Fig. 8; Table 1) revealed significant differences between the slopes of mean NVE and between the values of mean NVE recorded at minimum incline (2%). There was no significant difference in mean NVE at the maximum incline at which the BBA and GHA could perform (10% and 8.4%, respectively). Intra-species analysis showed that the mean NVE produced by the GHA at the minimum incline was significantly greater than that at maximal incline (Fig. 8; Table 1); however, no difference was seen in the BBA (Fig. 8; Table 1).

Discussion

This study has demonstrated important differences in the locomotory ability of black-browed and grey-headed albatrosses. GHA were able to achieve significantly higher walking speeds on level ground, whereas the BBA performed

on a significantly greater incline. Nest topography differed significantly: on average, BBA nests were in steeper areas and had steeper minimal approach angles. Therefore, at all attempts to move along the ground within their colony, BBA must deal with steeper inclines. GHA were able to perform at 0% incline at a mean maximum speed, which was significantly higher than that of BBA without reaching a significantly different \dot{V}_{O_2} . In addition, BBA can sustain a 'cruising' speed of 0.6 km h⁻¹ on a significantly steeper incline than GHA, although both reach similar \dot{V}_{O_2} maxima. The question is how are BBA able to perform better on the incline without incurring significantly higher metabolic costs than those of their congener?

It has been proposed that *L_s* should correlate with *L₁* (Hoyt et al., 2000), and that up to 20% of the energetic cost of locomotion is due to the muscular action used to swing the limb (Ellerby and Marsh, 2006; Marsh et al., 2006). Animals with longer limbs and strides tend to have lower transport costs, as the rate of vertical force generation decreases with longer stance periods (Kram and Taylor, 1990). Therefore, we might speculate that the longer *L₁* and *L_s* found in the GHA accounts for the lower

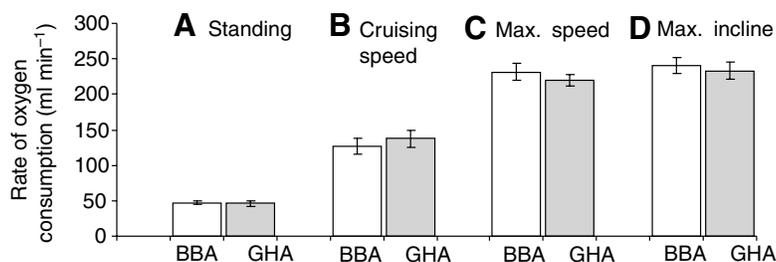


Fig. 6. Rate of oxygen consumption (\dot{V}_{O_2} in ml min⁻¹) for all the exercise trials (mean ± s.e.m.) conducted on 11 black-browed albatross (BBA) and 5 grey-headed albatross (GHA): (A) non-significant difference in between birds standing on the treadmill without any movement; (B) at cruising speed of 0.6 km h⁻¹ at 0% incline; (C) at maximum speed reached by each species; (D) at maximum incline reached by each species.

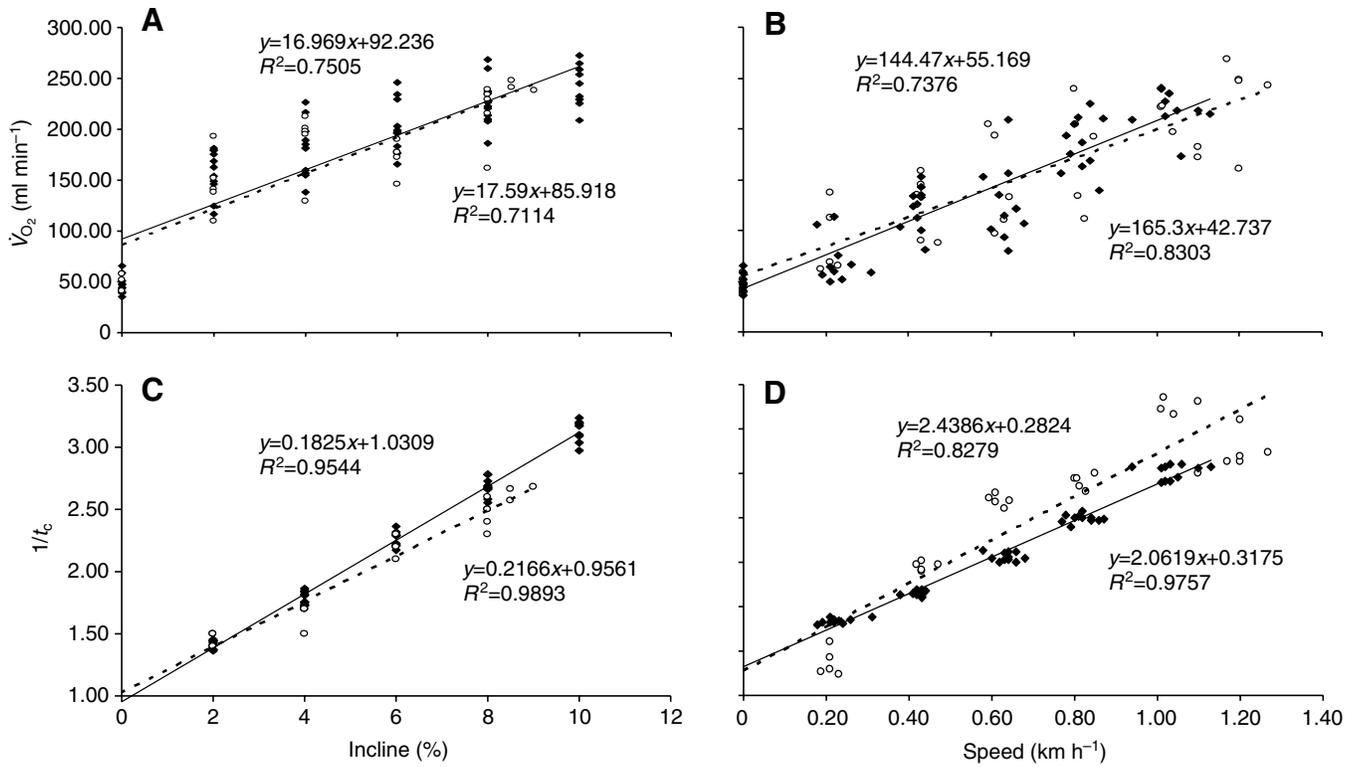


Fig. 7. (A) Rate of oxygen consumption (\dot{V}_{O_2} , ml min⁻¹) achieved by the grey-headed (open circles, $N=5$) and black-browed albatross (filled diamonds, $N=11$), when walking on the treadmill at 0.6 km h⁻¹ at varying % inclines. (B) Rate of oxygen consumption achieved by the grey-headed albatross and black-browed albatross when walking on the treadmill at varying speeds. (C) Rate of force generation ($1/t_c$) achieved by the grey-headed albatross and black-browed albatross when walking on the treadmill at 0.6 km h⁻¹ at varying % inclines. (D) $1/t_c$ achieved by the grey-headed albatross and black-browed albatross when walking on the treadmill at varying speeds.

rates of oxygen consumption recorded in comparison to the BBA when performing at the same speeds on the flat. Hoyt et al. suggested that, for a given species, longer limbs may decrease the force necessary to support body mass (Hoyt et al., 2000). However, the increased cost of swinging longer heavier limbs may nullify the simple univariate relationship between limb length and locomotory cost, resulting in no net gain (Hoyt et al., 2000; Marsh et al., 2004). As BBA have shorter L_1 and L_s

than GHA at the same speed on the flat, they must be utilising a greater stride frequency than GHA. Using a mathematical model, Kuo concluded that stride frequency is a significant determinant of the metabolic cost of swinging the limbs during walking (Kuo, 2001). However, mechanical work must be performed to redirect the centre of mass from the pendular arc in the transition from one step to the next (Kuo, 2002). The metabolic energy needed to perform this work could be minimized by taking short steps (Donelan et al., 2002).

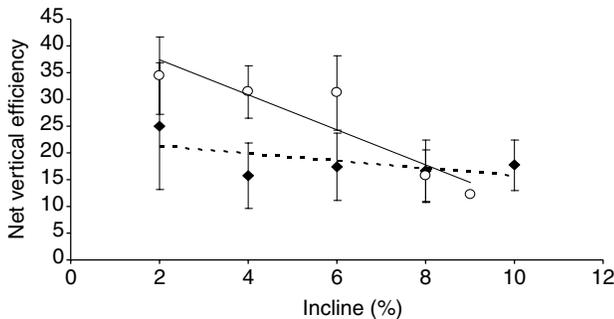


Fig. 8. Net vertical efficiency (mean ± s.e.m.) for 5 grey-headed albatross (GHA, open circles and solid line) and 11 black-browed albatross (BBA, filled diamonds and broken line), when walking on the treadmill with at different percent inclines ranging between 2–12%. Regression equation for GHA: $y=-3.29x+44.04$, $R^2=0.84$, and for BBA: $y=-0.69x+22.65$, $R^2=0.35$. The GHA data point at 9% represents only one animal; the others were unable to perform at this level.

GHA have a greater mean NVE when exercising below an 8% incline, at which point mean NVE becomes equal to that of BBA, above which they are unable to perform. Conversely, BBA show similar NVE regardless of the incline and are able to perform at a much greater incline than the GHA, suggesting that they have a single gait that it is optimised for steeper inclines. The shorter L_s combined with the greater rate of force production at the steeper inclines could reflect the use of quick, short and vertically powerful strides by the BBA, maximising the force production while minimising the effort of each leg needed to traverse the slope. This suggests that BBA have adopted a gait behaviour that minimises the cost of incline locomotion.

The present study has shown that these two species of albatross have evolved behavioural differences (L_s and $1/t_c$) and morphological adaptations (L_1) that minimise the cost of moving around their colony sites. It is clear that there is a relationship between terrestrial performance and topography of the colony and it is logical that the species that inhabits the steeper colony

site would be the best adapted for moving up an incline. Each species has evolved greater locomotor abilities in their respective environments that are not associated with differences in the metabolic cost of locomotion. The greater maximum speed of GHA on the level is not associated with a decreased rate of force generation, as would be predicted from their greater leg length. At moderate inclines the NVE of the GHA is significantly higher than that of the BBA. Although at the maximum incline at which the GHA can perform their NVE is similar to that of the BBA, the BBA can maintain a similar NVE on significantly steeper inclines, allowing similar rates of oxygen consumption at different maximal inclines.

The results of this study correspond well with the observed behaviour of both albatross species at the colony; GHA tend to run several steps prior to take-off whereas BBA walk to the nearest cliff edge or take off directly from their nest mound. However, it is difficult to determine whether this relationship is causal, as selection pressures may operate more strongly away from the colony. During calm or light wind conditions at sea, if an albatross wants to take off from the water it must run into the wind along the sea surface while beating its wings to gain sufficient lift, which is thought to be its most energetically costly activity (Warham, 1996; Weimerskirch et al., 2000). Although there is considerable overlap in feeding areas of BBA and GHA during the chick-rearing period, during the incubation period BBA females forage further north than male or female GHA (Phillips et al., 2004). Moreover, during the non-breeding periods these species migrate to quite distinct geographical regions that experience dissimilar prevailing weather systems (Croxall et al., 2005; Phillips et al., 2005). It is possible, therefore, that the differences in terrestrial performance reflect behavioural and morphological adaptations that minimise energy expenditure during take-off at sea, and that this influenced site topography preferences when colonies were established at breeding islands.

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