Basal Metabolic Rate of the Black-Faced Sheathbill (*Chionis minor*): Intraspecific Variation in a Phylogenetically Distinct Island Endemic

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ABSTRACT

Metabolic rate is a fundamental characteristic of all organisms. It covaries most significantly with activity, body mass, seasonality, and temperature. Nonetheless, substantial additional variation in metabolic rate, especially either resting rate or basal rate, is associated with a range of factors including phylogenetic position, ecological distinctiveness, range position, and diet. Understanding this variation is a key goal of physiological ecology. The black-faced sheathbill is a phylogenetically distinct, high-latitude, island-endemic bird occurring exclusively on several archipelagos in the southern Indian Ocean. Here we examined the idea that the unique phylogenetic position and ecology of the black-faced sheathbill may lead to a basal metabolic rate (BMR) different from that predicted by its body mass. When compared with BMR data available for all birds and a subset of island species, it was clear that the BMR of the black-faced sheathbill on subantarctic Marion Island, estimated at 15°C using indirect calorimetry (2.370 ± 0.464 W, mean ± SD; $n = 22$), for a group of birds with a mean mass of 459 ± 64 g, is no different from that expected based on body mass. However, variation in BMR, associated with habitat use and diet, even when correcting for variation in mass, was found. Sheathbills foraging year-round in comparatively resource-rich king penguin colonies have a higher BMR (2.758 ± 0.291 W, $n = 12$) than sheathbills that split their foraging between rockhopper penguin colonies and the intertidal zone (2.047 ± 0.303 W, $n =$ 10), which are poorer in resources. Because these populations coexist at relatively small spatial extents (the entire island is 290 km²), other factors seem unlikely as causes of this variation.

Keywords: Chionidae, endemism, energetics, insular, metabolic diversity.

Introduction

Basal metabolic rate (BMR) is the rate of metabolism of a resting, normothermic, postabsorptive, nonreproductive endotherm, measured during the inactive circadian phase at a thermoneutral temperature (McNab 1997). It accounts for upward of 40%–50% of the total daily energy budget in free-living individuals (Bryant 1997) and is a significant correlate of behavior, distribution, and life history (Brown et al. 2004; White et al. 2007*a*). In turn, BMR is influenced most significantly by body mass and to a lesser extent by temperature (White et al. 2007*b*; White and Kearney 2012) and also shows substantial residual variation. This residual variation has phylogenetic (Hayssen and Lacy 1985; Kozlowski and Konarzewski 2004), ecological (Lovegrove 2000; McNab 2003*a*, 2009), and geographic (McNab 2002; Wikelski et al. 2003) components.

Species or groups that are phylogenetically or ecologically distinct often have BMRs different from those expected from allometry or temperature alone (McNab 1995, 1996; Bozinovic et al. 2004). In birds, many taxa have been studied, often comprehensively (McKechnie and Wolf 2004; Jetz et al. 2008; McNab 2009). However, several significant clades have not been investigated. Many of these are unusually placed on the bird phylogeny, are restricted to islands, or have unusual life histories. In consequence, they might be expected to add substantial variation to the distribution of bird BMR (McNab 1992; White et al. 2012), although the likely scope of this additional variation remains poorly known.

A hitherto little-studied suite of factors that may further contribute to variation in avian BMR is associated with conspecific populations that have distinct habitats or diets or are separated spatially (McNab 2003*a*, 2009; Piersma et al. 2004; McKechnie and Swanson 2010). Such among-population and among-individual trait variation is increasingly being recognized as an important contributor to the structuring of assemblages (Bolnick et al. 2011; Violle et al. 2012). Investigating the magnitude and source(s) of intraspecific metabolic variation is therefore important for understanding BMR evolution (Konarzewski and Książek 2012) and the ways in which assemblages are structured.

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Here, we test the ideas that phylogeny and endemism should contribute to variation in BMR in addition to that expected from allometry and that colocated populations that experience quantitative and/or qualitative differences in resource availability should differ in energetic traits such as BMR. We do so using the black-faced sheathbill (*Chionis minor* Hartlaub) from subantarctic Marion Island. The family Chionididae is phylogenetically distinct, serving as an intermediate between the more typical wader-like Charadriiformes and the morphologically specialized marine clade comprising alcids, gulls, and allies (Livezey 2010). Comprising four morphologically (Bried and Jouventin 1997) and genetically (Viot et al. 1993) distinct subspecies, each restricted to their respective archipelagos in the southern Indian Ocean, black-faced sheathbills are members of the small ecological group of temperate island-endemic birds. Marion Island sheathbills are also well suited for examining intraspecific metabolic variation associated with factors related to foraging habitat and diet. Though all sheathbills can be described as opportunistic omnivores, the Marion Island population can be divided into two distinct and sympatric groups. One group (hereafter referred to as KP sheathbills) forages year-round in continuously occupied king penguin (*Aptenodytes patagonicus* Miller) colonies, where the sheathbills consume mostly the stomach contents of penguins obtained through kleptoparasitism, penguin carcasses, and excreta (Burger 1984). The second group (hereafter referred to as RH sheathbills) occupies eastern rockhopper penguin (*Eudyptes chrysocome filholi* Hutton) colonies during the penguins' breeding season, and their diet is similar to that of KP sheathbills during this period (Burger 1981*b*, 1984). However, when rockhopper penguins leave the island after their 5-mo breeding season (mid-November to mid-March; Crawford et al. 2003), RH sheathbills are forced to forage elsewhere for the remainder of the year. Many of these birds would traditionally forage for terrestrial invertebrates, but competition with invasive mice has lowered prey abundance to the point of dietary insignificance (Huyser et al. 2000; McClelland 2013). The majority of RH sheathbills currently forage in the intertidal zone, where they feed mainly on polychaete worms. The two sheathbill groups differ in body size, clutch size, chick production, and behavior (McClelland 2013). While the rate of philopatry is unknown, no breeding birds changed habitat groups over a 3-yr period ($n = 225$). Moreover, many territory-holding adults rarely traveled more than 200 m afield (G. T. W. McClelland and S. L. Chown, unpublished data), and some birds conceivably live beyond 2 decades within a few hundred meters of one another yet experience a disparate life history. Thus, the black-faced sheathbill on Marion Island offers a potentially tractable model to investigate the causes and consequences of intraspecific variation in avian metabolic rates.

Material and Methods

Study Site and Animal Capture

This study took place on subantarctic Marion Island (46°54′S, 37°45′E). The island is situated to the north of the Antarctic Polar Front and together with smaller Prince Edward Island

makes up the Prince Edward Island group. Though the two islands lay 19 km apart, sheathbills appear to be reluctant to leave shore, and no exchange of individuals between the two islands has been recorded. Marion Island has an area of 290 km² and a total coastline of 72 km. The island's climate is best described as oceanic, characterized by strong winds, high humidity and rainfall, and low daily temperature variation (mean monthly temperatures range between 3° and 8.5°C). A comprehensive overview of the climate, geology, and biology of the islands is provided by Chown and Froneman (2008).

Measurements took place during April and May 2011, several weeks after the sheathbill breeding season and the start of winter foraging behavior. Sheathbills were captured by hand within a 5-km stretch of coastline east of the research station (fig. 1). All individuals were selected from a 3-yr study population, and only adults that had bred or attempted to breed during the preceding breeding season were measured. Birds were weighed to the nearest 5 g using a 1,000-g Pesola spring scale (± 3 g; Baar, Zug, Switzerland). Measurements occurred near the end of the wing molt period, and molt status was determined from plumage examination (molt scores of ≥ 47; de Beer et al. 2001). The study, which includes individually marked birds (McClelland 2013), enabled us to distinguish birds from the RH and KP groups, and 12 and 10 birds were sampled from each group, respectively. Of these, 9 and 4 were female birds, respectively, sexed on the basis of mate comparison, where the smaller member of the breeding pair is considered female (Burger 1980).

Birds were housed in individual shade cloth cages (0.15 m³) in a room kept at outdoor ambient air temperature (5.0° ± 1.8°C SD, measured by a standard mercury thermometer, read every hour). All birds were released within 26 h of capture. The work was done under ethics permit 11NP_CHO01 from
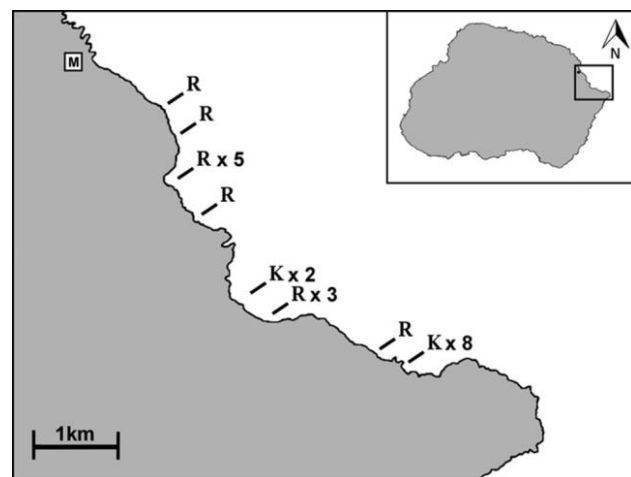

Figure 1. Sheathbill study area depicting the territory locations of measured king penguin (K) and rockhopper (R) sheathbills (x indicates the number of birds from each location if greater than 1) and the island research station (M).

Table 1: Avian species restricted to islands in which basal metabolic rate has been investigated

Species	M_b (g)	BMR (W)	Climate	Island size	Flight	Origin	n	Reference
Palila (*Loxioides bailleui*)	34.8	.447	Tr	I	Y	C	4	Weathers and Riper 1982
ʻApapane (*Himatione sanguinea*)	13.5	.300	Tr	I	Y	W/C	4/4	Weathers et al. 1983
Tui (*Prosthemadera novaeseelandiae*)	144.2	1.106	Te	L	Y	C	Unknown	McNab 2009
Kea (*Nestor notabilis*)	836.9	4.439	Te	L	Y	C	2	McNab and Salisbury 1995
Kākā (*Nestor meridionalis*)	369.3	2.142	Te	L	Y	C	2	McNab and Salisbury 1995
Greater vasa parrot (*Coracopsis vasa*)	454.0	4.372	Tr	L	Y	C	8	Lovegrove et al. 2011
Yellow-crowned parakeet (*Cyanoramphus auriceps*)	52.9	.492	Te	L	Y	C	7	McNab and Salisbury 1995
Red-crowned parakeet (*Cyanoramphus novaezelandiae*)	56.1	.622	Te	L	Y	C	8	McNab and Salisbury 1995
Antipodes parakeet (*Cyanoramphus unicolor*)	129.4	1.081	Te	S	Y	C	2	McNab and Salisbury 1995
Puerto Rican tody (*Todus mexicanus*)	6.3	.114	Tr	I	Y	W	26	Merola-Zwartjes and Ligon 2000
Black-faced sheathbill (*Chionis minor*)	459.0	2.370	Te	S	Y	W	22	This study
Takahē (*Porphyrio hochstetteri*)	2,758.3	6.886	Te	L	N	C	2	McNab and Ellis 2006
Inaccessible island rail (*Atlantisia rogersi*)	39.4	.225	Te	S	N	W	6	Ryan et al. 1989
Weka (*Gallirallus australis*)	813.5	1.828	Te	L	N	C	1	McNab and Ellis 2006
Guam rail (*Gallirallus owstoni*)	198.8	.917	Tr	S	N	C	2	McNab and Ellis 2006
Metallic pigeon (*Columba vitiensis*)	467.9	1.444	Tr	I	Y	C	2	McNab 2000
White-crowned pigeon (*Patagioenas leucocephala*)	251.9	1.344	Tr	I	Y	C	Unknown	McNab 2000
Nicobar pigeon (*Caloenas nicobarica*)	613.0	1.814	Tr	S	Y	C	3	McNab 2000
Western crowned pigeon (*Goura cristata*)	2,313.4	4.267	Tr	L	Y	C	6	McNab 2000
Pacific imperial pigeon (*Ducula pacifica*)	333.4	.794	Tr	S	Y	C	4	McNab 2000
Island imperial pigeon (*Ducula pistrinaria*)	394.2	1.072	Tr	I	Y	C	3	McNab 2000
New Zealand pigeon (*Hemiphaga novaeseelandiae*)	435.6	1.883	Te	L	Y	C	3	McNab 2000
Cloven-feathered dove (*Drepanoptila holosericea*)	198.0	.825	Tr	I	Y	C	2	Schleucher and Withers 2002
Blue duck (*Hymenolaimus malacorhynchos*)	717.1	3.142	Te	L	Y	C	3	McNab 2003b
Paradise shelduck (*Tadorna variegata*)	1,193.6	3.344	Te	L	Y	C	2	McNab 2003b
Black teal (*Aythya novaeseelandiae*)	488.4	2.333	Te	L	Y	C	2	McNab 2003b
Auckland teal (*Anas aucklandica*)	373.1	1.875	Te	S	N	C	2	McNab 2003b
Brown teal (*Anas chlorotis*)	528.8	2.319	Te	L	Y	C	2	McNab 2003b
Campbell Island teal (*Anas nesiotis*)	371.1	1.650	Te	S	N	C	2	McNab 2003b
Southern brown kiwi (*Apteryx australis*)	3,137.0	4.611	Te	L	N	C	3	McNab 1996
Great spotted kiwi (*Apteryx haastii*)	2,529.0	5.283	Te	L	N	C	2	McNab 1996
Little spotted kiwi (*Apteryx owenii*)	1,377.0	3.947	Te	L	N	C	2	McNab 1996

Note. M_b = body mass; BMR = basal metabolic rate. For climate, Te = temperate, and Tr = tropical. For island size, L ≥ 100,000 km², I ≥ 1,000 km², and S ≤ 1,000 km². For flight, volant = Y, and flightless = N. For origin, C = captive raised, and W = wild caught.

Stellenbosch University and with the approval of the Prince Edward Islands Management Committee.

Gas Exchange Measurements

Metabolic rate was estimated by indirect calorimetry from measurements of oxygen consumption ($\dot{V}_{O_2}$) obtained using an open flow-through respirometry system as set out in Lighton (2008) and set up at the island's research station. Only one bird was measured at a time. Birds were placed in a darkened 30-L (width and length = 300 mm, height = 333 mm) plastic chamber within a custom-built insulated environmental chamber. Each plastic chamber was airtight, with two short copper tubes affixed for air inlet and outlet. A wooden grate was placed in the bottom of the chamber for the bird to stand on. Air temperature within the environmental chamber (here considered ambient temperature, T_a) was measured using two calibrated Thermochron iButton data loggers (model DS1923, Dallas, TX).

Air was drawn from an unoccupied room (with an open window; high rainfall and humidity and low ambient temperatures meant that we did not use outside air directly) using an air pump (Microvood) and passed through Bev-A-Line tubing (Thermoplastic Processes, Georgetown, DE; ca. 9.5 mm internal diameter) to a silica gel/soda lime/silica gel column, which scrubbed carbon dioxide and water vapor. The air stream was then split into two lines, the flow rate of each regulated by a mass flow controller (model 840, Sierra Instruments, and MFC2, Sable Systems, Las Vegas, NV), factory calibrated, and then checked against a set of custom-built rotameters. One line supplied the respirometry

chamber at 8,000 mL min^{-1}, ensuring adequate mixing in the chamber and maintaining [O_2] depletion of <0.5% between the incurrent air and the excurrent air. The excurrent air from the chamber was subsampled with a subsampler mass flow meter unit (SS4; Sable Systems), passed through a soda lime/silica gel column, and then to an Oxzilla II oxygen analyzer (Sable Systems) to measure fractional [O_2] concentration. The second air stream flowed directly to the oxygen analyzer to establish a baseline and account for any temperature-related drift that may have occurred. Output from the oxygen analyzer was digitized using a Universal Interface II (Sable Systems) and recorded on a personal computer using Expedata data acquisition software (Sable Systems), with a sampling interval of 1 s. Baseline [O_2] was measured for 20 min before and after each $\dot{V}_{O_2}$ measurement.

The lowest 10-min mean $\dot{V}_{O_2}$ over the test period was assumed to represent resting values, following Liknes et al. (2002). Because carbon dioxide and water vapor were scrubbed before and after passing through the respirometry chamber, oxygen consumption was calculated using equation (9.12) of Lighton (2008). All measurements were obtained at night, during the rest phase of the birds' circadian cycle (Burger 1982). Measurements began at least 30 min after sunset and ended no later than 30 min before sunrise. Individual measurement periods lasted 3–6 h. To ensure that birds were awake and resting calmly during measurements, they were monitored inside the chamber with an infrared webcam (Genius eface 1325r). Water was provided ad lib., but food was withheld until after metabolic measurements, which occurred ≥9 h after capture. The allometrically expected passage rate for an average-sized sheathbill (459 g) is 109.7 min, following Ka-
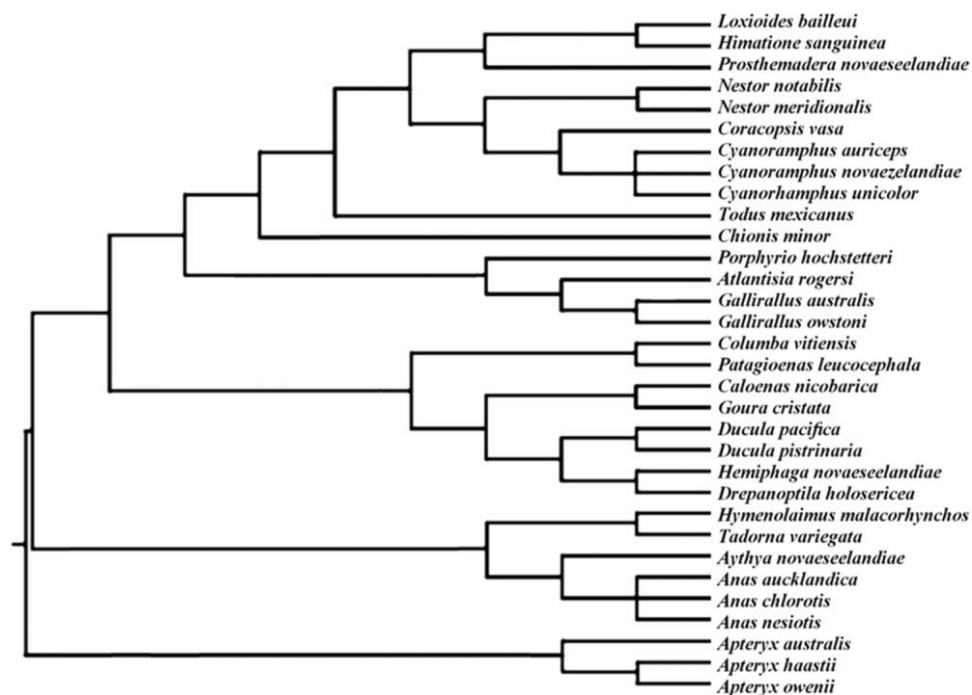

Figure 2. Phylogeny of 32 avian species occurring on islands in which basal metabolic rate has been investigated.

rasov (1990), and birds could reasonably be considered to be postabsorptive. The oxygen analyzer was tested for temperature-associated drift (i.e., baseline [O_2] was measured) every 30 min.

Seven individuals examined were subjected to a ramped T_a profile during each test to determine the thermoneutral zone (TNZ). Each bird experienced temperatures of 1°, 5°, and 15°C for 3 h, respectively, during a single measurement session. Sheath-bills alter their behavior when experiencing exceptionally high temperatures (G. T. W. McClelland, personal field observations), and we sought not to measure stress-related metabolism. We therefore chose 15°C as the maximum temperature, given that it is well within the maximum ambient and microclimate tem-peratures recorded for the island (Chown and Froneman 2008).

Oxygen consumption rate was corrected to milliliters of oxy-gen per hour at standard temperature and pressure, dry. Sheath-bills were assumed to have a respiratory quotient (RQ) of 0.8 dur-ing BMR measurements, which minimizes error in the estimated rate of energy expenditure when RQ is unknown (Koteja 1996). Each individual's rate of oxygen consumption was hence con-verted to metabolic rate (W) using a conversion factor of 20.1 kJ L^{-1} O_2 (Schmidt-Nielsen 1997). BMR was considered the lowest $\dot{V}_{O_2}$ across the range of temperatures measured (Doucette and Geiser 2008) and then subsequently determined for these lowest values for all birds over a consecutive 10-min period.

Statistical Analyses

To assess variation associated with temperature, and therefore to determine whether birds were likely to be within their TNZ, we compared metabolic rate among birds measured across the three temperatures using a linear mixed-effects model (Gałecki

and Burzykowskie 2013), with bird identity as a random factor and temperature and mass as fixed factors, implemented in the R package *lme4* (Bates et al. 2011) and fitted using maximum likelihood. Significance was assessed by comparing this model with a null model excluding temperature.

ANCOVA with body mass (M_b) as a covariate was used to investigate BMR variation associated with membership of ei-ther the KP or RH groups, sex, and molt status after data were checked for normality using Shapiro-Wilks tests. Collinearity among predictor variables was assessed by variance inflation factors (VIFs), adopting a VIF threshold of 5 (Zuur et al. 2010). Least squares means were used in post hoc comparisons. Anal-yses were performed in the statistical software R 3.0.0 (R De-velopment Core Team 2010).

To compare the BMR of sheathbills to that of other birds, we used the overall mean BMR and body mass of individuals measured from both groups. Sheathbill BMR was compared with that of birds in general using data for wild-caught pop-ulations of 137 species analyzed by McKechnie et al. (2006), who used a phylogeny based primarily on Sibley and Alquist (1990). Phylogenetically independent 95% prediction intervals for the BMR of *Chionis minor* were calculated using PDTREE, follow-ing Garland and Ives (2000). We then repeated this analysis after rearranging the data following the phylogeny proposed more recently by Hackett et al. (2008), to assess the robustness of these conclusions.

The comparison was then narrowed to island endemics us-ing BMR and M_b data for sheathbills in this study and an addi-tional 31 species from the literature (table 1). In view of the general paucity of BMR measurements for island birds, data were included irrespective of sample size or population origin (wild
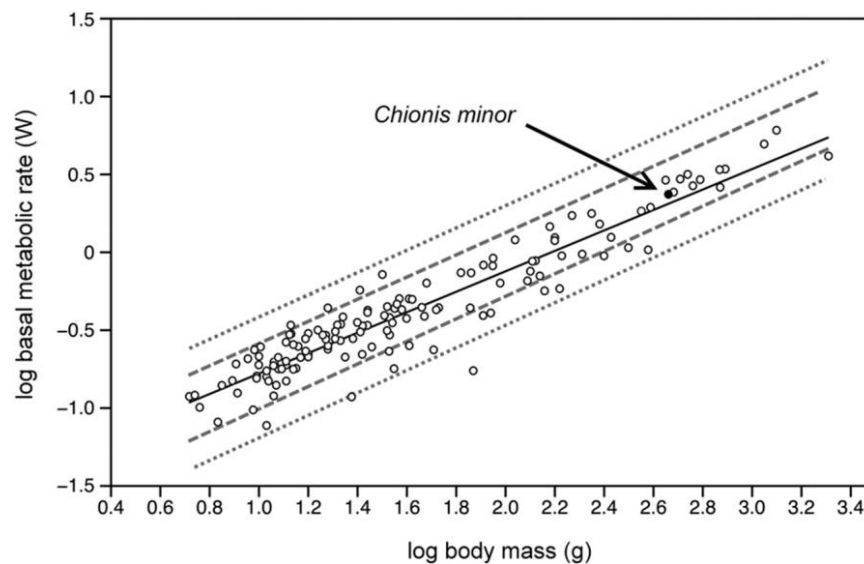

Figure 3. Ordinary least squares (i.e., nonphylogenetically independent) regression of the basal metabolic rate of 137 wild-caught avian species (black line; logBMR = $-1.437 + 0.656$logM_b). The gray dashed and dotted lines represent the phylogenetically independent 95% confidence and prediction intervals, respectively, based on the phylogeny proposed by Sibley and Alquist (1990). The body mass and basal metabolic rate values for the black-faced sheathbill are highlighted in black.
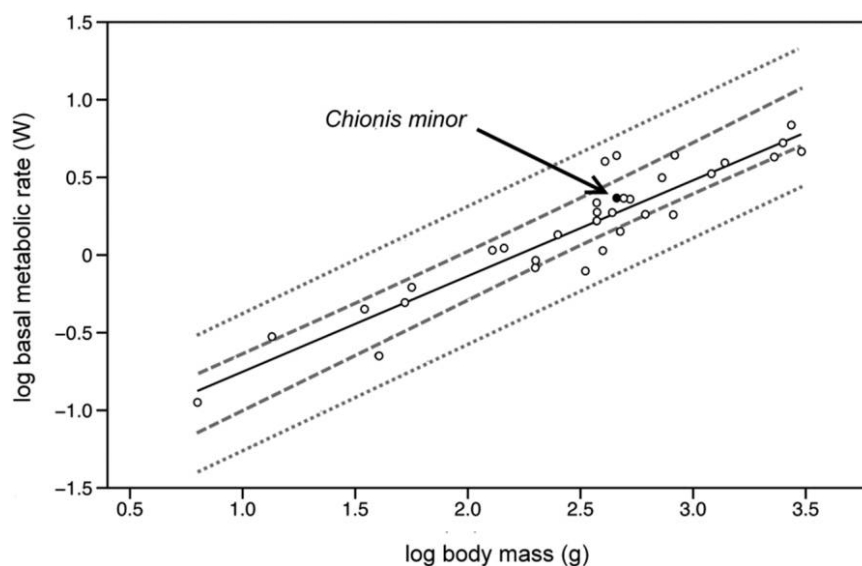
Figure 4. Ordinary least squares regression of the basal metabolic rate of 32 avian species restricted to islands (black line; $\log\text{BMR} = -1.369 + 0.617\log M_b$). The gray dashed and dotted lines represent the phylogenetically independent 95% confidence and prediction intervals, respectively, based on the phylogeny proposed by Hackett et al. (2008). The black-faced sheathbill is highlighted in black.

caught or captive raised) despite possible influences on results (McKechnie and Wolf 2004; McKechnie et al. 2006). We did not include birds restricted to the island of New Guinea, considering its recent (<17,000 yr) separation from Australia (Voris 2000). A phylogeny was constructed based on the topology proposed by Hackett et al. (2008), with relationships within the Psittaciformes, Columbiformes, Gruiformes, Anseriformes, and Apterygiformes based on Wright et al. (2008), Gibb and Penny (2010), Livezey (1998), Donne-Gousse et al. (2002), and Baker et al. (1995), respectively (fig. 2). Because all of the branch lengths in the phylogeny were not known, all branches in the model were set as equal. The phylogenetic variance-covariance matrix required for these analyses was obtained using the PDAP suite (Garland and Ives 2000) within the program Mesquite (Maddison and Maddison 2011) from the respective phylogenies. Phylogenetic signal was assessed following Revell (2010) using the R package *phytools* (Revell 2012). Since significant phylogenetic signal was detected (Pagel's $\lambda = 0.899$; 95% confidence interval $= 0.399$, significantly >0; $P < 0.001$), phylogenetically independent prediction intervals based on the sheathbill's position within the phylogeny were again calculated following Garland and Ives (2000).

Results

The lowest metabolic rates in the ramped T_a profile were recorded at 15°C, but values were not significantly different across the three temperatures (shown by no difference between the null model and the model including temperature; $\chi^2 = 2.5$, df $= 2$, $P = 0.29$), indicating that 15°C is not outside the TNZ. For this reason, and because 15°C falls within the range of TNZs observed in other Charadriiformes (Gabrielsen et al.

1988, 1991; Bryant and Furness 1995), we undertook further measurements at 15°C.

Mean mass of the 22 sheathbills was 459.0 g (SD $= 64$, min $= 360$, max $= 600$), and mean whole-animal BMR was 2.370 W (SD $= 0.464$, min $= 1.599$, max $= 3.165$). The slopes of the regressions were $\log\text{BMR} = -1.435 + 0.657\log M_b$ (GLM: $F = 1063.4$, df $= 1, 135$, $P > 0.001$, $r^2 = 0.887$) for all wild-caught populations and $-1.366\log\text{BMR} + 0.619\log M_b$ (GLM: $F = 254.9$, df $= 1, 30$, $P > 0.001$, $r^2 = 0.895$) for island birds. The BMR datum for sheathbills fell within the phylogenetically independent 95% confidence and 95% prediction intervals when compared to both other wild-caught populations (figs. 3, A1) and birds restricted to islands (fig. 4). The former conclusion held for analyses based on the phylogenies of Sibley and Alquist (1990) and Hackett et al. (2008).

Body mass and BMR differed significantly between the two sheathbill populations (table 2). Mean KP sheathbill body mass was 20.4% greater than that of RH sheathbills (Student's t-test: $t = 4.22$, df $= 20$, $P < 0.001$). Controlling for body mass, BMR differed significantly by habitat type but not by sex or molt score (table 3). Least squares means revealed that mass-corrected BMR

Table 2: Differences in mean body mass and whole-animal basal metabolic rate (WA BMR) in black-faced sheathbills breeding in rockhopper (RH) and king penguin (KP) colonies on Marion Island

Population	Body mass (g; $\pm$ SD)	WA BMR (W; $\pm$ SD)	n
RH sheathbills	421.3 $\pm$ 44.2	2.047 $\pm$ .303	12
KP sheathbills	507.5 $\pm$ 51.7	2.758 $\pm$ .291	10

Table 3: Results of ANCOVA, using body mass as covariate, analyzing basal metabolic rate in relation to foraging habitat, sex, and molt score in 22 adult black-faced sheathbills on Marion Island

	SS	F	df	P
Intercept	.026	.297	1	.593
Body mass	.139	1.584	1	.225
Foraging habitat	.664	7.572	1	**.014**
Sex	.005	.053	1	.821
Molt score	.001	.016	1	.902
Error	1.490	…	17	

Note. Foraging habitat refers to either eastern rockhopper penguin colony/intertidal zone or king penguin colony. Type III sums of squares (SS) are reported. Significant relationships are shown in bold.

in KP sheathbills was 23.9% higher than that of RH sheathbills ($F = 9.144$, df $= 1, 19$, $P = 0.007$).

Discussion

Black-faced sheathbills are both phylogenetically and ecologically distinct from many other avian taxa, given their position within the Charadriiformes and status as one of the globe's few temperate island endemics (del Hoyo et al. 2013). In consequence, it was predicted that metabolic rates in this species might be unusual by comparison with other birds. By contrast, the present data suggest that the BMR of sheathbills is typical for a bird of its size. Sheathbill BMR fell within the 95% prediction intervals of the regression for BMR of both wild-caught birds and island-restricted species. Though the prediction intervals in both analyses were relatively wide, partially a reflection of the distant relationship between sheathbills and other species in the respective phylogenies (Garland and Ives 2000), the relatively close proximity of the black-faced sheathbill to the regression line suggests that narrower intervals would do little to alter this conclusion. Alternative phylogenetic topologies are also unlikely to modify this result, considering that the differing topologies suggested by Sibley and Alquist (1990) and Hackett et al. (2008) both failed to find sheathbills exceptional.

Mass-corrected BMR (i.e., when body mass is included as a covariate in the ANCOVA) was found to vary by up to 24% between the KP and RH groups. The most plausible potential driver of this variation is differences in resource availability associated with use of these two different kinds of habitats. The RH sheathbills feed both in rockhopper penguin colonies and in the intertidal zone, foraging for polychaetes (McClelland 2013). Polychaete worms have lower energetic values (kJ g⁻¹ wet mass) than most benthic invertebrates (Griffiths 1977) and provide considerably less energy than the food items consumed most frequently in penguin colonies (table 4). Sheathbills do not actively seek out individual polychaete worms but must ingest them along with algae (*Porphyra* sp.; Burger 1981*a*), which is indigestible to sheathbills (G. T. W. McClelland and S. L. Chown, unpublished data). This need to consume large amounts of poor-quality material alongside polychaetes would presumably make it difficult

to compensate for their low energetic value by increasing foraging rate. In addition, the accessibility of the intertidal zone is contingent on tides and sea surface conditions, which interfere with foraging 25.6% of days (McClelland 2013). During the winter months, RH sheathbills therefore likely forage on a diet that is of less quality and predictability than KP sheathbills. Thus, sheathbills occupying a superior habitat had higher mass-corrected metabolic rates in comparison to sheathbills occupying a lower-quality habitat despite all individuals experiencing identical abiotic environmental (temperature, rainfall, humidity, solar radiation, and wind) conditions.

Many birds exhibit substantial seasonal variation in BMR (McKechnie 2008; McKechnie and Swanson 2010; Nzama et al. 2010), and it is worth noting that our data reflect a time of year when the two sheathbill groups experience a large difference in food quality and availability. Future studies are necessary to elucidate whether the observed disparity in BMR is present throughout the year or whether metabolic rates in KP and RH sheathbills converge for the 5-mo rockhopper penguin breeding season when food quality, availability, and territorial behaviors for both groups of sheathbills are likely to be similar (Burger 1981*a*).

BMR is often thought to be associated with habitat quality, and several hypotheses have been proposed to account for the phenomenon, including the food habits hypothesis (McNab 1986), which posits that species or populations that exploit a diet of high quality, availability, and/or predictability are likely to exhibit high mass-corrected BMRs, while lower BMRs are more likely to occur when the diet is of low quality, availability, and/or predictability. The two sympatric yet distinct groups of black-faced sheathbills on Marion Island represent a natural common-garden experiment, at least as far as climatic factors are concerned, for examining the factors underlying such variation. At this point, it is not clear whether the differences are a consequence of phenotypic plasticity or adaptation. Further work would require both genetic data and common-garden experiments (e.g., such as those of Wikelski et al. 2003) to elucidate the underlying basis of the BMR variation.

Sheathbills are the only terrestrial-endemic birds present on Marion Island and the only terrestrial bird species present on all four Southern Ocean archipelagos. The intraspecific vari-

Table 4: Energy value of the main food items consumed by black-faced sheathbills foraging in king penguin colonies and the intertidal zone on Marion Island

Habitat and food item	kJ g⁻¹ wet mass
King penguin colonies:	
Kleptoparasitism[a]	4.5–6.8
Penguin carcasses[a]	4.9–11.6
Penguin excreta[a]	2.1
Intertidal zone:	
Polychaete worms[b]	2.68–4.58

[a]Burger 1984.
[b]Steimle and Terranova 1985 and references therein (published mean values of species within class Polychaeta).

ation in BMR recorded in this study may play an important role in the species' ability to persist where others have not. Island birds often undergo a niche expansion, demonstrated by an increased range of morphologies and foraging behaviors when compared to their mainland progenitors (Van Valen 1965; Blondel 2000; Whittaker and Fernández-Palacios 2007). There is no reason to assume that this broadening of traits does not extend to physiology. Unfortunately, at present, too few studies have examined intraspecific variation within island species to assess whether this is the case. For example, a search of the literature found only one other endemic bird species (Puerto Rican tody *Todus mexicanus* Lesson; Merola-Zwartjes and Ligon 2000) that has been studied to a degree that would allow meaningful intraspecific analysis (wild caught, $n > 10$). The var-

iation among the KP and RP sheathbills suggests that greater focus on the energetics of endemic birds may reveal substantial variation associated with island living.
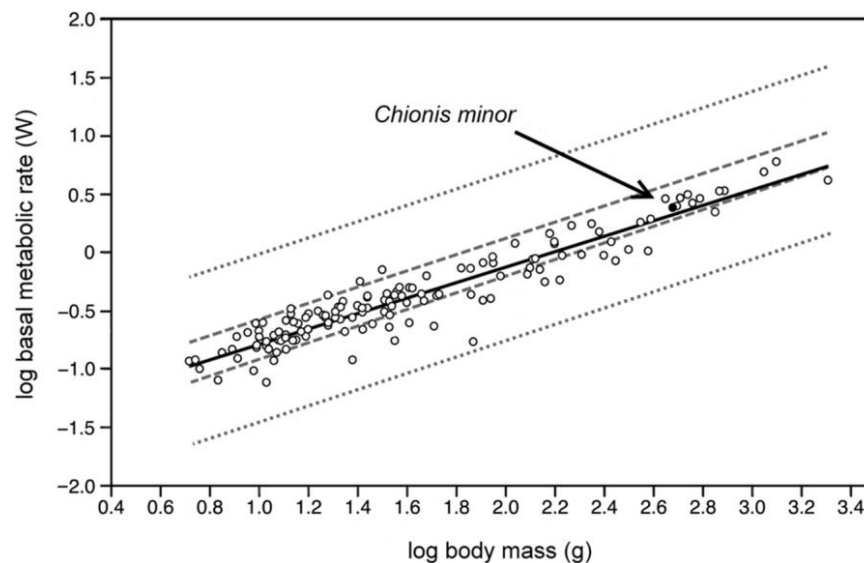
APPENDIX

Figure A1. Ordinary least squares (i.e., nonphylogenetically independent) regression of the basal metabolic rate of 137 wild-caught avian species (black line; $\log BMR = -1.437 + 0.656 \log M_b$). The gray dashed and dotted lines represent the phylogenetically independent 95% confidence and prediction intervals, respectively, based on the phylogeny proposed by Hackett et al. (2008). The body mass and basal metabolic rate values for the black-faced sheathbill are highlighted in black.

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