

Foraging effort in Magellanic penguins: balancing the energy books for survival?

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Abstract The determination of activity-specific energy expenditure of wild animals is key in ecology and conservation sciences. Energy management is crucial for seabirds during the breeding season when they need to maintain a positive balance between energy intake and the metabolic costs for them and their young. We analysed information from accelerometers to estimate the energy expenditure of Magellanic penguins (*Spheniscus magellanicus*) foraging at sea during the early chick-rearing period from four Patagonian colonies (i.e. Punta Norte, Bahía Bustamante, Puerto Deseado and Puerto San Julián). We studied how activity-specific energy consumption affected total energy expenditure during foraging and considered how this related to the current status and trends of breeding populations. The derived diving energy expenditure of penguins differed between sites, with inter-colony differences being primarily due to variability during the bottom and ascent phases of the dives: bottom phase energy expenditure was largely determined by the total distances travelled during the search, pursuit, and capture of prey, rather than the time per se allocated

to this phase. Those colonies where the rate of population change was lowest also expended the most energy per trip due to greater times spent underwater and/or undertaking a higher number of dives per trip. Finally, the total energy consumption as well as the rate of energy expenditure per trip was good indicators of trends in breeding populations.

Introduction

The mechanisms by which animals obtain and/or expend energy depends largely on their foraging behaviour, growth and reproduction, and thus affects life history strategies (e.g. Stearns 1977; Brown et al. 2004). For central place foragers (sensu Orians and Pearson 1979), such as seabirds, managing time and energy during the breeding season is crucial as breeding adults need to meet both their own energy needs and those of their brood within the short-time windows necessary for effective provisioning (e.g. Orians and Pearson 1979; Ropert-Coudert et al. 2004). Effective strategies for this are tempered by the availability and distribution of prey in time and 3-dimensional space (e.g. Suryan et al. 2000; Grémillet and Charmantier 2010; Wilson et al. 2011).

In diving birds, such as penguins, variability in foraging strategy is particularly obvious in differential depth usage, this being modulated by features manifest in the dive profiles (e.g. angle of descent and ascent, bottom time, vertical velocities, etc.) and the number of dives made per hour (e.g. Wilson et al. 2004, 2010, 2011; Shepard et al. 2009, 2010; Sala et al. 2012a, 2014). The general premise here, as elsewhere, is that birds should attempt to maximize prey ingestion in relation to energy expenditure (e.g. Pyke 1984; Halsey et al. 2003), and the criticality of this has been recognized in many species-specific conservation issues (e.g. Langton et al. 2011; Lewison et al. 2012).

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Accelerometers have been shown to help quantify both the activity of animals in a suite of different environments (e.g. Gómez-Laich et al. 2008; Wilson et al. 2008; Gleiss et al. 2011 and references therein) and their activity-specific energy expenditure (Wilson et al. 2006, 2010; Shepard et al. 2008a; Green et al. 2009; Gleiss et al. 2011; Gómez-Laich et al. 2011). In particular, the recent recognition of a powerful proxy for movement-derived power use, based on dynamic acceleration [overall dynamic body acceleration (ODBA)] accessible from animal-attached recorders (e.g. Wilson et al. 2006; Halsey et al. 2009a, b; Shepard et al. 2009; Gleiss et al. 2011 and references therein), has made it possible to allude to energy expenditure in free-living animals across a range of species. This, combined with a particular quirk in penguin foraging ecology whereby undulations in the dive profile correlate with prey ingestion (e.g. Simeone and Wilson 2003; Bost et al. 2007; Hanuise et al. 2010; Sala et al. 2012a), means that we can examine how penguins manage their energy expenditure over time and space in relation to energy acquisition (see Sala et al. 2012a), ultimately deriving metrics for colony well-being from an energetic perspective (see Ballance et al. 2009).

The Magellanic penguin (*Spheniscus magellanicus*) is a significant top predator of the Patagonian Shelf ecosystem with many of its prey species being of appreciable commercial value (e.g. Skewgar et al. 2007; Pastous Madureira et al. 2009; Yorio et al. 2010). Thus, studies of penguin foraging requirements and the mechanisms by which these birds balance their energy budgets are important both in its conservation and in appropriate management of marine resources in Patagonian waters. In Argentina alone, the Magellanic penguin nests in 63 colonies with a total population of ca. 900,000 breeding pairs approximately 60 % of the global breeding population (Schiavini et al. 2005; Bird-Life International 2013).

In this study, we examined energy expenditure, derived from dynamic acceleration, from device-equipped Magellanic penguins, to attempt to determine the possible connection between this and the current status and trends of breeding sites, following a mechanistic approach (see Lewis et al. 2006). The specific objectives of this work were: (1) to analyse how changes in energy allocated to the different at sea activities affects total energy expenditure, (2) to provide an estimate of energy expenditure by foraging Magellanic penguins from four colonies along the coast of Argentina, and (3) to establish whether energy expenditure at sea may be related to the current status and population trends of breeding colonies.

Based on findings reported in previous studies for the same species, in the same colonies and, in some cases, for the same group of individuals studied here (see Sala et al. 2012a, b, 2014), we propose the following directional hypothesis (see Underwood 1990, 1997):

The colonies where penguins have the highest energy expenditure at sea during the early chick-rearing period are those that show the lowest reproductive success.

The hypotheses expressed in statistical terms are:

$$H_0 : m_{PD} = m_{PSJ} = m_{BB} = m_{PN}$$

$$H_1 : m_{PD} > m_{PSJ} \geq m_{BB} > m_{PN}$$

where H_0 , H_1 , m , correspond to: null hypothesis, alternative hypothesis, sample mean of each variable (from each colony: PD, Puerto Deseado; PSJ, Puerto San Julián; BB, Bahía Bustamante; and PN, Punta Norte), respectively. Basically, we propose this directional H_1 because in previous studies, we found a greater foraging and diving effort in those colonies located in the centre of breeding distribution, BB and PD (Sala et al. 2012a, b, 2014), and a higher number of total dives made by penguins from PSJ (Sala et al. 2012a, 2014).

Our main prediction would argue that on average (1) the more energetically costly dives are, (2) the higher the power use is, and (3) the higher the values of cumulative energy expenditure during foraging trips at sea, the less successful associated colonies will be in terms of reproduction, which will lead to the lowest values of positive rates of population change.

Methods

Sites, study periods, and population trends

Field work was conducted during the early chick-rearing period, between November and December 2005, 2006, 2007, and 2008, at four colonies along the Patagonian coast of Argentina: PN (42°04'S, 63°49'W), BB (45°10'S, 66°29'W), PD (47°45'S, 65°52'W), and PSJ (49°16'S, 67°42'W). The rates of population change used in this work are those presented by Sala et al. (2012b) and can be seen in Table 1 of that paper. The data set used and analysed in this work are derived from the same general database used in other studies on the Magellanic penguin (Sala et al. 2012a, 2014).

Deployment of devices

A total of 57 Magellanic penguins brooding small chicks were equipped with one of the two different types of recording technology: Daily Diaries or GPS-TDlogs (Table 1; see below for details). For this, birds were carefully removed from their nests using a clipboard (Wilson 1997) and then equipped by attaching the devices to the feathers of their lower backs, to minimize hydrodynamic

Table 1 Details of device deployments on Magellanic penguins during the early chick-rearing period (November–December 2005–2008) at four Patagonian colonies

Site	Study year	Type of device	No. of birds equipped	No. of birds with data	No. of birds with complete trips	No. of dives
Punta Norte	2008	GPS-TDlog	10	9	9	6,447
		Daily Diary	5	5	1	2,508
Bahía Bustamante	2005	Daily Diary	6	3	3	1,483
		GPS-TDlog	6	1	1	641
	2006	Daily Diary	6	4	1	1,467
		Daily Diary	1	1	1	512
Puerto Deseado	2006	Daily Diary	8	5	3	3,922
Puerto San Julián	2007	GPS-TDlog	7	6	6	6,126
		Daily Diary	8	6	5	6,254
Total			57	40	30	29,360

drag (Bannasch et al. 1994), using overlapping strips of waterproof tape (Wilson et al. 1997). Every effort was taken to minimize the stress caused to the birds during manipulation, and the procedure was completed in less than 5 min, after which the birds were returned to their nests. All devices were retrieved after a single foraging trip, being recovered within hours of the birds returning from the sea. Thus, no single individual contributed more data to the set than any other. All birds equipped with devices continued to breed normally during the study period.

Daily Diaries

Thirty-four birds were equipped with multi-channel archival tags (Daily Diaries; Table 1) (see Wilson et al. 2008 for details), which recorded data with 22-bit resolution at rates of 6–9 Hz in 13 channels. However, recording channels relevant for the present study were tri-axial body acceleration (range -4 to 4 g) (Gómez-Laich et al. 2008; Shepard et al. 2008b) and pressure (0.5–20 bar). The three (orthogonal) axes for the acceleration transducers were calibrated by rotating the devices through all combinations of pitch and roll (0° – 360°) so that output from the transducers could be converted into real ‘g’ (Wilson et al. 2006, 2008). Accuracy on all channels was better than 1 % of full-scale deflection except for depth, where accuracy was better than 0.01 %. The devices were made to be streamlined and had maximum dimensions of $70 \times 40 \times 10$ mm (L \times W \times H), constituting 1.8 % of the penguin cross-sectional area. They weighed 68 g, which is less than 1.5 % of the mean weight of an adult Magellanic penguin (mean: 4 kg; range 2.7–7.2 kg; Williams 1995).

GPS-TDlogs

Twenty-three Magellanic penguins were also equipped with GPS loggers (GPS-TDlog, Earth and Ocean Technologies, Kiel, Germany) (Table 1), which recorded depth,

temperature, latitude, and longitude. The horizontal accuracy of the positional fixes (recorded at 1 Hz when the penguins were at the surface) was better than 5 m for 90 % of fixes (GPS-TDlog Manual). Depth and temperature data were recorded at 0.5 Hz and were accurate to 0.03 bar and 5 mK, respectively. Data were stored in a 2-MB flash memory. Loggers had a hydrodynamic, waterproof housing measuring $96 \times 39 \times 27$ mm (L \times W \times H), comprising ~6.5 % of the cross-sectional area of the bird, and a total mass of 75 g, which is ca. 1.7 % of the mean Magellanic penguin body mass (Williams 1995).

Energy expenditure

Mean instantaneous ODBA values for periods when the animals were diving were obtained following Wilson et al. (2006), using a running mean over two seconds to isolate the ‘static’ (gravity-based) component from the ‘dynamic’ (animal-movement-based) acceleration (see Shepard et al. 2008b). The different phases within a dive (descent, bottom and ascent) and the maximum depth reached were calculated using custom-made software (Swansea University, Swansea, Wales, UK). The program displayed depth data against time graphically and then placed cursors at the start, at the end, and at the inflection points of each dive profile, to indicate the descent, bottom (where birds generally do most prey capture; Simeone and Wilson 2003) and ascent phases (see Sala et al. 2012a for details). The appropriateness of the cursor positions was checked visually, always by the same user. Once each dive phase had been identified, its mean instantaneous ODBA value was obtained.

The mean instantaneous ODBA value for the resting periods on the sea surface (i.e. when birds were floating) is more a measure of wave action than any activity by the bird and thus cannot be used to derive power use (cf. Gómez-Laich et al. 2013). However, a measure of power use during resting in water can be derived from the literature using values from the congeneric Humboldt penguin (*Spheniscus*

humboldti) (5.95 W kg^{-1} ; Luna-Jorquera and Culik 2000) determined using gas respirometry. For this, we assumed an average weight of ca. 4 kg for Magellanic penguins (Williams 1995; see Wilson et al. 2004) so that resting metabolic rate for a Magellanic penguin in water was taken to be 23.8 W.

ODBA can be considered as analogous to energy (Gleiss et al. 2011) so that summed ODBA values over time relate to total energy expenditure while rates of ODBA activity relate to metabolic power (see Qasem et al. 2012). Accordingly, we calculated the total ODBA derived from the different activities performed by penguins during their foraging trips (i.e. total ODBA for each period of behaviour) by multiplying the mean instantaneous ODBA values (g s^{-1}) for each period of specific behaviour by the time invested on it (s), as this equates with the summed ODBA values over that period of time. These values have units of acceleration (g) and should mirror the total investment of energy for each particular behaviour (see below). A linear proxy for the total energy expenditure per foraging trip of each instrumented bird was calculated by summing the total ODBA values for all at sea activities. However, to compare the energy expenditure of Magellanic penguins during foraging trips at sea with the results obtained in other studies and also to make the results more widely comprehensible, ODBA values were converted to units of joules per second following Wilson et al. (2010), who derived a relationship of:

$$\text{Metabolic power} = 117.7 \times \text{ODBA}_{\text{mean}} + 22$$

where metabolic power is expressed in Watts and the ODBA values are mean ODBA values per second (i.e. as a rate of ODBA activity that relates with the metabolic power; see above).

To compare the total estimated energy expenditure (EEE) by penguins from different colonies during foraging, we included in our analysis only those individuals with complete trip data from Daily Diaries (see Table 1). However, since we had reduced numbers of individuals with these characteristics, we used the robust colony-specific relationship between the total ODBA and the maximum dive depth (see below), generated from an exploratory analysis, in order to obtain energy expenditure values per dive for those penguins also equipped with GPS-TDlogs. In these cases, we added the total ODBA accumulated in dives to that accumulated during surface recovery periods (see above) and thus gave an estimate of total energy expenditure per trip for penguins equipped with GPS-TDlogs.

Using previous classifications developed to identify sections of penguin foraging trips into outbound, foraging, and inbound phases (see Sala et al. 2012a), we also calculated section-dependent power use and energy use between different colonies. Basically, penguins leaving the colony

were considered to be undertaking the outbound section of the trip until the moment the first dive exceeded a depth of 10 m after which the birds were considered to be foraging (Rey et al. 2012; Sala et al. 2012a). Foraging behaviour could be further confirmed using acceleration and depth data from the Daily Diaries because variation in the depth profile took the form of undulations (see Sala et al. 2012a for a discussion on this) accompanied by increases in flipper beat frequencies associated with prey chases shown by the heave acceleration (Wilson et al. 2010). The end of the foraging phase and the start of the return phase was also clear, being defined by regular, shallow (<10 m) dives with a clear parabolic shape (Williams 1995; Rey et al. 2010; Sala et al. 2012a).

In summary, we analysed a total of 16,146 dives performed by 24 of the 28 Magellanic penguins that were equipped with Daily Diaries (see Table 1) (four birds, two from BB, one from PD and one from PSJ had erroneous acceleration records and were excluded from the analysis).

Statistics

We grouped data from both sexes because previous studies showed no intersexual differences in the foraging trip characteristics of Magellanic penguins during the early chick-rearing period (Rey et al. 2010, 2012). In order to control for pseudoreplication in diving behaviour, we used generalized linear mixed-effects models (GLMM) fitted by restricted maximum likelihood (REML) with Tukey's post hoc contrasts (Crawley 2007; Zuur et al. 2009). In these analyses, colony was included as a fixed factor and bird identity as a random factor. Since, in all cases, diving variables followed a *Poisson* distribution, we used GLMMs with *Poisson* error distribution and log-link function corrected for overdispersion (Crawley 2007; Zuur et al. 2009). Equations showing the relationship between diving parameters and depth were constructed with the significant parameters obtained for each mixed effect model (Zuur et al. 2009). We selected the function (or model) that best fit the data (i.e. linear or quadratic) using the Akaike Information Criterion (AIC), choosing the one that had the lowest AIC score (Burnham and Anderson 2002).

With respect to the foraging trip-based parameters (i.e. single values per bird equating to e.g. total energy expenditure \times trip $^{-1}$) and to compare between colonies, we used the nonparametric statistical test of Kruskal–Wallis with Dunn's post hoc contrasts (and verified in each comparison for the homocedacy assumption by a Bartlett's test; Zar 1999).

All statistical analyses were performed using the open source statistical package R version 3.0.1 (R Development Core Team 2013) with a level of significance of $P < 0.05$.

Table 2 Estimation of energy consumption during dives ($N_{\text{Dives}} = 16,146$) split into phases (i.e. descent, bottom and ascent) made by 24 Magellanic penguins during the early chick-rearing period at four colonies of Patagonia Argentina

Colony (n)	Punta Norte (5)	Bahía Bustamante (8)	Puerto Deseado (5)	Puerto San Julián (6)	$X^2(df = 3)^2$	P
Mean power descent (W)	66.0 (5.9) [56.4–74.0]	68.4 (6.8) [54.2–80.8]	73.2 (9.8) [62.5–88.1]	70.9 (6.7) [58.5–81.9]	3.5	0.16
EEE descent (J)	1,122.4 (172.0) [873.9–1,342.8] ^a	1,296.5 (360.2) [785.2–2,177.7] ^b	945.8 (317.8) [588.9–1,712.9] ^d	663.8 (83.0) [511.9–786.2] ^{a,b,d}	17.4	<0.001
Mean power bottom (W)	64.4 (6.0) [56.5–72.4] ^c	68.0 (10.0) [51.9–86.9]	79.4 (7.7) [63.5–90.1] ^c	71.8 (8.4) [56.0–72.4]	6.7	0.042
EEE bottom (J)	2,125.3 (204.5) [1,777.6–2,523.1]	2,482.6 (645.7) [1,929.2–3,808.6] ^b	2,857.1 (455.4) [1,918.1–3,332.5] ^d	1,633.7 (335.6) [1,127.9–2,124.8] ^{b,d}	13.6	0.002
Mean power ascent (W)	53.9 (8.3) [39.9–64.9] ^{a,c}	55.7 (7.7) [41.5–67.5] ^c	72.0 (5.0) [60.8–76.6] ^{c,e}	63.7 (7.7) [45.1–74.8] ^a	12.2	0.004
EEE ascent (J)	729.4 (158.2) [427.3–911.4]	989.3 (252.4) [613.4–1,493.5] ^b	972.7 (303.1) [510.3–1,502.5] ^d	514.2 (33.0) [477.1–570.7] ^{b,d}	16.1	0.001
Mean power dive (W)	61.4 (6.7) [50.9–70.4] ^c	64.0 (7.7) [49.2–77.0]	74.9 (6.5) [62.3–84.2] ^c	68.8 (7.3) [53.2–81.2]	8.0	0.023
EEE dive (J)	3,806.8 (423.3) [3,032.2–4,204.3] ^a	4,671.5 (1,181.4) [3,573.4–7,343.1] ^b	4,693.3 (994.9) [2,896.7–6,535.4] ^d	2,696.2 (448.0) [2,061.6–3,221.1] ^{a,b,d}	16.5	0.001

Mean values are given (SD), along with range [Min–Max]. Mean values and significant statistical test are shown in bold. The data were obtained from Daily Diaries recorders (see ‘Methods’). The sample size (number of birds) per colony is shown in parentheses. EEE = estimated energy expenditure (see text)

Generalized linear mixed-effects models (GLMM) with a Tukey’s multiple comparison test to compare between colonies were used. The significant differences ($P < 0.05$) in the results of post hoc Tukey’s contrast are shown by the superscript letters as follow: ^a Punta Norte versus Puerto San Julián; ^b Bahía Bustamante versus Puerto San Julián; ^c Punta Norte versus Puerto Deseado; ^d Puerto Deseado versus Puerto San Julián; and ^e Bahía Bustamante versus Puerto Deseado

Results

Energy expenditure during diving

Table 2 summarizes the values relating to the energy expenditure of dives and each of its phases (i.e. descent, bottom and ascent) from penguins from the four study colonies.

Descent phase of dives

The mean power for penguins associated with the descent phase of a dive was similar across the four colonies (GLMM: $X_3 = 3.5$, $P = 0.16$; Table 2). However, foraging penguins from PSJ spent significantly less energy than the other birds during their descents (GLMM: $X_3 = 17.4$, $P < 0.001$; Table 2), having values approximately half those of BB birds (663.8 vs. 1,296.5 J, respectively; Table 2).

Bottom phase of dives

The mean power during the bottom phase differed slightly between colonies (GLMM: $X_3 = 6.7$, $P = 0.042$; Table 2). However, consideration of the entire period at the bottom of the dives showed that birds from BB and PD expended the greatest amount of energy during this phase (GLMM: $X_3 = 13.6$, $P = 0.002$; Table 2). In all four colonies, the energy expended during the bottom phase increased

linearly with the number of undulations (‘wiggles’) undertaken by penguins (PN: $r^2 = 0.41$, $F_{1,2506} = 1,706$, $P < 0.001$; BB: $r^2 = 0.24$, $F_{1,3460} = 1,114$, $P < 0.001$; PD: $r^2 = 0.41$, $F_{1,3920} = 2,674$, $P < 0.001$; PSJ: $r^2 = 0.38$, $F_{1,6252} = 3,808$, $P < 0.001$). In fact, the total vertical distance travelled (m) by the birds during the bottom phase best explained the variation in energy expended at that stage (Fig. 1). This relationship was particularly strong in PSJ, where the total vertical distance travelled at the bottom phase explained 72 % of the variability in the energy expenditure during that phase of dives (Fig. 1).

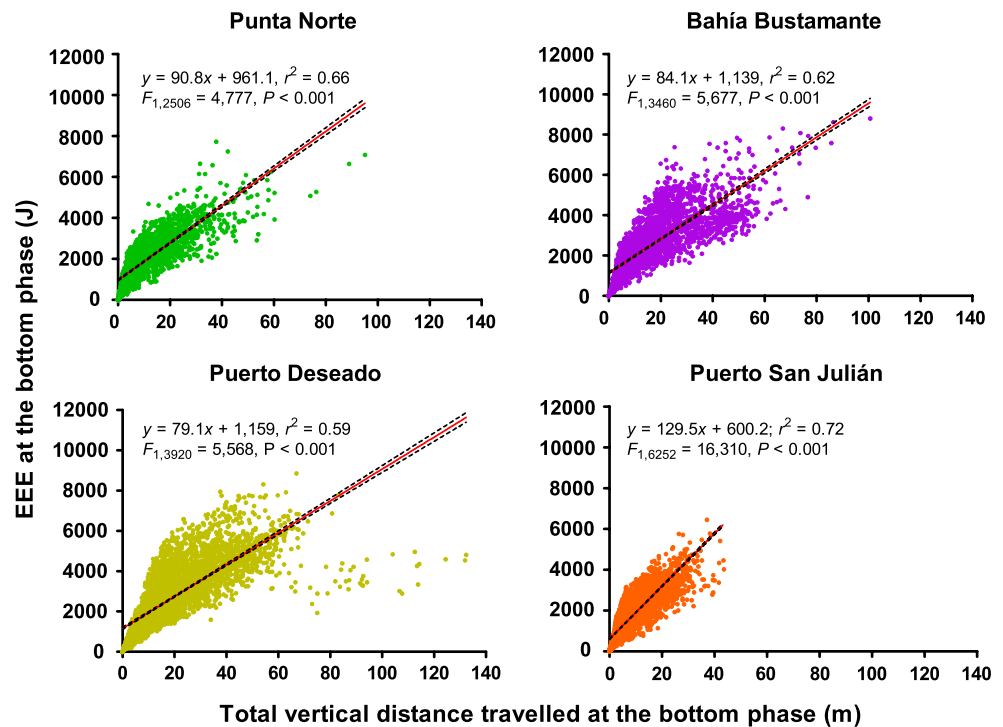
Ascent phase of dives

The mean power during ascent was significantly different between colonies (GLMM: $X_3 = 12.2$, $P = 0.004$; Table 2) where, for example, penguins from PD had greater mean power values (by some 32 %) than birds from PN and BB (Table 2). The overall energy used during the ascent phases also varied greatly between colonies (Table 2), with birds from BB and PD using most energy at this time (GLMM: $X_3 = 16.1$, $P = 0.001$; Table 2).

Entire dive

Although penguins from PD had the highest value of mean power during entire dives, they only differed significantly

Fig. 1 Relationship between the total vertical distance travelled (m) by penguins during the bottom phase of dives and the total energy expended (EEE) (J) at that time for the four study colonies. The red line represents the curve that best fitted the data and the black dashed lines show 95 % confidence intervals



to individuals from PN (74.9 vs. 61.4 W, respectively; GLMM: $X_3 = 8.0$, $P = 0.023$; Table 2). The maximum energy expended values for dives were recorded in PD and BB (4,693.3 and 4,671.5 J, respectively; Table 2), this being some 74 % higher than birds from PSJ (Table 2).

Energy expenditure and diving depth

There was a strong relationship between the energy expended during dives and maximum depth reached. For all data pooled, the EEE values were related to maximum depth via:

$$\text{EEE dive} = -1.47(\text{Maximum dive depth})^2 + 206.4(\text{Maximum dive depth}) + 1,389$$

($r^2 = 0.77$, $F_{1,16143} = 3,309$, $P < 0.001$) and relationships between the two parameters were also significant when each of the colonies was considered separately (Fig. 2). Colony-specific patterns shown in overall EEE per dive (Fig. 2) were also apparent in the descent EEE values (PN: $y = -0.21x^2 + 53.4x + 239.0$, $r^2 = 0.97$, $F_{2,13} = 252.0$, $P < 0.001$; BB: $y = -0.33x^2 + 64.6x + 96.4$, $r^2 = 0.98$, $F_{2,14} = 425.9$, $P < 0.001$; PD: $y = 40.3x + 156.6$, $r^2 = 0.99$, $F_{1,16} = 1,464$, $P < 0.001$; PSJ: $y = 46.2x + 115.4$, $r^2 = 0.97$, $F_{1,6} = 257.8$, $P < 0.001$) and the ascent phases (PN: $y = 0.18x^2 + 8.33x + 473.3$, $r^2 = 0.93$, $F_{2,13} = 103.9$, $P < 0.001$; BB: $y = -0.24x^2 + 44.6x + 194.4$, $r^2 = 0.92$, $F_{2,14} = 89.5$, $P < 0.001$; PD: $y = -0.34x^2 + 66.1x - 142.5$,

$r^2 = 0.92$, $F_{2,15} = 102.1$, $P < 0.001$; PSJ: $y = 29.0x + 171.6$, $r^2 = 0.95$, $F_{1,6} = 136.9$, $P < 0.001$).

The total energy used for the bottom phase of dives, including sudden acceleration of pursuit and capture of prey (i.e. wiggles), varied markedly with maximum dive depth (Fig. 3). The relationships obtained from PN, PD, and PSJ birds showed a bell-shaped function (i.e. negative quadratic), with maximum values of total ODBA in the depth ranges of 35–65, 30–50, and 25–30 m, respectively (Fig. 3). However, birds from BB increased energy expenditure in the bottom phase approximately linearly with maximum dive depth (Fig. 3).

Energy expenditure during the foraging trip

Outbound

The total energy calculated allocated to the outbound phase of the foraging trip did not differ statistically between colonies (KW: $H_3 = 1.7$, $P = 0.22$; Table 3). In contrast, however, the calculated rate of energy expenditure per unit time (i.e. metabolic power) during this time was higher (by up to 46 %) for penguins commuting from BB and PD (35.7 and 36.9 W, respectively) than birds from the other two colonies (Table 3).

Foraging

Penguins from PD birds were calculated to have spent, on average, 87 % more energy during foraging than

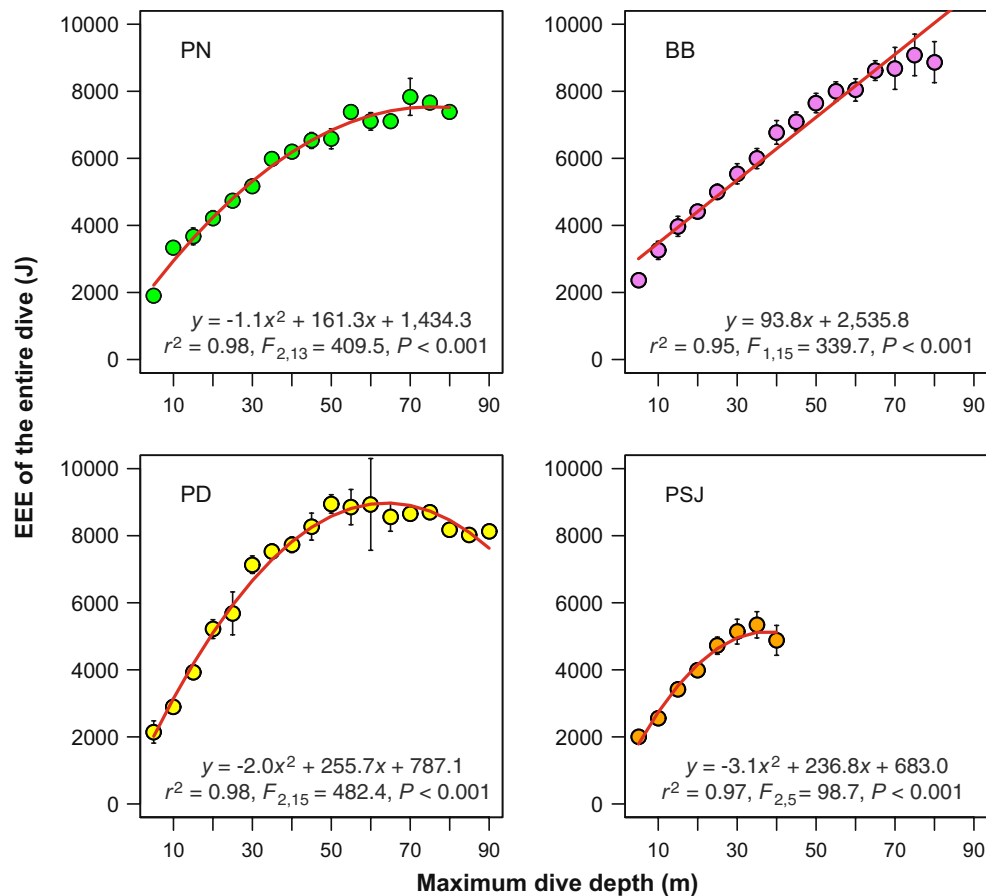


Fig. 2 Total energy expended per dive (EEE) (J) as function of maximum dive depth (m) for penguins from each colony (PN Punta Norte, BB Bahía Bustamante, PD Puerto Deseado, PSJ Puerto San Julián).

The red lines correspond to the curves that best fit the data. The values (coloured circles) correspond to the overall means for intervals of 5 m depth \pm SE

individuals from PN (2,903 vs. 1,553 kJ, respectively; Table 3) although the estimated metabolic power did not statistically differ between colonies (Table 3).

Inbound

Penguins from PN were calculated to have invested most energy in the inbound phase of the foraging trip, being more than double that birds from PD (KW: $H_3 = 4.6$, $P = 0.045$; Table 3), even though PN birds had the lowest metabolic power (KW: $H_3 = 6.6$, $P = 0.019$; Table 3). In contrast, metabolic power was calculated to be highest for individuals from BB and PD (ca. 70 % higher, on average, than PN) (Table 3).

Entire foraging trip

At the level of the entire foraging trip, we found that the most energetically costly trips were those conducted by penguins from PD and PSJ (Table 3), even though birds from BB and PD had highest metabolic power values (Table 3).

Energy expenditure and rate of population change

Our calculated energy metrics were good indicators of the rates of population change of the four colonies, reported by Sala et al. (2012b). The colonies with the highest rates of population increase were those with the least energy expenditure resulting from their time at sea (Fig. 4). Thus, those colonies where the penguins spent more energy during their foraging trips, both absolutely (i.e. EEE of the entire trip [kJ]) and per second at sea (i.e. metabolic power, as rate of EEE, of the entire trip [W]), had the lower rates of population change (Fig. 4a, b).

Discussion

Here, we have studied, for the first time, the energy expenditure of the major at sea activities undertaken by Magellanic penguins operating from four different colonies along the Patagonian coast (ca. 1,150 km coastline) (cf. Wilson et al. 2010) and have thus elucidated the different energetic

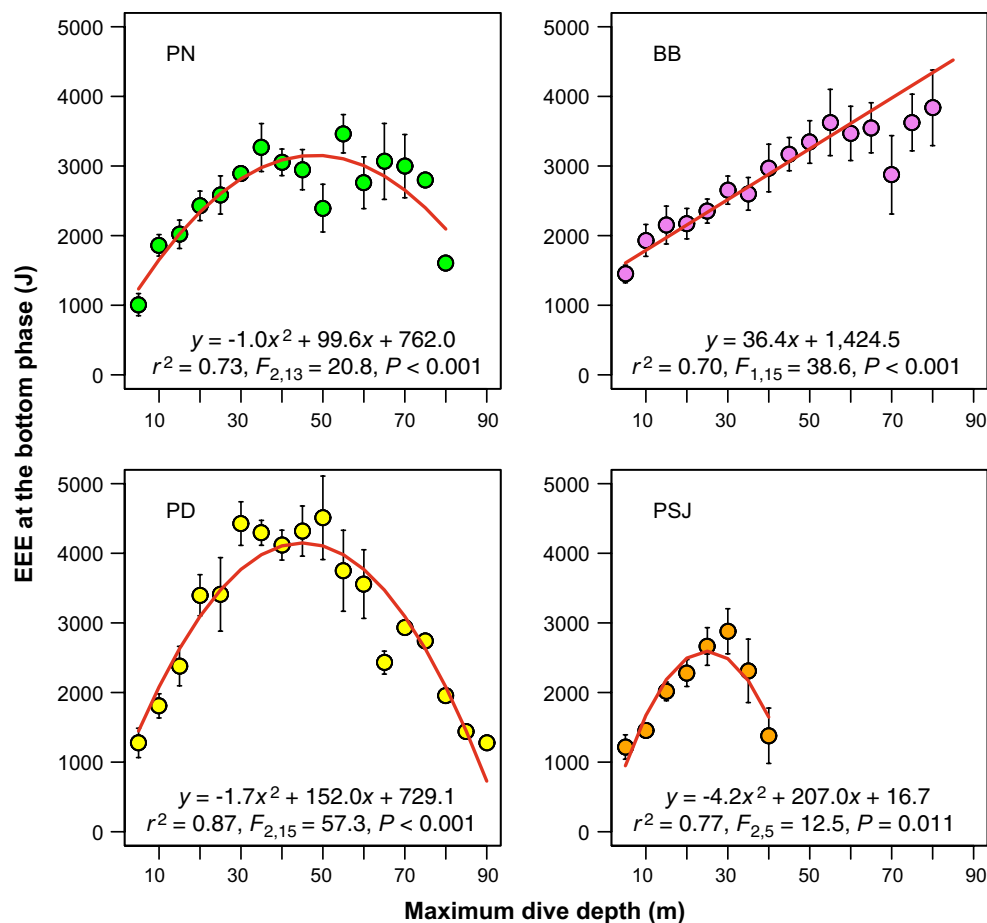


Fig. 3 Total energy expended (EEE) (J) during the bottom phase of dives as function of maximum dive depth (m) for penguins from the study colonies (PN Punta Norte, BB Bahía Bustamante, PD Puerto

Deseado, PSJ Puerto San Julián. The red lines correspond to the curves that best fit the data. The values (coloured circles) correspond to the overall means for intervals of 5 m depth \pm SE

components that are likely to be linked to current population trends (see Sala et al. 2012b, cf. e.g. Hennicke and Culik 2005; Lewis et al. 2006; Ballance et al. 2009).

We have established that, in energetic terms, longer, deeper dives, particularly those associated with high vertical distances travelled during the bottom phase (i.e. over the pursuit and/or prey capture phases) of dives, markedly increase the energy expenditure of foraging trips (Tables 2 and 3). We expect this behaviour to affect breeding success and the recruitment of relevant colonies (for a discussion of this, please see Sala et al. 2012b).

Diving energy expenditure

Descent phase of dives

Our ODBA values indicate that the descents of dives are the most energetically onerous behaviours of foraging penguins and that, as pointed out by Wilson et al. (2010), the energy allocated to descent is also strongly associated

with dive depth. Thus, the reason that penguins from BB allocated most energy to this process (Table 2) are related both to the absolute depth of dives and the highest rates of descent exhibited by these birds (Sala et al. 2014), both of which are major factors modulating power use in these buoyant birds (Wilson et al. 2011). These costly deeper dives are presumably related to penguins from BB consuming most benthic prey such as Hake (*Merluccius hubbsi*) (Sala et al. 2012a, see Gandini et al. 1999), a stark contrast to the birds of PSJ, which feed on near-surface-dwelling Fuegian Sprat (*Sprattus fuegensis*) (Sánchez and Ciechomski 1995; Sánchez et al. 1995; Sala et al. 2012a) in shallow waters (see Sala et al. 2014), expending little energy and having low mean power requirements for the descent phase of their dives (Table 2) to catch them.

Bottom phase of dives

Bottom phase durations tend to increase with dive depth for penguins (Wilson et al. 1996; Peters et al. 1998;

Table 3 Estimation of energy consumption of the three foraging trip segments (i.e. outbound, foraging area and inbound) and the whole trip made by 30 Magellanic penguins during the early chick-rearing period from four colonies of Patagonia Argentina

Colony (<i>n</i>)	Punta Norte (10)	Bahía Bustamante (6)	Puerto Deseado (3)*	Puerto San Julián (11)	$H_{KW(df=3)}$	<i>P</i>
EEE outbound (kJ)	523.3 (176.4) [273.2–850.3]	403.3 (162.4) [237.6–664.1]	359.1 (223.5) [114.9–553.3]	526.0 (304.4) [148.1–1,112.0]	1.7	0.215
Power outbound (W)	25.3 (4.3) [21.8–36.7] ^a	35.7 (4.3) [30.2–41.4] ^a	36.9 (3.9) [32.8–40.5]	29.1 (9.3) [17.6–44.4]	7.6	0.011
EEE foraging (kJ)	1,553 (633) [976–2,775] ^b	2,086 (709) [1,077–2,992]	2,903 (958) [1,825–3,656]	2,561 (900) [1,553–4,598] ^b	9.6	0.004
Power foraging (W)	40.6 (17.7) [31.2–89.4]	54.4 (20.3) [42.1–95.4]	63.0 (7.7) [55.2–70.6]	46.3 (14.4) [28.5–69.3]	4.5	0.053
EEE inbound (kJ)	677 (390) [164–1,385]	343 (163) [127–578]	249 (221) [95–502]	451 (187) [213–742]	4.6	0.049
Power inbound (W)	30.7 (5.0) [26.6–42.8] ^a	43.5 (9.1) [30.6–55.9] ^{a,c}	52.7 (2.7) [50.3–55.6]	33.1 (11.6) [17.9–52.8] ^c	6.6	0.019
EEE entire trip (kJ)	2,753 (739) [2,111–4,415]	2,832 (767) [1,694–3,628]	3,511 (1,317) [2,035–4,567]	3,538 (966) [2,292–5,429]	4.8	0.044
Power entire trip (W)	31.4 (5.0) [27.2–44.9] ^a	42.5 (3.4) [36.4–46.3] ^a	47.0 (18.0) [27.1–62.3]	38.3 (9.9) [27.5–52.7]	5.3	0.036

Mean values are given (SD), along with range [Min–Max]. Mean values and significant statistical tests are shown in bold. Data were obtained from GPS-TDlogs and Daily Diary loggers (see ‘Methods’). Mean values and significant statistical tests are shown in bold. The sample size (number of birds) per colony is shown in parentheses. EEE = estimated energy expenditure (see text)

Kruskal–Wallis test with a Dunn’s multiple comparison contrast to compare between colonies was used. The significant differences ($P < 0.05$) in the results of post hoc Dunn’s contrast are shown by the superscript letters as follow: ^a Punta Norte versus Bahía Bustamante; ^b Punta Norte versus Puerto San Julián; and ^c Bahía Bustamante versus Puerto San Julián

Luna-Jorquera and Culik 1999), but our data show that there is variable energy expenditure in these bottom phases according to locality (cf. Table 2; Fig. 3). BB and PD, for example, had the highest energy expenditure during this phase (using up to 75 % more energy than in PSJ; Table 2). Here, most variation in energy expenditure is likely to be related to the capture of prey since increasing speed normally requires a cubed power input (Wilson et al. 2002). Only one clear prey capture strategy has been described for the Magellanic Penguin, consisting of birds lunging at their prey from the underneath (Boswall and MacIver 1975; Wilson et al. 2010), using their positive buoyancy to help them accelerate towards their prey (Wilson et al. 2010) and producing the characteristic ‘wiggle’. Multiple prey captures during single dives, which are the norm for Magellanic penguins (Simeone and Wilson 2003; Rey et al. 2012; Sala et al. 2012a), however, require that birds redescend the water column following their ascending lunge at prey (cf. Fig. 1); the power requirements for this will depend on the depth (because depth modulates body air volume and therefore upthrust), swim speed, and dive angle (Wilson et al. 2010, 2011), and these are likely to vary with prey type. Although we do not know how capture strategies vary with prey type, clearly, the power implications in the pursuit in relation to energy gain will determine the overall net prey value.

Ascent phase of dives

Although most of the ascent phase of the dive is reported to be passive, whereby penguins use the upthrust from their body-associated air to rise in the water column (Wilson et al. 2010), it was notable that penguins of PD expended about 33 % more energy at this time than birds from PN and BB (Table 2). The implication here is that PD birds actively swam more than their conspecifics at this time. This strategy is hard to explain, since it increases the effective cost of transport for these animals, lowering their energy-based efficiency. Shepard et al. (2009) report, however, that birds provisioning broods must balance energy-efficiency with time-efficiency. It may thus be relevant that Sala et al. (2012b) report PD birds spending the longest at sea during foraging, which will equate with the lowest chick provisioning rates. Incurring higher power costs to return to the surface might be tenable if they resulted in a faster dive cycle duration with concomitant higher chick provisioning rates (cf. Shepard et al. 2009). This is what actually happens, as the penguins from this colony show the highest values of ‘dive effort’ (Zimmer et al. 2011), measured as dive duration divided by the dive cycle duration (see Sala et al. 2014). Indeed, this general premise can explain why PD birds had such overall high-power usage during dives (Table 2).

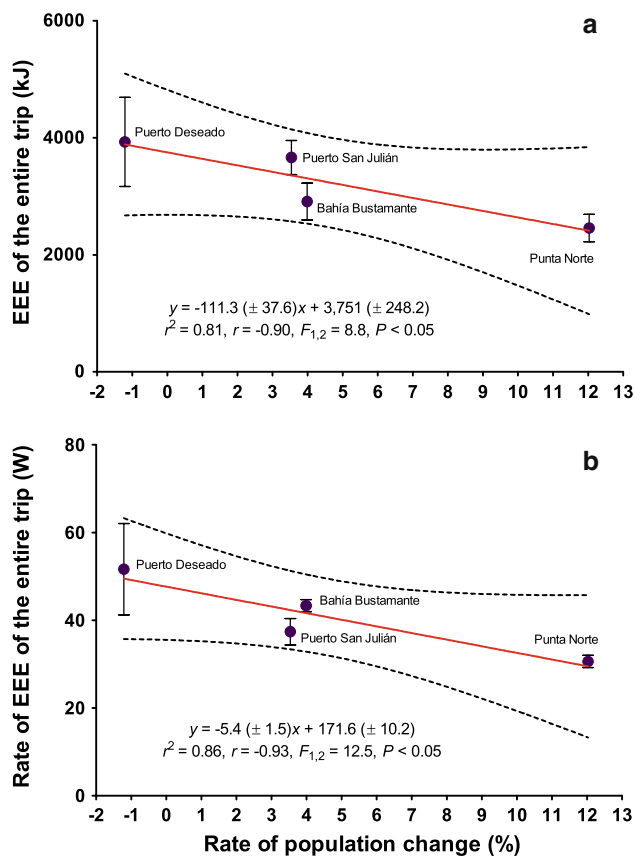


Fig. 4 **a** Total estimated energy expenditure (EEE; kJ \pm SE) and **b** mean metabolic power use (i.e. rate of EEE; W \pm SE) for complete foraging trips made by penguins from different colonies as a function of population growth rates at four different breeding sites along the coast of Patagonia. The red lines represent the functions that best fitted to the data and the black dashed lines show the 95 % confidence intervals

Energy expenditure during foraging trips

Travelling to and from foraging areas

The variation in the calculated metabolic power during travel to (outbound) and from (inbound) foraging sites highlights apparently different travel and search strategies used by the birds from the different colonies (Table 3). Various authors have reported that penguins normally execute short, shallow dives during the commuting stages between breeding and foraging sites (e.g. Rey et al. 2010), which should lead to efficient horizontal travel (Wilson 1995). However, birds may also begin searching for prey by executing deeper, albeit highly directional, dives (Sala et al. 2012a, 2014) which should expose them to prey, if present at depth, but waste time, and possibly energy, if not. A careful look at the energetics of travel as a function of depth, incorporating both horizontal and vertical cost of transport metrics in tandem with foraging success will be a

fascinating study area to examine how penguins might bet-hedge according to perceived prey densities in the different areas. What we can say here is that it seems no coincidence that the colony with the greatest rate of population change studied by us, PN, shows the highest proportion of foraging dives (in contrast to those of travelling) (for a discussion of this please see Sala et al. 2014).

Foraging

Within foraging areas, metabolic power was highest in PD, with BB birds coming a close second, although the derivation of this power (i.e. EEE foraging [kJ]) was quite different (Table 3). Although PSJ penguins spent less energy per dive (Table 2), they performed most dives and had the highest rate of diving (see Sala et al. 2012a, 2014), something that accords with their shallow dives (Fig. 2; see Sala et al. 2014), which led to, overall, them having high energetic requirements. Conversely, although BB penguins had low rates of diving (Sala et al. 2012a, 2014), they dived deep (see Sala et al. 2014), investing appreciable amounts of energy per dive (Table 2). Penguins from PD and PSJ, however, feed on prey with lower values of wet mass and energy content compared to birds from the other two colonies (Sala et al. 2012a; see above) and thus have to spend longer at sea, and underwater, to make up for this energetic shortfall (see Sala et al. 2012a, b, 2014), which explains the greater total amounts of energy invested in foraging by birds from these two sites compared to PN or BB penguins (Table 3).

Entire foraging trip

Overall, our gross values for metabolic power over entire Magellanic foraging trips compare well with those reported by Hennicke and Culik (2005) for the congeneric Humboldt Penguin, a bird of similar size (Williams 1995) (e.g. 60.8 ± 7.9 and 47.0 ± 18.0 W per trip for Humboldt penguins and PD, respectively; Table 3), as they do for the total energy expended per foraging trip (e.g. 3,935 kJ for Humboldt penguins and 3,538 kJ for Magellanics from PSJ; see Table 3). The Humboldt penguin work was based on models using information based on empirical laboratory studies on metabolic rates of diving and resting birds (Luna-Jorquera and Culik 2000), considered the ‘gold standard’ for activity-specific metabolic rate determination (Halsey 2011 and references therein). While the similarity in overall values between our studies and those of Hennicke and Culik (2005) lends confidence to the two approaches, it is important to note that lab-based metabolic studies do not faithfully recreate conditions of the wild. Thus, for example, the radical decrease in power needed to swim at increasing depths due to air volume changes with pressure

(Wilson et al. 1992) can only be alluded to using tags on wild birds. There is a similar situation with respect to the dive angle. Importantly, however, variation in the model parameters by Hennenke and Culik (2005) can lead to substantial variation in overall energy costs, which define the operational envelope under which these penguins forage. Our data from Magellanic penguins, in addition to reflecting activity-specific power during, for example, the different phases of the dive (Table 2) and the different phases of the foraging trip (Table 3) indicate that the manner in which birds react to variation in prey distribution and abundance according to distance from the colony and depth profoundly affects both the rate at which they expend energy and the rate at which they provision their brood. Indeed, rather than being a species with a well-defined allocation of time or energy foraging in a stylized manner (cf. Boersma et al. 2009), Magellanic penguins show considerable plasticity (Sala et al. 2014). This variable allocation of effort and time to localities in the 3-dimensional habitat that they exploit is presumably something that explains their breeding success despite taking diverse prey types (Wilson et al. 2005; Sala et al. 2012a) across their wide latitudinal range.

In this work, BB was the only colony for which we have studied more than one season (Table 1). By using the same database employed here, Sala et al. (2014) found no interannual differences in the basic diving parameters (i.e. maximum dive depth; time of descent, bottom phase, ascent and total dive time; rates of descent and ascent, etc.), closely linked to energy expenditure (cf. Wilson et al. 2010, 2011). However, this concerns only to one site and we cannot preclude that interannual differences may have also affected our results and that interannual variability in the oceanographic environment where Magellanic penguins forage differs between sites. Southern marine ecosystems, in general, and the area exploited by Magellanic penguins from the studied colonies in particular, are usually characterized by their stability (Acha et al. 2004; Rivas et al. 2006). This presumably accounts for the remarkable interannual consistency in the foraging routes taken by Magellanic penguins from Punta Tombo as documented by Boersma et al. (2009) (cf. Sala et al. 2012b) and other Patagonian seabirds (e.g. Quintana et al. 2010, 2011; Harris et al. 2012). Evidence of individual consistency in foraging behaviour within and amongst seasons reinforces the notion that the environment surrounding the studied colonies (Acha et al. 2004) and, presumably, targeted prey are stable enough over time, perhaps even years.

Energy expenditure and rate of population change

Several studies have indicated that food availability around seabird breeding areas limits population sizes, but authors have found both density-dependent (e.g. Lewis et al. 2001;

Forero et al. 2002) and density-independent mechanisms (e.g. Boersma and Rebstock 2009) are important. In contrast, Sala et al. (2012b) found no relationship between growth rate and colony size, indicating that extrinsic effects are the main determinant of recent population trends, there being no strong evidence for density dependence in the study area and period evaluated here.

Sala et al. (2012b) discussed how foraging effort variables, taken simply in terms of the horizontal dimension of trips (i.e. trip duration, maximum distance from the colony, foraging path length, etc.), are related to the population trends of the various colonies. They argued that, in absent of evidence of density-dependent processes to explain population changes, metrics of foraging effort at sea can help explain current status and population trends (see Sala et al. 2012b). Although studies of this type are scarce (see Boersma and Rebstock 2009), Hennenke and Culik (2005) relate different degrees of foraging effort from two Humboldt penguin colonies in Chile to reproductive performance (measured by reproductive success and growth rate of chicks), reporting lowest reproductive performance from birds operating from the colony with the greatest foraging effort. The authors attribute these differences to density-independent factors such as availability and abundance of food at sea, more than any other process on land.

Interestingly, a recent publication shows how detailed inspection of diving behaviour and effort of Magellanic penguins from the same colonies studied here enhance this picture. Sala et al. (2014) note, for example, that birds from BB and PD have lower levels of population growth rate (see Sala et al. 2012b) while feeding on a relatively large number of different species (see Sala et al. 2012a and references therein) incurring some of the highest indicators of diving and/or foraging effort. Conversely, the penguins of PN and PSJ are primarily monophagic (see Wilson et al. 2005 and references therein) and use well defined, relatively shallow depths, exploiting these with lower rates of descent and/or ascent (Sala et al. 2014), which are less costly in terms of energy (see Wilson et al. 2010 and cf. Table 2). Although in the latter case, penguins from PSJ must make a greater number of total dives, as a result of consuming prey with lesser energy revenue (see above; Sala et al. 2012a), which greatly increases total energy expenditure at sea (Table 3), limiting, to some extent, the potential growth of this colony (see Fig. 4).

Conclusions

The results presented here accord with our three predictions and so give support to our hypothesis. Thus, work in this paper also implies that power use and total energy expenditure may help explain population trends (see Sala

et al. 2012b) because both these effort-based variables are good indicators of rates of population changes (Fig. 4). While correlation does not necessarily indicate causation, there is a growing body of evidence that suggests that we should be mindful of the energetics of foraging to explain population processes (Hennicke and Culik 2005; Grémillet et al. 2006; Lewis et al. 2006; Petersen et al. 2006; Ballance et al. 2009) and we may even consider using them as short-term indicators of current status and health of their populations. While we are fully aware of the possible improvements to our methodological approach to obtaining energy expenditure of animals using ODBA (see Gleiss et al. 2011 and references therein), but consider that our attempt is markedly better than doing nothing in a world where the rate of extinction of species is ongoing ten times faster than we thought (see Pimm et al. 2014), and where any energetic data may help make management decisions.

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