

# Cold birds under pressure: Can thermal substitution ease heat loss in diving penguins?

Javier Ernesto Ciancio<sup>1</sup> · Flavio Quintana<sup>1,2</sup> · Juan Emilio Sala<sup>1</sup> · Rory P. Wilson<sup>3</sup>

Received: 11 February 2015 / Accepted: 6 January 2016  
© Springer-Verlag Berlin Heidelberg 2016

**Abstract** Thermoregulation could represent a significant fraction of the total energy budget of endotherms under unfavourable environmental conditions. This cost affects several traits of the ecology of an organism such as its behaviour, distribution, or life history. Heat produced by muscle contraction during activity can be used to pay for heat loss or thermoregulation in many species (known as “thermal substitution”). This study seeks to unite the effects of temperature, depth, and activity on the energetic costs of endotherm divers using the Magellanic penguin as model species and to evaluate whether penguins may benefit from thermal substitution. This species operates under highly variable temperature and depth conditions along its breeding range and provides an ideal natural experiment. A developed thermodynamic model describing foraging activity predicted that the major element affecting heat loss was depth, exacerbated by temperature. Birds living in colder waters are predicted to be able to minimize costs by executing shallower dives and benefit from thermal substitution by swimming faster, particularly during deeper dives. The model was evaluated in two contrasting scenarios: (1) when birds swim near the surface commuting

to the foraging areas and (2) when birds dive to depth to forage. Activity data from tags on free-living penguins indicated two of these predictions were apparent; penguins generally travelled faster while commuting at the surface in colder waters, while birds from warmer water colonies dived deeper while foraging. Contrary to predictions, however, penguins swam slower at deeper depths during both descent and ascent phases of foraging dives. These results suggest that penguins may benefit from thermal substitution by swimming faster when birds perform shallow dives commuting to and back from foraging areas, but they provide no evidence of behavioural response (via swimming faster) for thermoregulation when diving to depth to forage. Reasons for this are discussed and include the relevance of prey abundance in 3-d space and maximizing dive duration by conserving oxygen reserves. The way the bird operates will have profound consequences for the energy needed and therefore necessary energy acquisition rates. Expansion of our findings to other diving endotherms might help explain both global activity patterns and energy flow in ecosystems.

---

Responsible Editor: S. Garthe.

---

Reviewed by Undisclosed experts.

---

✉ Javier Ernesto Ciancio  
ciancio@cenpat-conicet.gob.ar; javier.ciancio@gmail.com

<sup>1</sup> IBIOMAR, Centro Nacional Patagónico, Blvd. Brown 2915, 9120 Puerto Madryn, Chubut, Argentina

<sup>2</sup> Wildlife Conservation Society, Amenabar 1595, C1426AKC Ciudad Autónoma de Buenos Aires, Argentina

<sup>3</sup> Biosciences, College of Science, Swansea University, Swansea SA2 8PP, UK

## Introduction

The physical environment affects metabolic rate primarily via effects that relate to temperature (Schmidt Nielsen 1997; McNab 2002), so understanding how heat balance (the heat exchange between the environment and an organism) occurs is critical for understanding species metabolism and consequently behaviour, distribution, and ultimately, life histories (Brown et al. 2004; Humphries and McCann 2014). In ectotherms that are not aestivating, metabolic rate is usually taken to be a simple function of body temperature, with defined  $Q_{10}$  (a parameter that summarizes the effect of raising temperature 10 °C on the rate of

a chemical reaction, Angilletta et al. 2004), so any environmental process that contributes to body heat increase (e.g. insulation) or decrease (e.g. wind speed) essentially determines metabolic rate directly. Active homeotherms (not torpid or hibernating) are more complex because, operating within a narrow range of body temperature, any process that relates to heat gain or loss has to be counteracted by increased metabolic rate (Schmidt Nielsen 1997). This has profound implications for their ability to operate in thermally extreme environments because increased metabolic rate has to be counteracted by increased consumption, something that has to be tenable in terms of accessibility of food resources and the rate at which they can be physically acquired by the animal.

Penguins are endotherms with high operating body temperatures (37–39 °C Prinzinger et al. 1991) and have long been studied with respect to their adaptations to cold (Le Maho 1977), with a primary emphasis being on Emperor penguins *Aptenodytes forsteri* because these birds incubate eggs during the Antarctic winter where climatic conditions are extreme (Groscolas 1986; Ponganis et al. 2003). But penguins operate in both air and water, which have fundamentally different heat conductivities and specific heats with, for any given temperature, water being considerably more thermally costly than air (Kooyman et al. 1976), resulting in consequently elevated metabolic rates (Culik et al. 1994; Luna-Jorquera and Culik 2000). A prime finding of research on this area is, for example, that penguins in cold water have a resting metabolic rate (RMR) that is some 2–3 times higher than that in air at a similar temperature [Kooyman et al. (1976), Baudinette and Gill (1985), Culik and Wilson (1991); but see Fahlman et al. (2005) for recently fed penguins]. Resting metabolic rate is, however, rather a simple situation and only relates to a fraction of the activities of free-living penguins. Penguins normally spend most time at sea swimming and diving at a variety of speeds (Wilson et al. 2002), which modulate heat loss, exploiting variable depths, which should accordingly compress the feather air layer, reducing insulation with depth (Wilson et al. 1992). Swim speed should also affect heat production since higher speeds necessitate greater metabolic effort (e.g. Culik et al. 1994) which produces more heat.

Heat produced by muscle contraction during different activities or by digestion of food (specific dynamic action SDA) could be used to pay for heat loss, thus diminishing the metabolic costs of animals operating in cold water. This physiological phenomenon called “thermal substitution” occurs in a diverse array of taxa including both terrestrial and aquatic animals (Lovvorn 2007; Humphries and Careau 2011) and has been proposed as driver of their behaviour under certain circumstances (McNamara et al. 2004; Liwanag et al. 2009). For example, thermal substitution

via the SDA and from exercising muscles has been demonstrated in diving ducks, but the presence of thermal substitution from exercising muscles depends on exercise level (Kaseloo and Lovvorn 2005, 2006). Despite its importance for describing animal energetics, there is little understanding of the magnitude of thermal substitution in nature (Lovvorn 2007) and, in particular, there is no clear evidence of penguin benefit or use. In a review of environmental and allometric variables affecting substitution, Humphries and Careau (2011) suggested that thermal substitution is more likely to occur in intermediate-size animals, experiencing temperate ambient temperatures (e.g. for terrestrial mammals of ~1 kg in ~15 °C). This could be the case for the Magellanic penguin *Spheniscus magellanicus*, our model species in this study. One condition for substitution to occur is that ambient temperature ( $T_a$ ) should be below a lower critical temperature ( $T_{LC}$ ), at which thermoregulation requires additional production of heat (Humphries and Careau 2011). Unsurprisingly, because of the high heat capacity and thermal conductivity of water, animals in water show higher  $T_{LC}$  values (De Vries and Van Eerden 1995) and tend to be exposed to conditions where substitution is more likely to occur (Enstipp et al. 2006).

In an attempt to understand how water temperature, dive depth, and activity might affect aquatic endotherms generally, we constructed a simple thermodynamic model to determine the rate of heat loss of the Magellanic penguin while swimming near the surface or diving to depth to forage. This species breeds all along the Patagonian Continent, from Beagle Channel to Peninsula Valdés (Williams 1995), a latitudinal range of 40°–55° S, and is consequently exposed to a wide range of water temperatures. Our model incorporates the effects of swim depth and swim speed on heat loss in two environmental conditions selected to be contrasting: (1) when birds swim near the surface commuting to the foraging areas and (2) when birds dive to depth to forage. We then considered how swimming and diving activity might modulate the metabolic rate of foraging Magellanic penguins, specifically considering consequences derived from thermal substitution. Finally, we used animal-attached tags to examine the diving behaviour of free-living penguins at various sites along the Magellanic penguin latitudinal range to examine whether birds varied their behaviour according to environmental conditions so as to benefit from thermal substitution.

## Methods

### Overview of the heat balance of a Magellanic penguin

Heat balance of organisms experiencing temperatures lower than their body temperatures is determined by the difference

**Table 1** Parameters used in the models

Parameter	Description	Value/units	Source
<b>Heat loss model</b>			
$k_1$	Conductivity of air	0.024 W m <sup>-1</sup> °C <sup>-1</sup>	
$k_2$	Mentioned but not used in model		
$k_3$	Coefficient	0.26 s m <sup>-1</sup>	Derived from analysis in text
$k_4$	Coefficient	4.87 m <sup>-2</sup>	Derived from analysis in text
$A$	Transverse surface area	0.204 m <sup>2</sup>	Derived from Walsberg and King (1978) for a 4-kg M. penguin
$V_s$	Volume of air in plumage at the surface	0.00084 m <sup>3</sup>	McCafferty et al. (1997)
$v_{\text{norm}}$	Regular travelling speed	2.1 m s <sup>-1</sup>	Wilson et al. (2004)
$T_{\text{peng}}$	Penguin body temperature	38.5 °C	Wilson and Grémillet (1996)
$T_{\text{water}}$	Water temperature	11 °C	Wilson et al. (2004)
	Penguin weight	4 kg	
<b>Heat production model</b>			
$a$	Coefficient	2.95	Luna-Jorquera and Culik (2000)
$b$	Coefficient	-6.35	Luna-Jorquera and Culik (2000)
$c$	Coefficient	5.81	Luna-Jorquera and Culik (2000)
$k_5$	Coefficient	5.9 W kg <sup>-1</sup>	Luna-Jorquera and Culik (2000)

between heat production and that transferred to the environment (Hudson and Bernstein 1981). It is unlikely that penguins operate in water at temperatures that are ever above their thermoneutral zone: various respirometry works detailing the RMR of penguins in air and water (e.g. Culik and Wilson 1992; Culik et al. 1994; Luna-Jorquera and Culik 2000) indicate, rather, that no penguin species actually operates in water within its aquatic thermoneutral zone because the RMR in water is not as low as that in air [Richman and Lovvorn (2011), but see Fahlman et al. (2005) and Stahel and Nicol (1982) for exceptions]. Considering this, we modelled the heat loss and heat production of Magellanic penguins in two separate models before combining them to estimate the heat balance of the species while foraging in the ocean and detail this process below:

### Heat loss

We assumed that the insulative capacity of the bird's plumage would not change at any water temperature below that at thermoneutrality since there are good energy conservation reasons for birds to minimize their heat loss (by e.g. reducing peripheral circulation) at the point where thermoneutrality is lost. We note though that issues such as blood perfusion to peripheral tissues, such as those of the flipper, will result in heat loss beyond this, despite birds having mechanisms in place such as burst perfusion to minimize this (Wilson et al. 1998). The rate of heat loss ( $dE/dt$ ) can be described by the modified standard Fourier law equation:

$$\frac{dE}{dt} = k_1 A \left( \frac{\Delta T}{L} \right) \quad (1)$$

where  $\Delta T$  is the average difference in temperature between the bird's core tissues ( $T_{\text{peng}}$ ) and the water ( $T_{\text{water}}$ ),  $k_1$  is the conductivity of the insulator,  $A$  is the transverse surface area (or the cross-sectional area of the heat path), and  $L$  is the thickness of the insulator (see Table 1 for parameter model values).

In a moving animal, increasing speed increases heat loss via forced convective heat transfer according to, among other things, the temperature distribution in the fluid flowing in the heated surface (Mitchell 1976) and the fluid conservation equations: mass, momentum, and energy that determine the distribution of temperatures in the water moving around the animal. This process is complex and will change according to animal shape (Mitchell 1976). McCafferty et al. (1997) reported that in their flying bird example (*Tyto alba*), heat loss increases in an approximately linear fashion with speed. We use this simplified form and therefore represent the rate of heat loss ( $dE/dt$ ) by an approximation of:

$$\left( \frac{dE}{dt} \right)_{\text{swim}} = k_2 v + \left( \frac{dE}{dt} \right)_{\text{rest}} \quad (2)$$

where  $v$  is the speed,  $k_2$  is a coefficient, and  $(dE/dt)_{\text{rest}}$  is the heat lost by the resting bird.

Combining Eqs. (1) and (2), the rate of heat loss by a swimming penguin would be:

$$\left( \frac{dE}{dt} \right)_{\text{swim}} = k_2 v + k_1 A \left( \frac{\Delta T}{L} \right) \quad (3)$$

or, because even the heat lost due to speed will be described by the Fourier equation;

$$\left(\frac{dE}{dt}\right)_{\text{swim}} = vk_3 \left[ k_1 A \left( \frac{\Delta T}{L} \right) \right] + k_1 A \left( \frac{\Delta T}{L} \right) \tag{4}$$

where  $k_3$  is a measure of how fast heat is lost as a function of speed. Finally, the predicted heat loss conditions for birds swimming near the surface do not prevail at depth. Air is a major factor in Magellanic penguin insulation (Wilson et al. 1992), but it changes in volume with depth according to Boyle’s law. The air layer thickness in the feathers, which equates with insulative capacity of the plumage, will change in direct accordance with this because the penguin surface area will change negligibly with depth. Thus,  $L = k_4 V$  and  $V = LA$  So

$$L = \frac{1}{A} V \quad \text{and} \quad k_4 = \frac{1}{A} \tag{5}$$

where  $k_4$  is a constant and  $V$  is the volume of air in the feathers. We use Walsberg and King (1978) to estimate the surface area of a penguin ( $A$ ), see Table 1 for parameter values. The volume of air ( $V_D$ ) at depth  $D$  (m) is given by Boyle’s law and related to the volume of air in the feathers at the surface via:

$$V_D = \frac{V_S}{\left[1 + \frac{D}{10.3}\right]} \tag{6}$$

where  $V_S$  is the volume of air in the feathers at the surface. The most radical scenario for heat loss with depth would occur if all the penguin insulation were derived from the air instead of incorporating some insulation from the skin and some subcutaneous fat. Assuming this to be the case for the moment, we can substitute  $V$  in Eq. (5) with  $V_D$ :

$$L = \frac{1}{A} \left( \frac{V_S}{\left[1 + \frac{D}{10.3}\right]} \right) \tag{7}$$

Finally replacing  $L$  in Eq. (4):

$$\left(\frac{dE}{dt}\right)_{\text{swim}} = vk_3 \left[ k_1 A \left( \frac{\Delta T}{\frac{1}{A} \left( \frac{V_S}{\left[1 + \frac{D}{10.3}\right]} \right)} \right) \right] + k_1 A \left( \frac{\Delta T}{\frac{1}{A} \left( \frac{V_S}{\left[1 + \frac{D}{10.3}\right]} \right)} \right) \tag{8}$$

Penguins have, however, two major forms of insulation, that from the air in the plumage, which is compressible with depth (Wilson et al. 1992), and insulation resulting from subcutaneous fat and the skin (Porter and Gates 1969). For simplicity, we consider the subcutaneous fat and the skin as a thickness of incompressible matter comparable, in essence, to air (although it will, of course, have a different thermal conductivity which will mean that a particular thickness of fat will be the

equivalent of a different thickness of air). It can be thus be added to the denominator in Eq. (4) substituting for  $L$  so that;

$$\left(\frac{dE}{dt}\right)_{\text{swim}} = vk_3 \left[ k_1 A \left( \frac{\Delta T}{[L_{\text{skin}} + L]} \right) \right] + k_1 A \left( \frac{\Delta T}{[L_{\text{skin}} + L]} \right) \tag{9}$$

### Heat production

A penguin that swims close to the water surface, where, simplistically, we may consider the feather air layer thickness to be the same as that in a bird resting in water, expends energy to overcome drag, which rises as a squared function of the speed, and produces metabolic heat accordingly. Various publications provide empirical polynomial functions that describe how penguins expend energy as a function of swim speed (Culik et al. 1996; Luna-Jorquera and Culik 2000), of the form:

$$P_{\text{swim}} = av^3 + bv^2 + cv + k_5 \tag{10}$$

where  $P_{\text{swim}}$  is the power used during swimming,  $v$  is the swim speed, and  $a$ ,  $b$ ,  $c$ , and  $k_5$  are coefficients. Here, any point above the intercept (where the speed = 0) should describe a metabolic term that is the power associated with the process of travelling, producing heat that can be used to offset the heat deficit. All other things being equal, increasing swim speed should produce increasing heat, which could be used to offset the heat deficit, potentially substituting thermoregulatory costs.

Because heat production by muscles of a swimming bird should be of the order of 85 % of the power needed to swim (muscle net efficiency or aerobic efficiency range 9.8–24.1 %; Gaesser and Brooks 1975), this parameter is affected by many different factors including speed (e.g. see Kvist et al. (2001)), while  $k_5$  is the power used to rest in water (Eq. 10). The heat produced during swimming  $(dP/dt)_{\text{swim}}$  for a 4-kg Magellanic penguin is accordingly 85 % of the power used:

$$P_{\text{swim}} = 0.85 \left( av^3 + bv^2 + cv + k_5 \right) 4 \tag{11}$$

So when

$$(dE/dt)_{\text{swim}} = P_{\text{swim}} \tag{12}$$

we can use these conditions to estimate the coefficient  $k_3$ , combining Eqs. 4 and 11;

$$vk_3 \left[ k_1 A \left( \frac{\Delta T}{L} \right) \right] + k_1 A \left( \frac{\Delta T}{L} \right) = 0.85(av^3 + bv^2 + cv + k_5)4 \tag{13}$$

When the heat produced via the metabolic processes used in powering the musculature for swimming exceeds that normally lost, the excess heat can simply be lost by, e.g., perfusing appendages [but see Wilson and Grémillet

(1996)]. However, during surface swimming at normal speeds (between 1.4 and 2.5 m s<sup>-1</sup>; Wilson et al. 2002) in water at “normal” temperatures, we assume that the power used by penguins is enough to maintain body temperature (Wilson and Grémillet 1996). This means that the value for  $k_3$  can be given within the following term whereby  $L$  in Eq. (13) is replaced by the term expressed in Eq. (7) following rearrangement:

$$\left(\frac{k_1 A^2 \Delta T}{V_s}\right)(1 + 0.097D)(vk_3 + 1) \leq 3.2(av_{\text{norm}}^3 + bv_{\text{norm}}^2 + cv_{\text{norm}} + k_5) \quad (14)$$

where  $v_{\text{norm}}$  is the normal swimming speed. The normal speed for a Magellanic penguin swimming at the surface (1 m depth) at 11 °C is 2.1 m s<sup>-1</sup> (Wilson et al. 2004) so that  $K_3$  is given by:

$$k_3 = \frac{56.01V_s}{v_{\text{norm}}k_1A^2\Delta T(1 + 0.097D)} - \frac{1}{v} \quad (15)$$

Finally, we estimate the heat flux of a swimming penguin combining both models as:

$$\text{Heat flux} = \text{produced heat (Eq. 11)} - \text{heat lost (Eq. 9)} \quad (16)$$

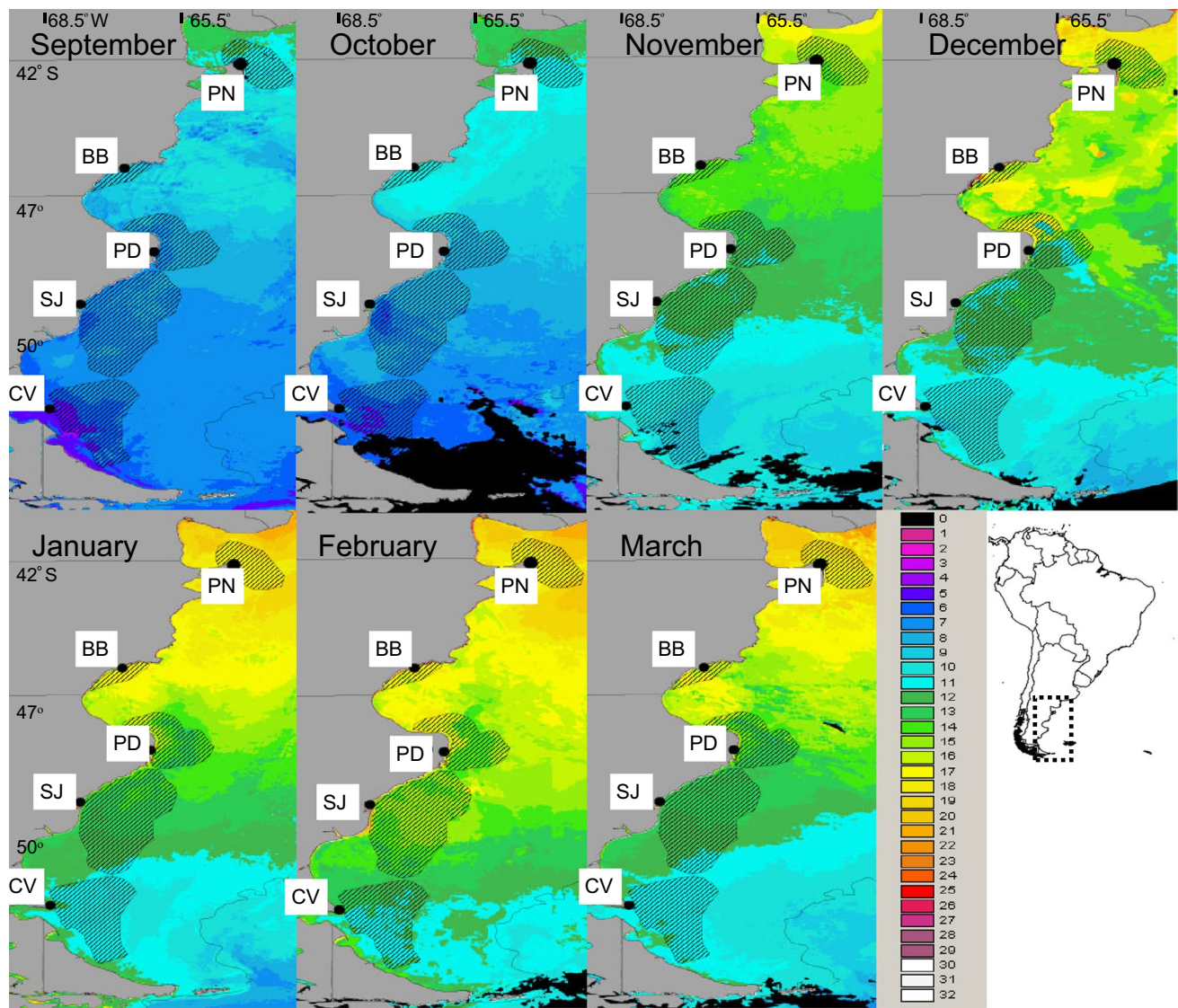
### Magellanic penguin thermal environment

To describe the temperatures where Magellanic penguins forage during the whole breeding season, published distribution maps of Magellanic penguin foraging areas and sea surface temperature (SST) maps were digitized into layers in a geographic information system (GIS) (Fig. 1). Five colonies were chosen along the species latitudinal range (Table 2), and as an approximate estimate of foraging range, we took the greatest foraging range reported in the literature, by either GPS (Boersma et al. 2009), dead-reckoning, or geolocation tags (Wilson et al. 2005). Sixty-five NOAA 14 and 16 satellite images from the CENPAT database (years 1999–2002) were chosen after visual inspection, and average monthly SST was estimated for each colony foraging area polygon (Fig. 1). In addition to this, the thermal environment of free-living breeding Magellanic penguins in the early breeding season (late November–early December) was estimated from temperature loggers deployed during the years (2005–2008) (see below for details). For this, temperatures were estimated as a function of depth and locality using temperature sensors on pressure sensor-equipped dead-reckoning devices.

### Magellanic penguin swimming and diving patterns data analyses

We studied penguin swimming and diving patterns in two contrasting situations of their foraging phase in the ocean:

penguins travelling horizontally near the surface to and from the foraging sites performing shallow dives (<2 m) with less obvious oxygen restrictions and low hydrostatic pressure changes, and penguins conducting more vertical dives for foraging under the effect of varying and generally higher pressure. For this, a total of 57 penguins from 5 colonies were equipped with either depth-temperature loggers on-board dead-reckoner devices [Daily Diary, Swansea University, Wales Table 2, see Wilson et al. (2008) and Wilson et al. (2010) for a description of the technology] or GPS-depth loggers [In Punta Norte, B. Bustamante, P. Deseado, and San Julián Colonies, GPS-TDlog, Earth and Ocean Technologies, Kiel (Germany) which recorded time, latitude, longitude, and speed at 1 Hz with an accuracy of positional fixes considered to be better than 5 m for 90 % of the fixes, see Sala et al. (2012) for details]. To attach the units, we used tape (Wilson et al. 1997) to secure them to the lower back following recommendations of Bannasch et al. (1994). Birds, which were brooding small chicks, were equipped for a single foraging trip after which the loggers were removed. Depth data from all the devices, which were collected at a minimum frequency of 1 Hz (max 9 Hz), were analysed to provide frequency data for the maximum depths reached during dives. In addition, data on swim speed relative to the water depth were recorded at 0.5 Hz for 5 penguins foraging from Cabo Vírgenes colony (52.3° S 68.3° W) using a dead-reckoner (Wilson et al. 2005) with a calibrated paddle wheel (Bannasch et al. 1994). The GPS-depth loggers were used to determine mean surface horizontal travel (ground) speed in 31 birds from three colonies (Punta Norte, Bahía Bustamante, and San Julián) after defining the outbound, foraging, and inbound section of a foraging trip according to Sala et al. (2012) (the surface speed during foraging will refer hereafter to the speed between patches of prey in the foraging area). During travelling periods (not performing deep dives to forage), penguin trajectory underwater is highly linear as birds move rapidly between breeding and foraging sites, and this is reflected in GPS positions of birds (which can only be obtained when penguins are at the surface) (Sala et al. 2012) so that speed errors due to deviations from a straight line course are minimal. To investigate whether there was a relationship between penguin surface travel speed derived from GPS (response-dependent variable) and SST and between swim speed relative to the water depth derived from paddle wheel of penguins, we used linear mixed-effects models (LME, Zuur et al. (2009)). We used individuals as random effects to control for lack of independence between repeated measures over the same penguin. For surface travel speed, trip section (with levels outbound, foraging, and inbound) and SST (numeric covariable) were treated as fixed effects. We incorporated an exponential function for the variance (varExp function,



**Fig. 1** Sea surface temperatures (SST, see text for sources) in the Magellanic penguin foraging range during the breeding season (September–March). Foraging areas (indicated by *greyed* out areas) were taken for birds from Puerto Deseado (PD) and San Julián (SJ) from Boersma et al. (2009), and areas for birds from San Julián and Cabo

Vírgenes (CV) were taken from Wilson et al. (2005). Bahía Bustamante (BB) foraging area was taken from (Yorio et al. 2010). As a conservative approach, the largest foraging area reported on literature is shown. The scale indicates degree Celsius, with zero values (*black*) corresponding to clouds where no measures could be taken

Pinheiro and Bates (2001)) to deal with variance heterogeneity related to sea surface temperature. For the analysis of speed at depth estimated using paddle wheels at Cabo Vírgenes, we used depth as random effect and modelled in three separated models, one for each diving phase (descent, bottom, and ascent phases). The models were fitted by restricted maximum likelihood (REML) using the lme function from nlme package in R (R Development Core Team 2011). Finally, we used two generalized linear model

(GLM, glm function in R) with a gamma distribution and log link function to evaluate the effects temperature (fixed, mean SST for November–December and mean temperature at the depth interval of 20–30 m) on the maximum depth utilized by penguin when foraging for all the devices that carried depth sensors. All statistics and computation were performed in R software, and also for estimations of the dive parameters (e.g. dive duration), the R package diveMove was used (Luque 2007).

**Table 2** Location of colonies, years studied, number and type of devices, dives and trip characteristics, and seawater temperatures in the water column measured by free-living birds carrying recording equipment during the austral spring (late November–early December)

Colony	Lat.	Year	Number of:		Duration of dives (s)			Surface speed ( $\text{m s}^{-1}$ ) (SD)			Duration, T (h) (SD)	Depth intervals (m) – temperature ( $^{\circ}\text{C}$ )							
			GPS	DR	Dives	FO	IN	OUT	FO	IN		OUT	0–10	10–20	20–30	30–40	40–50	50–60	>60
Punta Norte	42.08S	08	10	4	8956	72.4	62.2	71.6	1.04 (0.1)	0.61 (0.3)	1.30 (0.3)	24.5 (6.5)	13.90	13.23	13.16	13.09	13.12	13.28	13.19
Bustamante	45.11S	05/6/7	9	7	5629	87.1	37.2	49.5	1.65 (0.3)	2.02 (0.4)	1.94 (0.2)	38.7 (18.3)	13.72	11.97	11.52	11.39	11.08	10.89	10.38
P. Desierto	47.75S	06	1	5	5245	67.5	38.6	53.9	2.7	2.9	3.00	41.3 (14.9)	13.20	10.32	10.21	10.13	10.41	10.51	
San Julián	49.28S	07	12	4	15,121	49.9	41.7	52.4	1.72 (0.3)	1.14 (0.8)	2.4 (0.7)	27.0 (7.5)	10.15	9.38	9.13	8.82			
C. Virgenes	52.36S	00		5	3240	52.2	–	–	–	–	–	18.1 (6.8)	6.22	6.26	6.09				

“Number of” refers to the number of tagged birds with GPS (GPS) and with dead-reckoner devices (DR), or the number of dives analysed (Dives). Duration of dives refers to the mean duration of dives in the three phases of a foraging trip analysed: foraging (FO), inbound (IN), and outbound (OUT) as defined in Sala et al. 2012. Surface speed refers to speed calculated from GPS data while travelling at the surface (in FO phase, the surface speed is the speed between prey aggregations within the foraging area). Duration T refers to the mean duration of foraging trips expressed in hours. Water temperatures are expressed by mean values within 10-m-depth intervals

## Results

### Model outputs

A first output of our model was that, as water temperature decreased, the overall heat loss increased linearly (Fig. 2a). For penguins swimming near the surface, however, the effect of decreasing temperature was not predicted to have a particularly dramatic effect on heat flux (note that hereafter, when birds lose heat, we will refer to it as a negative heat flux and positive when they gain heat). Birds swimming near the surface at  $2.1 \text{ m s}^{-1}$  (the “normal” swim speed of Magellanic penguins, Wilson et al. (2004)) in water of  $14 \text{ }^{\circ}\text{C}$  had a positive heat flux of ca.  $6 \text{ W}$  (Fig. 2c), whereas in water of  $6 \text{ }^{\circ}\text{C}$ , they had a negative heat balance of some  $10 \text{ W}$  (Fig. 2c). Higher speeds increase heat loss; however, since heat production also increases and disproportionately so (because of the cubic function of power requirements with increasing speed) [see (Eq. 10)], overall heat flux becomes less negative or even positive so that even small increases in swim speed during high speed swimming (particularly above  $2.1 \text{ m s}^{-1}$  for example) readily mitigated the heat lost by birds in colder water (Fig. 2a, b).

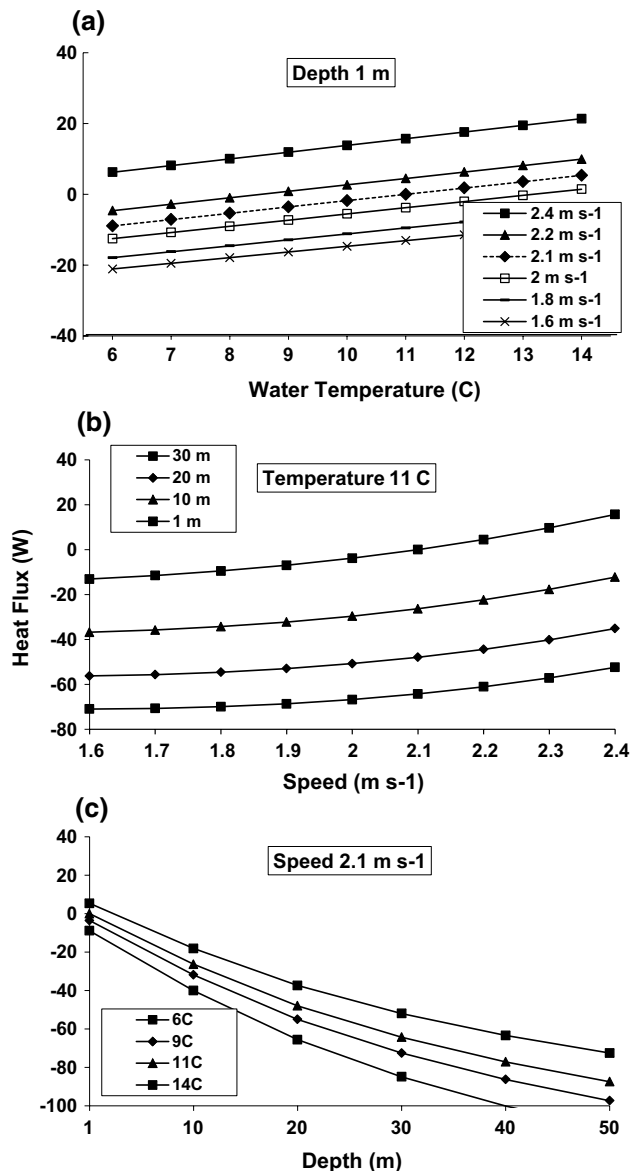
Depth, however, had a profound effect on heat flux (Fig. 2b) due to the compression of the insulating air layer with increasing hydrostatic pressure, with Magellanic penguins swimming in water of  $11 \text{ }^{\circ}\text{C}$  at  $2.1 \text{ m s}^{-1}$  predicted to be losing energy as heat at a rate of about  $80 \text{ W}$  at a depth of just  $30 \text{ m}$  (Fig. 2b, c). Increasing speed reduced net heat flux somewhat (Fig. 2b), but the effect of depth was dramatic and exacerbated disproportionately by temperature (Fig. 2c).

### Predictions stemming from the model

Our model indicates that a prime problem in managing heat loss for foraging Magellanic penguins is that of depth, followed by the exacerbating effect of temperature. Other things being equal, we would therefore expect birds living in colder waters to tend to execute shallower dives while foraging. In addition, if birds are to engage in thermal substitution, we would expect greatest swim surface and diving speeds to occur in birds from populations that live in coldest waters and dive deepest. Note that these predictions are based solely on heat flux calculations derived from our model. The applicability of the model and other factors that may change expectations are discussed later.

### Magellanic penguin thermal environment

Magellanic penguins breeding in the Patagonian coast face a wide range of temperatures along the reproductive cycle



**Fig. 2** Relationship between predicted heat flux (W) and: **a** water temperature for a Magellanic penguin swimming at a depth of 1 m at different speeds. This scenario (and those detailed below) assumes that at a water temperature of 11 °C and a swim speed of 2.1 m s<sup>-1</sup>, the heat produced by the action of swimming exactly balances the heat lost (for definition of all terms used in the model see Table 1). **b** Swim speed for a Magellanic penguin swimming at various water depths. **c** Depth for a Magellanic penguin swimming in water at various temperatures. Because of model design, negative heat flux is when birds lose heat and positive when birds gain heat

and geographic range, with temperatures differing significantly between colonies and months (Fig. 1; Table 2). For example, the thermal environment at the surface (SST) ranged between means of 6.1 °C SST during September at Cabo Vírgenes and 18.2 °C during March in Punta Norte, encompassing a maximum range of 4–20 °C (Fig. 1). Temperature also varied with depth, and the rate of change of

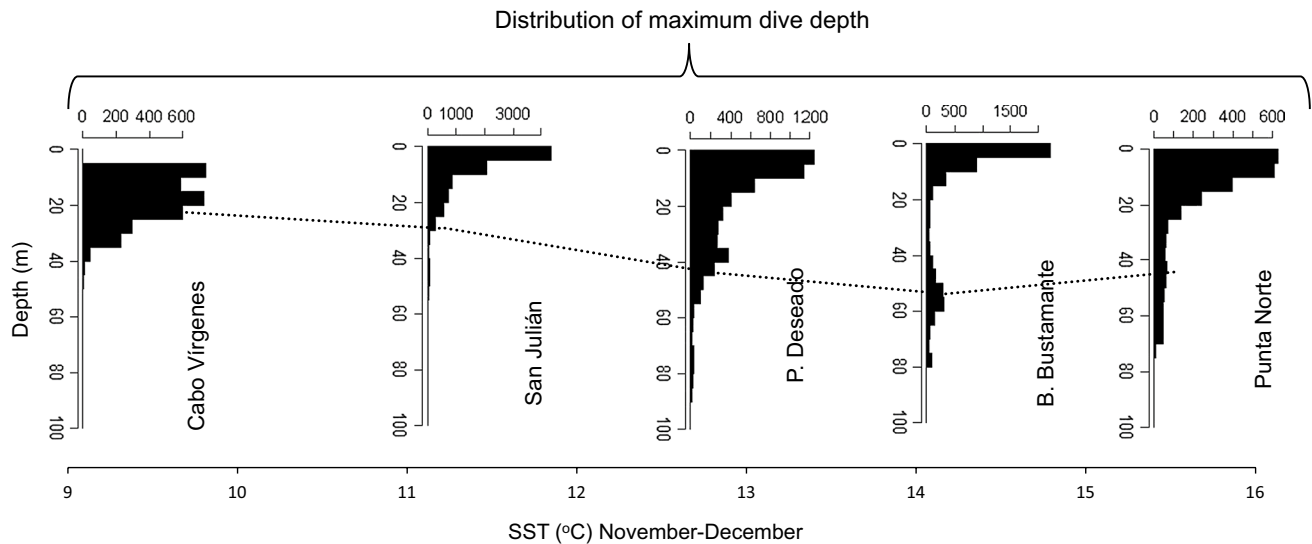
temperature with depth varied between colonies: During the period where devices were deployed (late November to early December), some colonies showed strong stratification in the top 10 m, e.g. P. Deseado, where water temperature fell from 13.2 to 10.3 °C in the first 20 m of the water column, while others showed poor stratification, e.g. Punta Norte (Table 2). The most severe thermal conditions occurred at Cabo Vírgenes, where the water surrounding the colony had temperatures ranging between 4 and 7 °C during the austral spring for the entire water column (Table 2; Fig. 1).

### Magellanic penguin behaviour under defined environmental conditions

Given the results of our model, we evaluated three hypotheses, two (i and iii) in which penguins might benefit by engaging in thermal substitution by swimming faster: (i) birds swimming near the surface (at depths of <2 m) to commute between the colonies and the foraging areas should swim faster in colder temperatures, (ii) other things being equal (this ignores confounding factors such as prey availability—see later), birds diving for foraging in colder water should dive shallower, and (iii) birds diving deeper for foraging should swim faster to counteract the increased heat loss due to insulator air layer compression. Our findings with respect to these hypotheses are presented below for our instrumented free-living birds.

- (i) *Overall surface travel speed while commuting:* birds that forage in colder surface waters (Fig. 1) travel at higher speeds (Table 2). The LME model showed a significant effect of temperature on surface travel speed [ $F_{(1,29)} = 14.4, p < 0.001$ ] for birds commuting to and between foraging areas, and this effect was independent of foraging trip section (no significant interaction between temperature and trip section:  $F_{(2,58)} = 1.34, p = 0.26$ ). Speed correlated negatively with seawater temperature (speed coefficient =  $-0.18$ ; 95 % CI =  $[-0.33, -0.02]$ ), showing that Magellanic penguins travel faster in colonies surrounded by colder waters.
- (ii) *Foraging depths:* the GLM analyses showed a significant effect of colony surrounding water temperatures in the maximum depth of foraging birds for both SST ( $F_1 = 52,094, p < 0.001$ ) and mean temperature at the depth interval of 20–30 m ( $F_1 = 63,410, p < 0.001$ ). Birds from the more northerly, and therefore warmer (Fig. 1), colonies dived deeper than birds from colonies located farther south (Fig. 3). The mean value for percentiles larger than 75 % of the maximum depth decreased with latitudinal water temperature (values are 41.2, 56.48, 41.8, 21.1, 17.6 m depth for Punta





**Fig. 3** Maximum depth per foraging dive histograms on the five studied colonies compared to SST for the study period. Penguins in the north of the latitudinal range (Punta Norte and B. Bustamante) appeared to perform deeper dives than birds in the south (P. Deseado,

S. Julián, and C. Vírgenes). *Dashed line* represents the mean value for percentiles larger than 75 % of maximum depth. Notice how this value decreases with latitude-water temperature

Norte, Bustamante, P. Deseado, S. Julián, and C. Vírgenes colonies, respectively, dashed line in Fig. 3).

- (iii) *Speed versus depth while foraging*: contrary to model predictions, the five Magellanic penguins equipped with a calibrated paddle wheel (giving speed relative to the surrounding water) foraging from Cabo Vírgenes swam slower at deeper depths during both descent and ascent phases of the dive (Fig. 4). The LME models showed a significant negative effect of depth on travel speed for the ascent (coef =  $-0.010$ ,  $F_1 = 7.28$ ,  $p = 0.007$ ) and descent (coef =  $-0.013$ ,  $F_1 = 6.08$ ,  $p = 0.013$ ) phases but not during the bottom phase ( $F_1 = 1.61$ ,  $p = 0.204$ ). The considerable variability in swim speed during the bottom phase of dives resulted in no pattern being apparent.

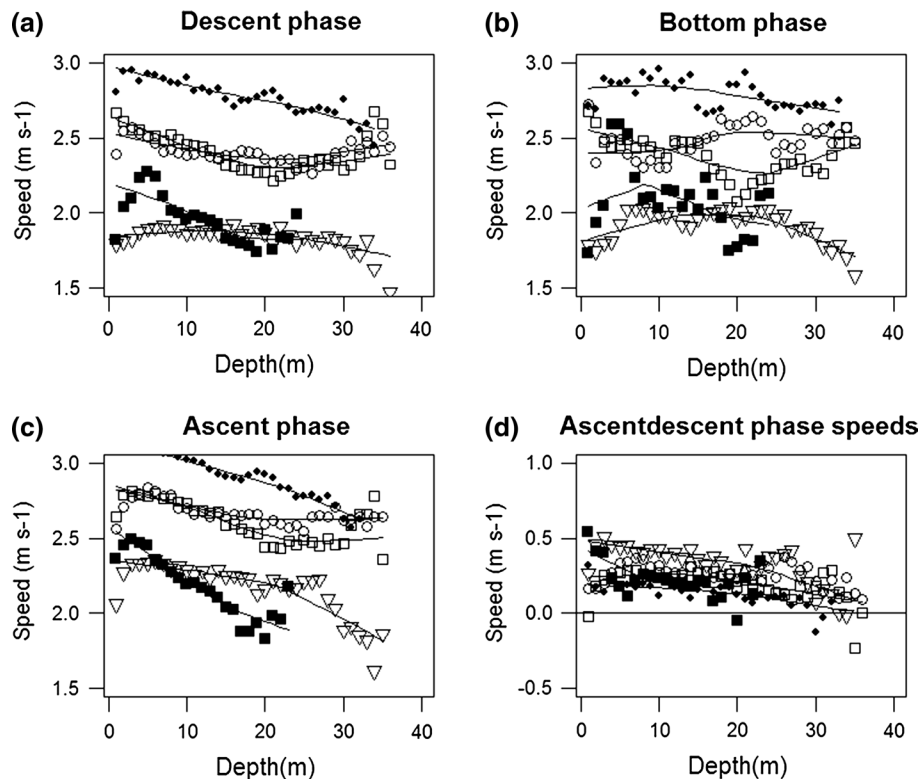
## Discussion

### Limitations of the model

Several thermodynamic models have been developed to understand life history traits of animals including seabirds (Hind and Gurney 1997; Grémillet et al. 1998; McNamara et al. 2004; Porter et al. 2006; Fort et al. 2009; Speakman and Król 2010). The complexity of these models ranges from simplified heat exchange models, considering only the effect of body shape (Mitchell 1976), to complex representations considering morphological, physiological, and behavioural properties of the animal, even modelling

the environment effect through climate models (Fort et al. 2009). The primary purpose of our model was to derive general trends, rather than to produce specific values, to test our thermal substitution scenario. Such a reductionist approach can always be criticized for lack of attention to detail (Hilborn and Mangel 1997), but does help clarify the potential importance of fundamental environmental parameters such as depth and temperature as done here. A specific aim of our work was to attempt an examination of the role of heat flux in potentially modulating the swimming and diving behaviour of penguins from a thermodynamic perspective. Thus, although this simplistic approach on free-living animals assumed to be optimizing for multiple parameters cannot control for many of these (such as prey distribution), it can serve as a useful pointer to highlight the value of observed behaviours and where future research might be directed.

We note some factors that may have affected the outcome of our model, which may help explain why some of our observations of penguin behaviour did not always match our predictions. For example, the model may have over-emphasized heat flux because we assume full homeothermy across all tissues, which is overly simplistic (Schmidt et al. 2006). In addition, we did not consider the metabolic power associated with specific dynamic action (Brody 1945) which could theoretically help in producing heat needed for thermoregulation (McCue 2006; Lovvorn 2007) although the costs of heating penguin prey, at ambient temperature, can be extreme (Wilson and Culik 1991). Indeed, the simple ingestion of cold food by penguins is



**Fig. 4** Mean speed relative to water (estimated with calibrated paddle wheels for the descent, bottom, and ascent phases of the dives as well as the ascent minus the descent speeds) at depth (1-m intervals) for five Cabo Vírgenes Magellanic penguins during the foraging phase of the foraging trip regardless the maximum depth of the dive. Different symbols represent different individuals. In general, birds swam slower at greater depth regardless of whether they were ascending or descending. At equivalent depths birds ascended faster than

they descended, presumably due to buoyancy (Wilson et al. 2008; Wilson et al. 2010), the difference between ascending and descending speeds decreased with depth and was about zero at depths close to 40 m. Lines were fitted with “loess” function in R (locally weighted polynomial regression). Only foraging dives to depth were included in this analysis (number of dives: 29,941 descent, bottom 36,175, and 31,257 ascent phases)

likely responsible for the dramatic drops in temperature observed in some regions of the abdomen (Culik et al. 1996; Handrich et al. 1997; Schmidt et al. 2006). The observation of lowered temperatures within the outer shell of the body due to the process of ingesting cold food and having thermal windows in particular areas, such as the brood patch, has led to considerable debate about the extent and function of such drops (see e.g. Culik et al. 1996; Handrich et al. 1997; Ponganis et al. 2001, 2003; Schmidt et al. 2006) and what mechanisms of blood perfusion (and simple heat transmission; Butler and Jones 1997) might be employed and to what end. What is clear is that any section of the body that has a lowered temperature will also have a lowered heat flux to the environment so, if such labile heterothermal volumes are maintained as such, they will result in an overall reduction in heat loss from the bird to the water. It is notable though that even radical reductions in the orders of 20 °C, such as has been observed close to the brood patch in diving king penguins (e.g. Schmidt et al. 2006), will not stop heat flux entirely for as long as they are

higher than ambient water temperature. What is also clear is that some parts of the body, e.g. the inferior vena cava (Ponganis et al. 2001), do not entertain substantial temperature drops (Ponganis et al. 2001, 2003). To these must be added some major tissues located towards the outside of the body shell, such as the pectoral muscle, which operate essentially normo-thermally (Schmidt et al. 2006). Thus, the size and peripheral location of the muscle groups involved in swimming will, via simple physical principles, inevitably lead to appreciable heat flux to the environment, even if there is some evidence of shunting of the heat to other areas of the body (Schmidt et al. 2006). Accordingly, the maintained high temperature of these regions requires energy investment which should be modulated by depth and speed in a manner similar to that described by our model.

The absolute importance of heat flux will, however, depend on the percentage of the body tissue that allows temperature drop and the position of all tissues with respect to the external surfaces. We also note that some heat will

be lost by the respiratory system, although this could only relate to breathing at the surface between dives (Lovvorn 2007). Similarly, differential exposure to radiation from the sun while floating at the surface (in the north there is low cloud cover, while the southernmost colony has the highest cloud cover ratio of the Patagonian coast) may also affect heat balance, again though, only at the surface.

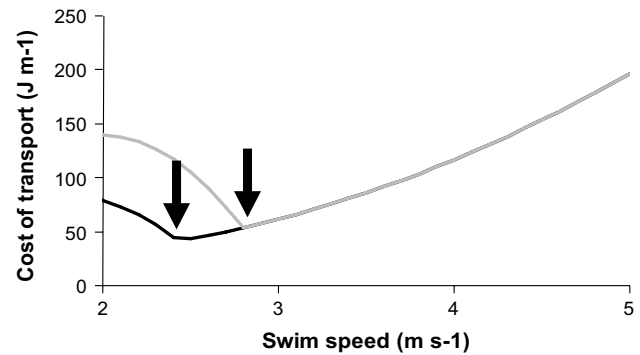
### Heat flux and oxygen conservation

A major consequence of high heat flux underwater and metabolic rate associated with maintaining body temperature is the impact on oxygen stores and correspondingly compromised dive durations. Suggestions that birds might allow body temperatures to drop during dives and correct for them during surface intervals by adopting high metabolic rates when oxygen is not limited (cf. Kvadsheim et al. 2005; Sparling et al. 2007 for mammals) are more complex than implied in the literature. First, Wilson and Grémillet (1996) noted how free-swimming, but not feeding (and therefore not subject to ingesta cooling the abdomen), congeneric African penguins *Spheniscus demersus* had systematically increasing stomach temperatures during swimming and decreasing temperatures during pauses at the surface. Secondly, to correct for heat loss during the dive, the power requirements during the surface period have to be greater by a factor that approximately equates with the ratio of dive to pause ratio. Thus, a bird that has a heat flux of  $-80$  W underwater for 100 s has to have a metabolic rate that equates to a heat production of ten times that during the expected 10-s short surface interval, something that would take its metabolic rate to unrealistic levels.

### Surface speed versus water temperature

A primary prediction stemming from our model is that penguins should be able to save energy by swimming faster in colder waters by capitalizing on thermal substitution. The direct thermal substitution scenario is, however, simplistic because increasing swim speed incurs accelerating power costs, taking animals away from their lowest costs of transport, the speeds at which the energy expenditure per unit distance is minimized (Tucker 1975; Schmidt Nielsen 1997). In fact, the effect of the thermal substitution phenomenon would be to shift the typically “U”-shaped cost of transport curve to the right (Fig. 5), demonstrating how the adoption of variable swim speeds according to water temperature should affect the costs of travel and, consequently, the costs of foraging.

Given that costs of transport can be effectively reduced for higher speeds up to a certain threshold which is water temperature dependent (this minimum is achieved at higher speed in colder waters, Fig. 5), it is probably no



**Fig. 5** Predicted cost of transport (which is derived by dividing the power use by the speed) as a function of swim speed for Magellanic penguins swimming under different scenarios. The values were derived using the model developed in this work which allows calculation of power as a function of speed and associated heat flux which, if body temperature is to be maintained, must be corrected by increased metabolic rate. The *grey line* shows a bird swimming in water at 10 °C, while the *black line* shows a bird at 15 °C, both at a depth of 1 m. Where the model-predicted heat loss exceeded heat production, the total costs exhibited by the birds under the two scenarios included these costs over and above the simple costs of swimming (see text). Note how the colder water shifts the point of minimum cost of transport (*arrows*) to the *right*

coincidence, therefore, that our penguins swam faster (as indicated by speed determined by our GPS-units) when commuting from colonies surrounded by colder waters. This would apply for penguins leaving the colony to forage and returning to it, which swim with marked directionality, undertaking short, shallow (<2 m) dives to enable them to commute to the foraging area as efficiently as possible (Sala et al. 2012). Nonetheless, it is striking that foraging phase shows this pattern too, when birds move between prey aggregations. Thus, penguins in colder water had overall faster travelling speeds irrespective of dive type, which accords with our predictions. Our predictions did not, however, prove correct when penguin dive to forage to deeper depths.

### Depth versus temperature

Our model results point to the importance of the air trapped in the feathers in modulating heat loss in penguins compared to other morphological (e.g. fat—which is negligible, for example, in cormorants compared to penguins—or skin thickness layer), physiological (body temperature), ecological (water temperature), or behavioural (swimming speed) features. Similarly, Grémillet et al. (1998) presented a theoretical treatise highlighting the critical role that plumage air layer thickness plays in the insulation of great cormorants *Phalacrocorax carbo* and European shags *Phalacrocorax aristotelis*. Given the importance of air as an insulator and the radical compression that air experiences with pressure

(see earlier), dramatically reducing the thickness of this insulative layer with depth, it is little surprising that depth is predicted to be the major factor determining heat loss in diving penguins. Such predictions are difficult to test under laboratory conditions, but Enstipp et al. (2006) found that captive double-crested cormorants *Phalacrocorax auritus* swimming in an exceptionally deep (10 m) tank under controlled temperature and feeding experiments consumed 22 % more energy than individuals diving to only 1 m depth, a difference that could be attributed at least partially to reduced insulation due to compression of the insulative air layer.

A superficial assessment would indicate that our model predictions with regard to the depth are borne out by our observations of dive depths used by penguins from different colonies down the Patagonian coast (Fig. 3). Although depth is predicted to be a primary modulator of metabolic rate in diving penguins, its effect is considerably exacerbated by temperature (Fig. 2). Despite this match between the model prediction and penguin behaviour, the dive depth of foraging penguins is presumably driven by other factors such as vertical prey distribution and bathymetry in the foraging area. While noting that the function of our model was to highlight how thermal effects might be expected to influence behavioural strategy, these other factors may be critical and may go against optimal behaviour with regard to heat flux. A good example is prey in the water column. When prey is not found near surface waters, penguins will have to dive deeper to find them, whatever the water temperature, incurring the consequent metabolic costs. We note though that vertical distributions of the main preferred prey species across the whole study area (Frere et al. 1996; Scolaro et al. 1999; Ciancio et al. 2015) do not differ substantially in their maximum depth distributions: anchovy, exploited by penguins from the northern colonies, is found up to 80 m depth (Hansen et al. 2001), while sprats, exploited by penguins from the southern colonies (Frere et al. 1996), are found up to 70 m depth (Casarsa 2005). Additionally, both prey species perform nictemeral vertical migrations (Hansen et al. 2001; Casarsa 2005) so they are available for penguins at different depth ranges during the light hours when Magellanic penguins forage (Wilson et al. 2005). Penguin from all studied colonies forage in the Patagonian Shelf in areas with maximum depths between 80 and 120 m, so the bathymetry, which typically extends beyond the lower depth limit of the prey (see above), would seem to play a minor role.

### Speed while diving for foraging versus depth

Our predictions for speed (relative to the surrounding water) versus depth derived from the model do not accord at all with our observations (Fig. 3), with penguins actually

slowing down with increased depth rather than speeding up to correct for increasing heat flux caused by decreased insulation thickness. It thus seems that speed during foraging dives is not regulated for any thermoregulation purpose and, rather, that other factors, such as oxygen preservation, modulate penguin behaviour. Clearly, increasing speed to counteract heat loss increases power requirements with concomitant increase in oxygen consumption, something that would reduce dive duration.

In conclusion is quite obvious that we have oversimplified the thermal flux situation. In a diving, feeding penguin, heat is lost to food, ingested at ambient temperatures and placed fairly centrally within the body cavity, as well as due to heat moving from the bird to the environment through the body external surface. Magellanic penguins minimize stomach peristalsis during foraging dives (Peters 1997), something that reduces transfer of heat from surrounding tissues to the stomach (Wilson et al. 1995), although non-stomach abdominal temperatures are still likely to drop somewhat (cf. Culik et al. 1996; Bevan et al. 1997; Handrich et al. 1997; Schmidt et al. 2006 for other diving bird species). Nonetheless, maximum stomach temperature drops recorded for Magellanic penguins by Peters (1997) never went below 32 °C (the vast majority was in excess of 36 °C), in agreement with data collected by Wilson and Grémillet (1996) for the congeneric African penguin. Based on the substantial drops in both non-stomach abdominal and stomach temperatures in sub-Antarctic and Antarctic diving birds (e.g. Bevan et al. 1997; Handrich et al. 1997; Schmidt et al. 2006) and the relatively small drops in the stomach temperature incurred by Magellanic penguins (Peters 1997) [non-stomach abdominal temperatures have not been measured for this species], we propose, for the Magellanic penguin, that regional heterothermy is less extreme than might be expected. Despite this, reduced local temperatures should operate to reduce heat flux to the environment to be lower than we estimate. However, the lack of reducing stomach temperatures over extended time in Magellanic penguins (Peters 1997), in contrast to, e.g. king penguins (Handrich et al. 1997), indicates that metabolic adjustments must correct for this. Part of this may come via thermal substitution during shallow surface dives (see above) which are interspaced with deeper foraging dives (cf. Peters 1997), but we also note that our equation for swimming power (Eq. 10) was derived from penguins swimming horizontally in a shallow swim canal. Here, although power requirements should mirror those of penguins commuting to and from foraging areas (Wilson et al. 2011), they will not accord well with deeper dives to forage. The descent requires power input due to both drag (a function of speed) and the energy necessary to overcome upthrust (which diminishes with depth). Thus, even if penguins maintain a constant speed (and constant dive angle)

during descent, they have high power requirements initially, decreasing with increasing depth, with metabolic heat production mirroring this (Wilson et al. 2011). Depending critically on dive angle and depth therefore, both of which modulate power in addition to speed (Wilson et al. 2011), descending Magellanic penguins may fully counteract heat flux to the environment or even increase body temperature (Wilson and Grémillet 1996; cf. Peters 1997—Fig. 42). The lack of an obvious swim speed according to depth during the bottom phase of the dive is likely due to the variability in speed during prey capture (Takahashi et al. 2004), which will tend to blur possible depth effects and make it difficult to determine whether the penguins are actually in net heat gain or loss. Since the ascent phase is purely passive (Wilson et al. 2010), however, the implication is that penguins will lose heat during this phase. Thus, diving Magellanic penguins might be experiencing rising body temperature during the descent phase of the dive and cooling during the ascent. Given that steeper dive angles are also associated with higher power (Wilson et al. 2011) and, therefore, higher heat production, we might consider that the systematic association between steep dive angles and increasing depth (and, importantly, the reverse) is not just a consequence of getting the birds to an operating depth, but might also help mitigate cooling.

The Magellanic penguin is expanding its geographic range, colonizing new oceanographic regions (Schiaivini et al. 2005). Our model is simplistic but provides a framework for understanding how temperature and depth should affect the energy expenditure of this penguin. Empirical data appear to support some of the expectations stemming from the model (related to surface speed and maximum depths) and suggest that this species may benefit from thermal substitution from heat derived from activity while travelling at the surface, but other factors may modulate penguin behaviour while diving to depth to forage. Experimental studies, under controlled conditions relevant to birds living in the wild, are needed to estimate realistic energy budget calculations to allow quantification of the thermal substitution effect. Ultimately though, the success of the species along its latitudinal range will depend *inter alia* on its capacity to provision the brood with food at an appropriate rate, after having balanced the energy requirements of the parents and this, in turn, will depend on the density and depth distribution of prey as well as the water temperature. The impact of the Magellanic penguin as a higher-order consumer on a marine ecosystem subjected to global warming scenarios (Buckley et al. 2012) follows on from this, and ecosystem models seeking to determine prey consumption in birds under different environmental conditions (Boyd 2002; Grémillet and Boulinier 2009; Hinke and Trivelpiece 2011; Garthe et al. 2012) may benefit by giving this approach consideration.

The general consequences of our approach extend to more than just Magellanic penguins. Overall, our work helps highlight that, generally, it should be energetically more taxing for aquatic endotherms, particularly small ones (cf. Schmidt Nielsen 1997) and species that use air as an insulator, to operate by diving to greater depths in colder water. We would predict that, after consideration of surface area:volume ratio effects (Schmidt Nielsen 1997), animals should be generally faster moving species (cf. e.g. sirenians, Kojeszewski and Fish 2007) versus odontocetes (Kojeszewski and Fish 2007) or have high power requirements to swim slowly (e.g. diving ducks versus penguins, Wilson et al. 1992), but also that behavioural modification should occur even intraspecifically according to variation in the environment within the species range. Given the predicted magnitude of variation in energy expenditure with depth and speed, the consequences for energy flow within marine ecosystems may be also profound.

**Acknowledgments** This research was funded by Agencia de Promoción Científica y Tecnológica (PICT 2010-203), CONICET (PIP 11220110100634) and Wildlife Conservation Society. We thank A. Gagliardini and J. Baba for assistance in satellite image analysis. A. Rivas made great comments to the manuscript and model. All device deployments were performed under permits of Dirección de Fauna y Flora Silvestre of Chubut and Consejo Agrario of Santa Cruz.

## References

- Angilletta MJ, Steury TD, Sears MW (2004) Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integr Comp Biol* 44:498–509
- Bannasch R, Wilson RP, Culik B (1994) Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *J Exp Biol* 194(1):83–96
- Baudinette R, Gill P (1985) The energetics of flying and paddling in water: locomotion in penguins and ducks. *J Comp Physiol B Biochem Syst Environ Physiol* 155:373–380
- Bevan R, Boyd I, Butler P, Reid K, Woakes A, Croxall J (1997) Heart rates and abdominal temperatures of free-ranging South Georgian shags, *Phalacrocorax georgianus*. *J Exp Biol* 200:661–675
- Boersma PD, Rebstock GA, Frere E, Moore SE (2009) Following the fish: penguins and productivity in the South Atlantic. *Ecol Monogr* 79:59–76
- Boyd IL (2002) Estimating food consumption of marine predators: Antarctic fur seals and macaroni penguins. *J Appl Ecol* 39:103–119
- Brody S (1945) *Bioenergetics and growth*. Reinhold, New York
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85:1771–1789
- Buckley LB, Hurlbert AH, Jetz W (2012) Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Glob Ecol Biogeogr* 21:873–885
- Butler PJ, Jones DR (1997) Physiology of diving of birds and mammals. *Physiol Rev* 77:837
- Casarsa L (2005) Morfología y comportamiento de los cardúmenes de sardina fueguina (*Sprattus fuegensis*) en dos sectores característicos del Atlántico Sudoccidental. Bachelor thesis, Mar del Plata

- Ciancio EJ, Botto F, Frere E (2015) Combining a geographic information system, dietary and habitat preferences, and stable isotope analysis to infer Magellanic Penguin diet in their austral distribution. *Emu*. doi:10.1071/MU14032\_AC
- Culik B, Wilson R (1991) Energetics of under-water swimming in Adelie penguins (*Pygoscelis adeliae*). *J Comp Physiol B* 161:285–291
- Culik BM, Wilson RP (1992) Field metabolic rates of instrumented Adelie penguins using double-labelled water. *J Comp Physiol B Biochem Syst Environ Physiol* 162:567–573
- Culik B, Wilson R, Bannasch R (1994) Underwater swimming at low energetic cost by Pygoscelid Penguins. *J Exp Biol* 197:65–78
- Culik BM, Putz K, Wilson RP, Allers D, Lage J, Bost CA, Le Maho Y (1996) Diving energetics in king penguins (*Aptenodytes patagonicus*). *J Exp Biol* 199:973–983
- De Vries J, Van Eerden MR (1995) Thermal conductance in aquatic birds in relation to the degree of water contact, body mass, and body fat: energetic implications of living in a strong cooling environment. *Physiol Zool* 68:1143–1163
- Enstipp MR, Grémillet D, Jones DR (2006) The effects of depth, temperature and food ingestion on the foraging energetics of a diving endotherm, the double-crested cormorant (*Phalacrocorax auritus*). *J Exp Biol* 209:845–859
- Fahlman A, Schmidt A, Handrich Y, Woakes AJ, Butler PJ (2005) Metabolism and thermoregulation during fasting in king penguins, *Aptenodytes patagonicus*, in air and water. *Am J Physiol Regul Integr Comp Physiol* 289:670–679
- Fort J, Porter WP, Grémillet D (2009) Thermodynamic modelling predicts energetic bottleneck for seabirds wintering in the northwest Atlantic. *J Exp Biol* 212:2483–2490
- Frere E, Gandini P, Lichstein V (1996) Variación latitudinal en la dieta del Pinguino de Magallanes *Spheniscus magellanicus*. *Ornitología Neotropical* 7:35–41
- Gaesser GA, Brooks GA (1975) Muscular efficiency during steady-rate exercise: effects of speed and work rate. *J Appl Physiol* 38:1132–1139
- Garthe S, Ludynia K, Hüppop O, Kubetzki U, Meraz J, Furness R (2012) Energy budgets reveal equal benefits of varied migration strategies in northern gannets. *Mar Biol* 159:1907–1915
- Grémillet D, Boulinier T (2009) Spatial ecology and conservation of seabirds facing global climate change: a review. *Mar Ecol Prog Ser* 391:121–137
- Grémillet D, Tuschy I, Kierspel M (1998) Body temperature and insulation in diving great cormorants and European shags. *Funct Ecol* 12:386–394
- Groscolas R (1986) Changes in body mass, body temperature and plasma fuel levels during the natural breeding fast in male and female emperor penguins *Aptenodytes forsteri*. *Comp Biochem Physiol B* 156(4):521–527
- Handrich Y, Bevan RM, Charrassin JB, Butler PJ, Ptz K, Woakes AJ, Lage J, Maho YL (1997) Hypothermia in foraging king penguins. *Nature* 388:64–67
- Hansen JE, Martos P, Madirolas A (2001) Relationship between spatial distribution of the Patagonian stock of Argentine anchovy, *Engraulis anchoita*, and sea temperatures during late spring to early summer. *Fish Oceanogr* 10:193–206
- Hilborn R, Mangel M (1997) The ecological detective: confronting models with data. Princeton University Press, New Jersey
- Hind AT, Gurney WS (1997) The metabolic cost of swimming in marine homeotherms. *J Exp Biol* 200:531–542
- Hinke J, Trivelpiece W (2011) Daily activity and minimum food requirements during winter for gentoo penguins (*Pygoscelis papua*) in the South Shetland Islands, Antarctica. *Polar Biol* 34:1579–1590
- Hudson DM, Bernstein MH (1981) Temperature regulation and heat balance in flying white-necked ravens, *Corvus cryptoleucus*. *J Exp Biol* 90(1):267–281
- Humphries MM, Careau V (2011) Heat for nothing or activity for free? Evidence and implications of activity-thermoregulatory heat substitution. *Integr Comp Biol* 51:419–431
- Humphries MM, McCann KS (2014) Metabolic ecology. *J Anim Ecol* 83:7–19
- Kaselloo PA, Lovvorn JR (2005) Effects of surface activity patterns and dive depth on thermal substitution in fasted and fed lesser scaup (*Aythya affinis*) ducks. *Can J Zool* 83:301–311
- Kaselloo P, Lovvorn J (2006) Substitution of heat from exercise and digestion by ducks diving for mussels at varying depths and temperatures. *J Comp Physiol B Biochem Syst Environ Physiol* 176:265–275
- Kojeszewski T, Fish FE (2007) Swimming kinematics of the Florida manatee (*Trichechus manatus latirostris*): hydrodynamic analysis of an undulatory mammalian swimmer. *J Exp Biol* 210:2411–2418
- Kooyman GL, Gentry RL, Bergman WP, Hammel HT (1976) Heat loss in penguins during immersion and compression. *Comp Biochem Physiol A Comp Physiol* 54:75–80
- Kvadsheim PH, Folkow LP, Blix AS (2005) Inhibition of shivering in hypothermic seals during diving. *Am J Physiol-Regul Integr Comp Physiol* 289:326–331
- Kvist A, Lindstrom A, Green M, Piersma T, Visser GH (2001) Carrying large fuel loads during sustained bird flight is cheaper than expected. *Nature* 413:730–732
- Le Maho Y (1977) The emperor penguin: a strategy to live and breed in the cold: morphology, physiology, ecology, and behavior distinguish the polar emperor penguin from other penguin species, particularly from its close relative, the king penguin. *Am Sci* 65:680–693
- Liwanag HEM, Williams TM, Costa DP, Kanatous SB, Davis RW, Boyd IL (2009) The effects of water temperature on the energetic costs of juvenile and adult California sea lions (*Zalophus californianus*): the importance of skeletal muscle thermogenesis for thermal balance. *J Exp Biol* 212:3977–3984
- Lovvorn JR (2007) Thermal substitution and aerobic efficiency: measuring and predicting effects of heat balance on endotherm diving energetics. *Philos Trans R Soc Lond B Biol Sci* 362:2079–2093
- Luna-Jorquera G, Culik BM (2000) Metabolic rates of swimming Humboldt penguins. *Mar Ecol Prog Ser* 203:301–309
- Luque S (2007) Diving behaviour analysis in R. *R News* 7:8–15
- McCafferty DJ, Moncrieff JB, Taylor IR (1997) The effect of wind speed and wetting on thermal resistance of the barn owl (*Tyto alba*). I: total heat loss, boundary layer and total resistance. *J Therm Biol* 22:253–264
- McCue MD (2006) Specific dynamic action: a century of investigation. *Comp Biochem Physiol Part A Mol Integr Physiol* 144:381–394
- McNab BK (2002) The physiological ecology of vertebrates: a view from energetics. Cornell University Press, New York
- McNamara J, Ekman J, Houston IA (2004) The effect of thermoregulatory substitution on optimal energy reserves of small birds in winter. *Oikos* 105:192–196
- Mitchell JW (1976) Heat transfer from spheres and other animal forms. *Biophys J* 16:561–569
- Peters G (1997) Die Regulation der Verdauungsprozesse bei Pinguinen (*Spheniscidae*). PhD thesis. Christian-Albrechts University Kiel
- Pinheiro JC, Bates DM (2001) Mixed-effects models in S and S-PLUS. Springer, New York
- Ponganis P, Van Dam R, Knowler T, Levenson D (2001) Temperature regulation in emperor penguins foraging under sea ice. *Comp Biochem Physiol A Comp Physiol* 129:811–820
- Ponganis PJ, Van RP, Levenson DH, Knowler T, Ponganis KV, Marshall G (2003) Regional heterothermy and conservation of core temperature in emperor penguins diving under sea ice. *Comp Biochem Physiol A Comp Physiol* 135:477–487

- Porter WP, Gates DM (1969) Thermodynamic equilibria of animals with environment. *Ecol Monogr* 39:227–244
- Porter WP, Vakharia N, Klousie WD, Duffy D (2006) Po’ouli landscape bioinformatics models predict energetics, behavior, diets, and distribution on Maui. *Integr Comp Biol* 46:1143–1158
- Prinzinger R, Pressmar A, Schleucher E (1991) Body temperature in birds. *Comp Biochem Physiol A Comp Physiol* 99:499–506
- R Development Core Team (2011) R: a language and environment for statistical computing. In: Computing RfFS (ed), Vienna, Austria
- Richman SE, Lovvorn JR (2011) Effects of air and water temperatures on resting metabolism of auklets and other diving birds. *Physiol Biochem Zool* 84:316–332
- Sala JE, Wilson RP, Frere E, Quintana F (2012) Foraging effort in Magellanic penguins in coastal Patagonia, Argentina. *Mar Ecol Prog Ser* 464:273–287
- Schiavini A, Yorio P, Gandini P, Raya Rey A, Boersma D (2005) Los pingüinos de las costas argentinas: estado y Conservación. *El Hornero* 20(1):5–23
- Schmidt Nielsen K (1997) Animal physiology: adaptation and environment. Cambridge University Press, Cambridge
- Schmidt A, Alard F, Handrich Y (2006) Changes in body temperatures in king penguins at sea: the result of fine adjustments in peripheral heat loss? *Am J Physiol-Regul Integrat Comp Physiol* 291:608–618
- Scolaro JA, Wilson RP, Laurenti S, Kierspel M, Gallelli H, Upton J (1999) Feeding preferences of the Magellanic Penguin over its breeding range in Argentina. *Waterbirds* 22:104–110
- Sparling CE, Fedak MA, Thompson D (2007) Eat now, pay later? Evidence of deferred food-processing costs in diving seals. *Biol Lett* 3:95–99
- Speakman JR, Król E (2010) Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. *J Anim Ecol* 79:726–746
- Stahel C, Nicol S (1982) Temperature regulation in the little penguin, *Eudyptula minor*, in air and water. *J Comp Physiol B Biochem Syst Environ Physiol* 148:93–100
- Takahashi A, Dunn MJ, Trathan PN, Croxall JP, Wilson RP, Sato K, Naito Y (2004) Krill-feeding behaviour in a chinstrap penguin compared to fish-eating in Magellanic penguins: a pilot study. *Mar Ornithol* 32:47–54
- Tucker VA (1975) The energetic cost of moving about: walking and running are extremely inefficient forms of locomotion. Much greater efficiency is achieved by birds, fishes and bicyclists. *Am Sci* 63:413–419
- Walsberg GE, King J (1978) The relationship of the external surface area of birds to skin surface area and body mass. *J Exp Biol* 76(1):185–189
- Williams TD (1995) The penguins: Spheniscidae. In: Perrins CM, Bock WJ, Kikkawa J (eds) Bird families of the world. Oxford University Press, Oxford, p 295
- Wilson RP, Culik BM (1991) The cost of a hot meal: facultative specific dynamic action may ensure temperature homeostasis in post-ingestive endotherms. *Comp Biochem Physiol A Physiol* 100:151–154
- Wilson RP, Grémillet D (1996) Body temperatures of free-living African penguins (*Spheniscus demersus*) and bank cormorants (*Phalacrocorax neglectus*). *J Exp Biol* 199:2215–2223
- Wilson RP, Hustler K, Ryan PG, Burger AE, Noldeke EC (1992) Diving birds in cold water: do Archimedes and Boyle determine energetic costs? *Am Nat* 144(2):179–200
- Wilson RP, Pütz K, Grémillet D, Culik BM, Kierspel M, Regel J, Bost CA, Lage J, Cooper J (1995) Reliability of stomach temperature changes in determining feeding characteristics of seabirds. *J Exp Biol* 198:1115–1135
- Wilson RP, Putz K, Peters G, Culik B, Scolaro JA, Charrassin J-B, Ropert-Coudert Y (1997) Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildl Soc Bull* 25:101–106
- Wilson RP, Adelung D, Latorre L (1998) Radiative heat loss in gentoo penguin (*Pygoscelis papua*) adults and chicks and the importance of warm feet. *Physiol Biochem Zool* 71(5):524–533
- Wilson RP, Ropert-Coudert Y, Kato A (2002) Rush and grab strategies in foraging marine endotherms: the case for haste in penguins. *Anim Behav* 63:85–95
- Wilson RP, Kreye JM, Lucke K, Urquhart H (2004) Antennae on transmitters on penguins: balancing energy budgets on the high wire. *J Exp Biol* 207:2649–2662
- Wilson RP, Scolaro JA, Grémillet D, Kierspel MAM, Laurenti S, Upton J, Gallelli H, Quintana F, Frere E, Muller G, Straten MT, Zimmer I (2005) How do Magellanic penguins cope with variability in their access to prey? *Ecol Monogr* 75:379–401
- Wilson RP, Shepard ELC, Liebsch N (2008) Prying into the intimate details of animal lives: use of a daily diary on animals. *Endang Species Res* 4:123–137
- Wilson RP, Shepard ELC, Gomez Laich A, Frere E, Quintana F (2010) Pedalling downhill and freewheeling up; a penguin perspective on foraging. *Aquat Biol* 8:193–202
- Wilson RP, McMahon CR, Quintana F, Frere E, Scolaro A, Hays GC, Bradshaw CJ (2011) N-dimensional animal energetic niches clarify behavioural options in a variable marine environment. *J Exp Biol* 214:646–656
- Yorio P, Quintana F, Dell’Arciprete P, González-Zevallos D (2010) Spatial overlap between foraging seabirds and trawl fisheries: implications for the effectiveness of a marine protected area at Golfo San Jorge, Argentina. *Bird Conserv Int* 20:320–334
- Zuur A, Ieno E, Walker N, Saveliev A, Smith G (2009) Mixed effects models and extensions in ecology with R. Springer, New York