

RESEARCH ARTICLE

***N*-dimensional animal energetic niches clarify behavioural options in a variable marine environment**

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SUMMARY

Animals respond to environmental variation by exhibiting a number of different behaviours and/or rates of activity, which result in corresponding variation in energy expenditure. Successful animals generally maximize efficiency or rate of energy gain through foraging. Quantification of all features that modulate energy expenditure can theoretically be modelled as an animal energetic niche or power envelope; with total power being represented by the vertical axis and *n*-dimensional horizontal axes representing extents of processes that affect energy expenditure. Such an energetic niche could be used to assess the energetic consequences of animals adopting particular behaviours under various environmental conditions. This value of this approach was tested by constructing a simple mechanistic energetics model based on data collected from recording devices deployed on 41 free-living Magellanic penguins (*Spheniscus magellanicus*), foraging from four different colonies in Argentina and consequently catching four different types of prey. Energy expenditure was calculated as a function of total distance swum underwater (horizontal axis 1) and maximum depth reached (horizontal axis 2). The resultant power envelope was invariant, irrespective of colony location, but penguins from the different colonies tended to use different areas of the envelope. The different colony solutions appeared to represent particular behavioural options for exploiting the available prey and demonstrate how penguins respond to environmental circumstance (prey distribution), the energetic consequences that this has for them, and how this affects the balance of energy acquisition through foraging and expenditure strategy.

Key words: survival, energy expenditure, optimal strategy, performance constraints, energetic niche, power envelope, behavioural plasticity, Magellanic penguin, *Spheniscus magellanicus*.

INTRODUCTION

There is extreme selection pressure for animals to manage energy judiciously (e.g. Stephens et al., 2007) because energy intake and expenditure do not always overlap spatially and temporally, requiring processing and storage that depend on a variety of ecological and physiological processes. The process of foraging, by which energy is acquired, has received particular attention because the success of foraging strategies ultimately depends on animals maximizing efficiency or their rate of energy gain (e.g. Ydenberg et al., 2007; Shepard et al., 2009) with the net energy gain from foraging covering all other (including non-foraging) costs. Models for optimization of foraging, however, often consider efficiency (e.g. Kacelnik, 1984), assuming that energy expenditure involved in calculations is linearly related to time (Shepard et al., 2009). Literature on energy expenditure shows that this is not generally true and that animals expend energy at different rates depending on the activity and its level (e.g. Culik et al., 1994). For example, the energy expenditure of travelling guinea fowl (*Numida meleagris*) varies substantially with incline (Rubenson et al., 2004) so that the specific slopes that guinea fowl choose (or the angle at which they

move up slopes) will have a profound effect on their overall efficiency.

The extent to which assumptions of constant energy expenditure during foraging affect optimality can be examined, however, by attempting to link all the factors that modulate energy expenditure together to derive power requirements (cf. Porter and Kearney, 2009) as a function of them. This would describe an energetic niche of the animal in question. Here, an assumed relationship between performance, such as moving at a constant speed up different inclines, and energy expenditure, which can be plotted on a two-dimensional graph of degree of incline (on the *x*-axis) against energy (on the *y*-axis), is combined with another measure of performance (such as load carrying) and energy expenditure in its own two-dimensional graph, to make a three dimensional graph consisting of an energy (or power) envelope (*y*-axis), which shows how energy expenditure relates to both animals moving up inclines and carrying variable loads (two horizontal axes) (cf. Watson et al., 2008). This is easily visualized but the process can be theoretically continued using more performance-related variables, such as speed, to create an *n*-dimensional energetic niche, which explains how the species

in question expends energy according to the way it performs. Indeed, this is a physiological parallel of Hutchinson's classic n -dimensional hypervolume definition of the niche (Hutchinson, 1958) and something that should help relate species physiological data (Kearney, 2009) to functional traits (Kearney et al., 2009) and the environment they exploit (Colwell and Rangel, 2009). Theoretically, the precise position of the animal on its n -dimensional energetic niche is determined by the animal itself; it should choose the extents of its behaviours (e.g. amount of load carried and degree of incline attempted) according to foraging conditions (such as prey abundance) (e.g. Ydenberg et al., 2007) so that net energy gain may be maximized. Although many studies have shown that animals change behaviour according to foraging conditions (e.g. Stephens et al., 2007) there are obvious practical difficulties in attempting to construct energetic niches for wild animals and examining the extent to which the animals operate in different places on their n -dimensional energetic niche according to conditions (cf. Fort et al., 2009).

In this paper, we create an easily visualized three-dimensional energy and power envelope for foraging Magellanic penguins based on simple mechanistic modelling in a movement towards creating the n -dimensional energetic niche for this species. We then use the model on data gathered from free-living penguins foraging at different locations on different prey to consider the extent to which the birds may operate at different points on the energy envelope according to location. Success in this should show that animals are indeed constrained by their performance envelopes but also that their specific behaviour will determine where they choose to operate on the envelope.

Air-breathing, diving animals are excellent for this approach because the time that they can remain underwater depends on their limited oxygen reserves and the rate at which they are depleted. Here, oxygen use equates linearly with energy expenditure (Stahel and Nicol, 1987). In addition, there are good quality data on energy expenditure in penguins (Bethge et al., 1997; Culik et al., 1996; Culik et al., 1994; Luna-Jorquera and Culik, 2000) that lend credibility to the modelling exercise.

MATERIALS AND METHODS

Device deployment

Between 1999 and 2003, studies were undertaken of 41 Magellanic penguins (*Spheniscus magellanicus* Forster 1781) breeding at one of four widely spaced colonies located along the coast of southern Argentina, covering virtually the entire species' latitudinal range. The colonies were: San Lorenzo (42°04' S, 63°21' W) – 13 birds; Puerto Deseado (47°45' S, 65°63' W) – 5 birds; San Julian (49°16' S, 67°42' W) – 7 birds; and Cabo Virgenes (52°24' S, 68°26' W) – 16 birds. Time–depth gauges were attached to a bird's lower back with tape (Wilson et al., 1997) and left in place for at least one foraging trip before being recovered (for details, see Wilson et al., 2005). All devices were retrieved and all birds continued breeding after unit removal. The units recorded depth at intervals of at least 0.5 Hz with a minimum of 8-bit resolution on transducers with maximum readings of up to 2 kPa. In addition to depth gauges, five birds breeding at Cabo Virgenes were also equipped with inter-mandibular angle sensors (IMASEN; Driesen & Kern GmbH, Bad Bramstedt, Schleswig-Holstein, Germany), a magnet-Hall-sensor-based system for determining the frequency and timing of prey ingestion (Wilson et al., 2002a). IMASENs were set to record beak angle at a minimum of 10 Hz.

Data were analyzed using specially written software; the program graphically displayed depth and (when available) beak angle data

against time. Points of inflection in depth defined the onset and end of the dive as well as the onset and termination of bottom phases. These data, and parameters derived from them (such as rate of change of depth), were written to an ASCII file pending further analysis, together with data on when prey were caught, with prey capture being identified by looking at changes in beak angle over time (Wilson et al., 2002a).

Estimation of energy used during foraging

To approximate the energy used by diving penguins, we need to consider the three basic phases of a dive, which differ in their mechanics (see below), and the factors that can influence them. We do this below before specifically considering the sensitivity of our model to variability in our assumptions.

The basic dive form adopted by penguins consists of (1) a descent phase from the surface to a specific depth, (2) a phase during which the bird swims along at a particular, relatively constant, depth and (3) an ascent phase. The course of energy expenditure during these three major phases is fundamentally different because of depth-mediated changes in volumes of air present in the lungs, which results in variable buoyancy (Sato et al., 2002; Wilson and Zimmer, 2004).

Descent phase

When penguins dive they have air in their feathers and air in the respiratory spaces. The air in the feathers amounts to $\sim 0.21 \text{ kg}^{-1}$ body mass (Wilson et al., 1992) whereas the air in the respiratory spaces has been approximated to 0.161 kg^{-1} by Kooyman, although this value might be depth dependent (see 'model sensitivity' below) (Kooyman, 1975). The air contained within the penguin is at its maximum volume at the surface. As the bird descends, however, this air becomes compressed according to Boyle's Law so that its volume (V_2 ; in litres) at any depth (D_2 ; m) is given by:

$$V_2 = V_1 / [1 + (D_2 / 10)], \quad (1)$$

where V_1 is the volume at the surface. The volume of air associated with the bird determines the upthrust (in newtons, where upthrust = gV ; g being the gravitational constant) because penguins have a body density that is almost identical to that of seawater (Wilson et al., 1992). The mechanical work (W) that the penguin must do during the descent, resulting from the upthrust, is determined by the depth change and the overall upthrust of the bird so that:

$$W = gV dD / dt. \quad (2)$$

The depth change over any time interval is given by the penguin's swimming speed (U ; m s^{-1}) and the dive angle [θ ; the angle between the bird's trajectory and the sea surface, which is here standardized as a 'swim' angle with negative values and is roughly constant during any one dive (Ropert-Coudert et al., 2001)] and given by:

$$dD / dt = U \sin \theta. \quad (3)$$

Note that the swim angle can be calculated by applying simple trigonometry to the rate of change of depth as the vertical component, and the swimming speed as the oblique component. The rate of work, or power output ($P_{o, \text{upthrust}}$; in W) that the penguin has to maintain to move between depths D_t and D_{t+1} is given by the rate of descent:

$$P_{o, \text{upthrust}} = g \{V_1 / [1 + (D_2 / 10)]\} \rho U \sin \theta, \quad (4)$$

where ρ is the density of seawater. However, a swimming penguin has to generate power for moving forward against drag as well as

upthrust. The equation for calculating the drag on a penguin gliding underwater is:

$$F_d = 0.5 U^2 \rho C_d A, \quad (5)$$

where C_d is the coefficient of drag [0.0368 for penguins (Culik et al., 1994)] and A is the cross-sectional area of the penguin at the point of its greatest girth [0.02083 m² (Oehme and Bannasch, 1989)]. We note that compression of respiratory air spaces in the penguin body with depth (cf. Sato et al., 2002) will tend to reduce penguin body volume with increasing depth and thus putatively affect drag. However, the penguin thorax is stiff and virtually invariant because of the ucnate processes linking the ribs, which makes the thorax robust allowing birds to cross the sea edge with minimal risk of damage. Thus, volumetric changes within the body (including those relating to stomach fullness) result in changes in the degree of bulging between the sternum and legs rather than in bird girth so that drag is likely to change little with depth. The rate of work done in this case is given by the force multiplied by the distance travelled per unit time, so that the power output ($P_{o, swim}$) is:

$$P_{o, swim} = 0.5 U^3 \rho C_d A U. \quad (6)$$

The total mechanical power output ($P_{o, total}$) for a penguin diving is the sum of Eqns 5 and 6 so that:

$$P_{o, total} = (0.5 U^3 \rho C_d A) + (g \{V_1 / [1 + (D_2 / 10)] \rho U \sin \theta\}). \quad (7)$$

To be biologically meaningful, however, mechanical costs need to be converted to aerobic costs (power input; P_i) by an aerobic efficiency (e.g. Lovvorn et al., 2009). This can be determined using data in the literature on oxygen consumption in penguins swimming at known speeds horizontally in swim channels (though typically at depths of <1 m) because 1 ml of oxygen is the substrate responsible for yielding ~20 J of energy (Stahel and Nicol, 1987). Here, the power output of swimming at particular speeds from Eqn 6 can be regressed against the known power input derived from oxygen consumption measurements made on the congeneric Humboldt penguin (*Spheniscus humboldti*) (Luna-Jorquera and Culik, 2000). The polynomial fit describing this gives:

$$P_i = 0.0004P_o^4 - 0.029P_o^3 + 0.8005P_o^2 + 8.8258P_o + 28.775, \quad (8)$$

which incorporates maintenance energy, and can be used to examine how overall instantaneous input power requirements of Magellanic penguins descending the water column vary according to depth and dive angle (Fig. 1A). The integral of this gives the total energy required for a penguin to descend from the surface to a specific depth. For this we used a mean swimming speed of 2.1 m s⁻¹ for all calculations involving U because Magellanic penguin swimming speed is virtually constant underwater, irrespective of dive phase, having a mode of 2.1 m s⁻¹ (90% confidence limits of 1.6 and 2.6 m s⁻¹) (Ropert-Coudert et al., 2002a; Ropert-Coudert et al., 2002b; Wilson et al., 2002b) with rates of descent being modulated primarily by changes in descent angle (Ropert-Coudert et al., 2001; Wilson et al., 2010).

Bottom phase

During the bottom phase, Magellanic penguins show little vertical movement (Simeone and Wilson, 2003) so we assume that they swim horizontally and only have to invest energy to overcome drag. As such, power output and input requirements can be derived from the relevant sections of Eqns 6 and 8, respectively. We assume that speed remains constant at the elected speed of 2.1 m s⁻¹ (see above), although this will not be the case for animals chasing prey at increased speeds (Wilson et al., 2002b). The extent to which prey

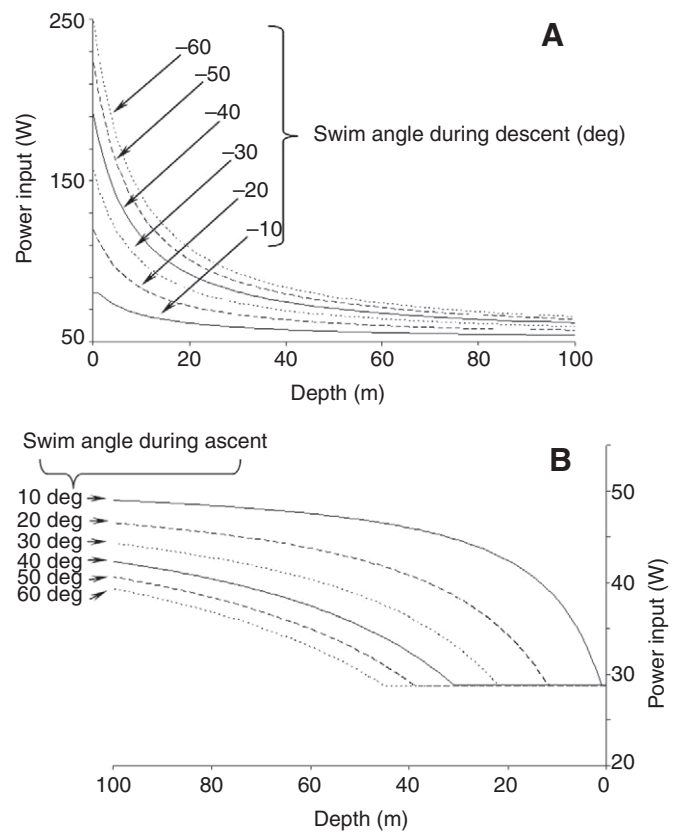


Fig. 1. Relationship between the calculated instantaneous power input of a 4 kg Magellanic penguin during (A) descent and (B) ascent of the water column as a function of depth for different descent and ascent angles.

are encountered and pursued, and the increases in speed that this entails, could theoretically represent a source of error for the calculations of energy expended during particular dives. Against this, however, is the relatively infrequent rate of prey encounter compared with the time spent swimming underwater (Wilson et al., 2004), the small amount of time spent per chase [2.02 s or ~3% of an average dive of 60 s where a single prey is encountered (Wilson et al., 2010)] and the fact that Magellanic penguins catch 89% of their prey during passive ascents using buoyancy to help them accelerate to catch their prey with minimal energy expenditure (Wilson et al., 2010).

Ascent phase

During the ascent, a penguin is aided by the upthrust, but its movement is hindered by drag. When the upthrust component:

$$F_{up} = g V \sin \gamma, \quad (9)$$

(where γ is the swim angle between the bird's trajectory and the sea surface, which has positive values) exceeds the drag (Eqn 5), the bird can rise to the surface passively. Otherwise, it has to invest energy to power itself to an extent defined by the difference between the drag force and the component given by the upthrust. For simplicity, we consider that any time the upthrust component exceeds the drag, the penguin proceeds to the surface at the nominal speed of 2.1 m s⁻¹, although there are occasions when speed does increase during the passive ascent (Wilson et al., 2002b). Modelling the theoretical increase in penguin speed with decreasing depth during the passive part of the ascent shows that speeds should rapidly

exceed that observed (Wilson et al., 2004). This indicates that birds must normally brake their ascent somewhat by increasing drag [which they do with their feet (Bannasch, 1995)]. At depths where the penguins must work to ascend, the mechanical power output is given by the rate of work done (the force times the distance per unit time; cf. Eqn 6) and the power input can be derived from Eqn 8. As in the descent phase, the power requirements of birds returning to the surface at various angles can be plotted against depth (Fig. 1B) and the total energy used for the ascent for any single dive is derived by integration.

Complete dive energy expenditure

The formulations for energy expenditure in Magellanic penguins during the three different phases of the dives are used to determine energy expenditure as a function of the amount of time spent in the different phases (which, in the case of the descent and ascent phases, is determined primarily by the descent and ascent angles). The total energy expended for the dive is the sum of all three phases, and this was calculated for each dive of each bird from each colony using the data recorded by the devices. The combination of descent and ascent angles and the duration of the bottom phase (at a swim angle of 0 deg) introduces effectively two more dimensions to the depth–energy relationship, which becomes a multi-dimensional energy envelope. Unfortunately, this cannot be visualized easily, but it can be circumvented by converting all consequences of swim angle for all three dive phases into total distance travelled during the dive using standard trigonometry, based on use of our assigned swimming speed and rate of change of depth, as recorded by the loggers. We thus produced a three-dimensional energy envelope with the two lateral axes consisting of maximum depth reached during a particular dive (which always occurred during the bottom phase) and distance travelled. This process converts the standard graph of dive duration *versus* depth, which is invariably used to describe the foraging behaviour of air-breathing marine divers (e.g. Ryan et al., 2007), into a plot of the energy invested per dive to specific depths according to penguin performance (as defined by rates of descent and ascent and the length of the bottom phase). The difference between dive duration as a function of maximum dive, for which there is considerable variance (e.g. Chilvers et al., 2004), and energy expenditure as a function of maximum dive depth indicates why the latter may more properly describe the extent of underwater activity: in essence, the energy expended by a diving penguin depends on time spent moving at different swim angles and depths, whereas this dependency is not apparent in simple duration considerations (see above).

Model sensitivity

The model assumes that Magellanic penguins dive with a constant volume of air, irrespective of depth. Although the volume of air in feathers is likely to remain invariant (at constant pressure), there is a suggestion that penguins might inhale more for deeper dives (Sato et al., 2002; Wilson and Zimmer, 2004), although the extent is unknown. Given that penguins always inhale prior to diving (Kooyman, 1975; Wilson et al., 2003), the volume of air in the respiratory system is unlikely to be much less than half that originally proposed by Kooyman (Kooyman, 1975) for ‘shallow’ dives and much more than half as much again for ‘deep’ ones (cf. Wilson et al., 2003) (giving a span of 0.161 kg^{-1}). This would give total limits (air in both the feathers and the respiratory spaces) of $0.28\text{--}0.441\text{ kg}^{-1}$ or approx. 22% more or less than that estimated above (0.361 kg^{-1}) with the actual value being depth dependent. However, the precise amount of air inhaled by penguins as a function

of dive depth has not been quantified (cf. Sato et al., 2002; Wilson et al., 2003) so calculated buoyancies at any given depth can be higher during deeper dives than in shallow ones and the energy envelope may change accordingly.

Beyond the volumes of air associated with the penguin, the calculation of the energy required to execute any particular dive is most sensitive to factors that relate to the rate of change of depth (vertical swimming speed), especially during the descent part of the dive, because this is when the animal is working against buoyancy, and power requirements may exceed those required for normal level swimming by approximately five times (cf. Fig. 1A,B). The rate of change of depth is modulated only by swim angle and swimming speed. Variation in swim angle affects instantaneous energy expenditure (Fig. 1), which highlights the substantial effect of depth on the energy envelope. If only the effect of swim angle during descent is considered, the range of power use over the full possible variation in angle (0–90 deg) varies from a factor of ~ 1.5 (for a bird at 50 m) to ~ 5 (for a bird at 1 m depth; Fig. 2A). Based on previously published data (Ropert-Coudert et al., 2001; Wilson et al., 2010), we argue that swim angle, which remains constant during the descent, is the primary modifier of energy requirements. However, the energy expenditure of diving birds is highly sensitive to speed because power output is related to the cube of speed (Wilson et al., 2004). Irrespective of swim angle, calculations using our model show that the difference in power input between swimming speeds of 1 and 3 m s^{-1} [which correspond with >95% confidence limits of speed data (Wilson et al., 2002b)] varies by a factor of 5 at any depth (Fig. 2B).

The specific issue of how the power required for speed, which is related to swim angle during the descent, might relate to the rate of descent can be examined by determining the overall power input requirements for penguins descending (at rates corresponding to those found in nature). These are solved for different descent rates by only altering speed (keeping swim angle constant) and comparing them with the case where only the swim angle is altered (keeping speed constant; Fig. 2C, Table 1). The exercise examines the worst case scenario because we assume that all the variability in descent rate is due to angle, whereas the opposing view, that all the variability in descent rate is due to variation in swimming speed, makes no concession for angle. Both scenarios, as expected, show increases in input power with increasing vertical speed, but the cubed relationship between power and swimming speed results in errors, varying between -39% at a vertical speed of 0.5 m s^{-1} , to $+71\%$ at 1.5 m s^{-1} (Fig. 2C) for power input. In the former case, the bird swimming at an angle of -30 deg would have to be swimming at $\sim 1\text{ m s}^{-1}$, almost two standard deviations away from the mean commuting speed of Magellanic penguins (Wilson et al., 2002b). In the latter case, the bird would have to be travelling at 3 m s^{-1} , which is more than three standard deviations away from the mean (Wilson et al., 2002b).

The above exercise demonstrates the extent to which our model is sensitive to variation in our assumptions. Importantly, the model is projected to show trends in energy expenditure with dive profile rather than absolute values, so, considering that built-in variation changes the actual patterns little, we suggest that our approach is reasonably robust.

Colony-specific responses

To account for repeated measures of energy estimates per individual, we constructed a series of general linear mixed effects models (GLMM) to examine the relationship between energy expenditure, dive depth and distance travelled as a function of colony of origin

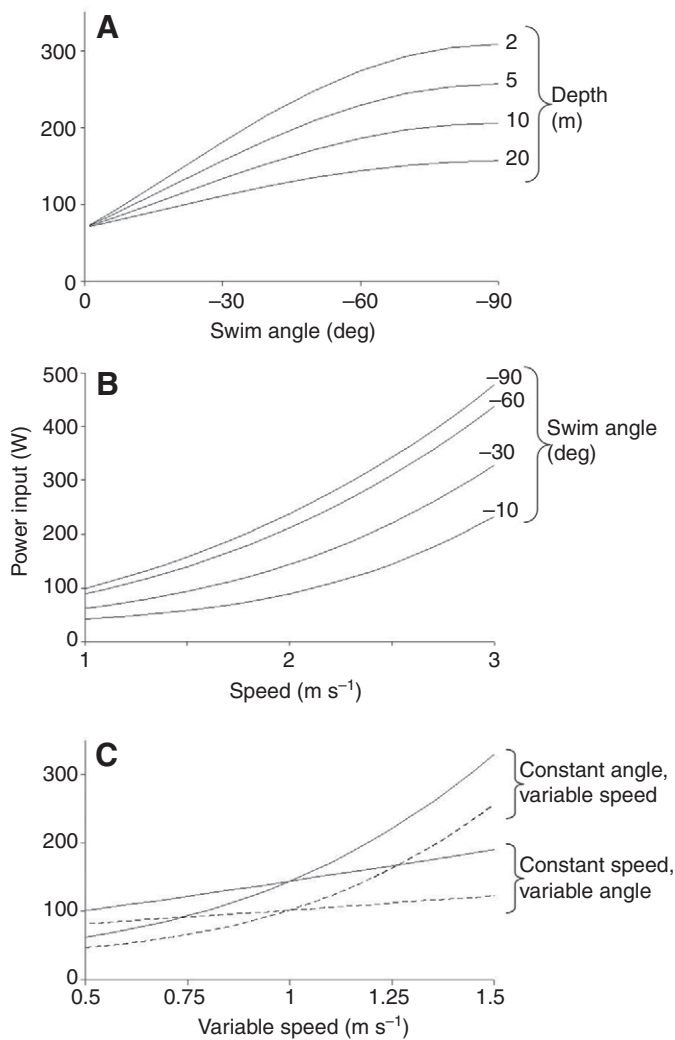


Fig. 2. (A) Relationship between calculated instantaneous power input of a 4 kg Magellanic penguin, swimming at 2.1 m s^{-1} during descent at defined angles at a variety of different depths. (B) Relationship between instantaneous power input and speed of a 4 kg Magellanic penguin swimming at a depth of 5 m during descent, at a variety of different descent angles. (C) Variation in power input required for a Magellanic penguin to descend at different vertical speeds according to whether the change in vertical speed is brought about by change in descent angle (speed held constant at 2.1 m s^{-1}) or actual speed (angle held constant at 30 deg). Solid lines, at 5 m depth; dashed lines, at 20 m depth.

[based on the `glmer` function in the R Package (R Development Core Team, 2009 ver. 2.9.1; <http://cran.r-project.org/>)]. Our explicit aim was to test the hypothesis that penguins from each colony used different regions of the energy–depth–distance envelope, as might be expected in birds exploiting different prey, which are likely to be distributed differently in the water column. Our modelling approach therefore examined nine model combinations of the three fixed terms (maximum depth, distance travelled, and colony of origin), with individual penguins coded as a random intercept effect in the GLMM structure. Our prediction would gain support if there were sufficient evidence for a three-way interaction between the fixed terms compared with a model including only the necessary two-way interaction between depth and distance (necessary because the energy expended, as defined above, depends on the depth

Table 1. Sensitivity of a model predicting power used by diving Magellanic penguins as a function of extremes of speed, depth and dive angle

Power (W)	Speed (m s^{-1})	Depth (m)	Swim angle (deg)
73.6	2.1	1.0	5.0
308.3	2.1	1.0	90.0
70.9	2.1	50.0	5.0
111.0	2.1	50.0	90.0
36.8	1.0	5.0	5.0
99.0	1.0	5.0	90.0
329.1	3.5	5.0	5.0
680.7	3.5	5.0	90.0

achieved and distance travelled). To deal with heteroscedasticity and non-Gaussian distributions, we log transformed the depth variables and used a Gaussian error distribution and identity link in the GLMM. We also tested for serial autocorrelation among energy values per penguin using the autocorrelation function `acf` in the R Package (no autocorrelation was found). Model comparison was based on the Bayesian information criterion (BIC), which is suitable for large datasets to infer the dominant correlations (Burnham and Anderson, 2002; Link and Barker, 2005). Models were ranked with the most parsimonious model(s) having the lowest BIC values and highest model weights (Burnham and Anderson, 2002). We also calculated the percentage deviance (%DE) explained by each model in the model set.

RESULTS

Total dive durations for all birds varied between 4 and 230 s (Table 2), and increased as a function of depth for penguins from the four different colonies (Fig. 3A), as did duration allocated to descent (Fig. 3B) and ascent (Fig. 3D) although the duration spent during the bottom phase was more complex (Fig. 3C). This treatise, however, only relates to time allocation and is the approach generally used by workers describing the diving behaviour of air-breathing marine animals (cf. Halsey and Butler, 2006). However, the relationships between derived penguin power requirements and depth for the descent (Fig. 1A) and the ascent phases (Fig. 1B) of the dive as a function of descent or ‘return to the surface’ angle make it clear that penguin choice of maximum depth and trajectory will influence the cost of dives substantially.

The GLMM revealed that the saturated model including the three-way interaction between maximum depth, distance travelled and colony of origin had the highest support among the nine models considered (Table 3). However, the %DE by this model was only marginally higher than the next most highly ranked model that included the two-way interaction between depth and distance (Table 3). This demonstrates that although the evidence is strong that penguins from each colony use a different component of the energy–depth–distance surface, the differences were small (Fig. 4).

The three-dimensional scatterplot of energy expended *versus* maximum depth reached and distance travelled (Fig. 4) is derived from multiple points, each relating to a specific performance over a single dive, but it builds up into something that resembles a three-dimensional energetic niche. Individual birds create paths of points over this energetic niche as they forage (Fig. 5). If this energy expended is converted into a representation of power use by factoring in the time (using an average derived from all phases in each dive), we can derive a power envelope where minimized power requirements become apparent during the deepest dives with the greatest distances swum (Fig. 6).

Table 2. Dive parameters of Magellanic penguins foraging from different colonies

Colony	Duration (s)		Bottom Mean (Max)	Depth (m)	
	Total Mean (Max)	Descent Mean (Max)		Ascent Mean (Max)	Mean (Max)
San Lorenzo	62 (230)	18 (103)	25 (112)	19 (168)	18.2 (92.6)
San Julian	55 (168)	11 (67)	31 (77)	13 (91)	12.1 (101.2)
Cabo Virgenes	54 (178)	13 (118)	28 (148)	13 (56)	15.6 (46.6)
Puerto Deseado	25 (114)	7 (50)	11 (89)	8 (58)	5.6 (36.5)

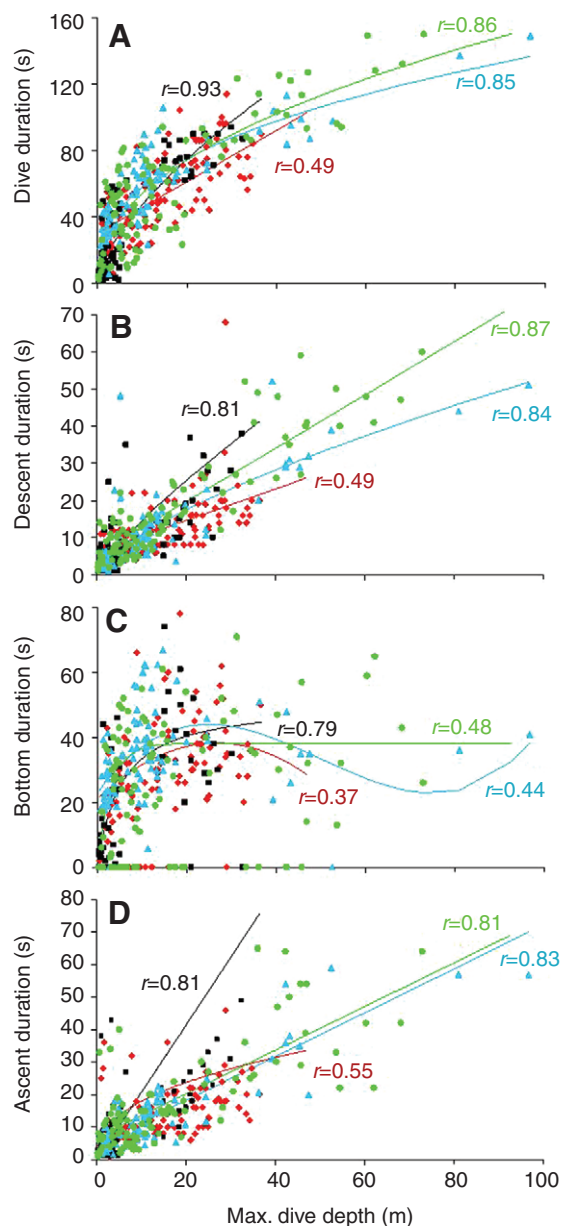


Fig. 3. Relationship between the maximum depth reached and (A) total dive duration, (B) descent duration, (C) bottom phase duration and, (D) ascent duration, using data thinned to give 100 random points for Magellanic penguins from each of four colonies in Argentina; red diamonds, Cabo Virgenes; blue triangles, San Julian; black squares, Puerto Deseado; grey circles, San Lorenzo. Lines of best fit and Pearson product-moment correlation coefficients (using non-thinned data) are shown in the corresponding colours (normality and equality of variances in the data were ascertained using Kolmogorov–Smirnov and Levene's tests, respectively).

The foraging behaviour of individuals from Cabo Virgenes showed that these birds have rates of descent (mediated through differing swim angles) that varies according to whether they had encountered prey in the previous dive or not. After data had been sorted to consider only dives to specific depths by particular individuals (to eliminate the effect of depth in modulating swim angle and thus, rate of descent – see above), all individuals descended at a steeper angle after a dive in which they had ingested prey (Table 4). Because steep swim angles during the descent result in higher power requirements (see earlier), which moves birds using such swim angles across the energy envelope, this suggests that inter-colony differences that we observe in area use of the energy envelope are likely to be derived from differences in prey distribution.

DISCUSSION

Energy or power envelopes demonstrate how particular behaviours influence energy expenditure. The use of a mechanistic model of the total energy required for a single dive that is based on performance is an appropriate method for this aspect of diving behaviour in air-breathing animals, such as penguins, because they do not have free access to oxygen during the dive. For activities undertaken in air, where energy expenditure can vary depending on a number of factors (as for example a terrestrial vertebrate running at different speeds up different inclines) a power envelope (Fig. 6) is more appropriate because there is no limitation to oxygen as occurs in air-breathing animals that dive. The definition of such envelopes promises to have wide applicability across species by revealing the range of options available to accommodate changing environmental conditions, even those that relate to climate change, for example (Walther et al., 2002).

The lower vertical limits on our derived energy envelope for diving Magellanic penguins (Fig. 4) define the minimum energy they must expend to perform particular behaviours, with the mechanics (drag, muscle efficiency etc.) of penguins dictating these limits. In penguins, consideration of swim angle is essential because the rate of work is angle dependent as air is transported down the water column, even when swimming speeds are constant. This situation is more complex than the analogous situation for terrestrial animals because, although the latter might have to contend with climbing a steep hill, air volume (and therefore, upthrust) varies substantially with depth and affects power requirements in a diving penguin (Fig. 1).

Unlike terrestrial animals, diving animals must also manage power so that oxygen reserves are not exhausted at any point during the projected dive (Costa et al., 2001; Halsey et al., 2003; Kooyman and Ponganis, 1994). For example, excessive use of power (and therefore oxygen reserves) at the onset of a dive can only be made possible by correspondingly reduced power during later phases of the dive (Castellini et al., 1992) or by reducing dive duration (e.g. distance travelled in Fig. 4). Generally, we note that penguins show greatest variation in power use during shallower dives but this

Table 3. Ranking of the nine general linear mixed-effects models investigating the relationship between energy expended, maximum depth achieved, distance travelled and colony of origin

Model	<i>k</i>	<i>LL</i>	Δ BIC	wBIC	%DE
E~DP+DT+CL+DP×DT×CL	18	-107710.9	0.0	1.000	31.35
E~DP+DT+CL+DP×DT	9	-107903.9	298.1	<0.001	31.23
E~DP+DT+DP×DT	6	-107930.9	322.8	<0.001	31.21
E~DP+DT+CL	8	-114370.9	13222.4	<0.001	27.11
E~DP+DT	5	-114391.3	13233.8	<0.001	27.10
E~DT	4	-125578.3	35598.1	<0.001	19.97
E~DP	4	-142280.3	69002.1	<0.001	9.32
E~CL	6	-156888.9	98238.7	<0.001	0.01
E~1	3	-156905.9	98243.4	<0.001	0.00

E, energy expended; DP, maximum depth achieved; DT, distance travelled; CL, colony of origin; wBIC, model weight; *k*, number of parameters; *LL*, maximum log-likelihood; Δ BIC, difference in BIC for each model from the most parsimonious model; %DE, percentage deviance explained.

All models include a random individual effect to account for repeated measures. Models are ranked according to the Bayesian information criterion (BIC). The saturated model accounted for >99% of the posterior model weight (wBIC) of the nine models considered.

variance decreases substantially with increasing maximum depth (Fig. 6), presumably because birds that are far from the surface cannot afford to have a high metabolic rate because it compromises limited oxygen reserves. The real benefits of varying power during the dive, however, must be equated with the costs incurred (composed of both metabolic power and duration) during recovery periods at the water surface between dives. Because the rate at which oxygen is taken up by the body depends on the difference in partial pressure of oxygen between air and body tissues (Butler and Jones, 1997), animals that dive with large body oxygen stores need proportionately longer to replenish them, making long dives less efficient than short dives [see Wilson and Quintana (Wilson and Quintana, 2004) and references therein].

Our results demonstrate that penguins from different colonies operate on different parts of our derived energy envelope and we

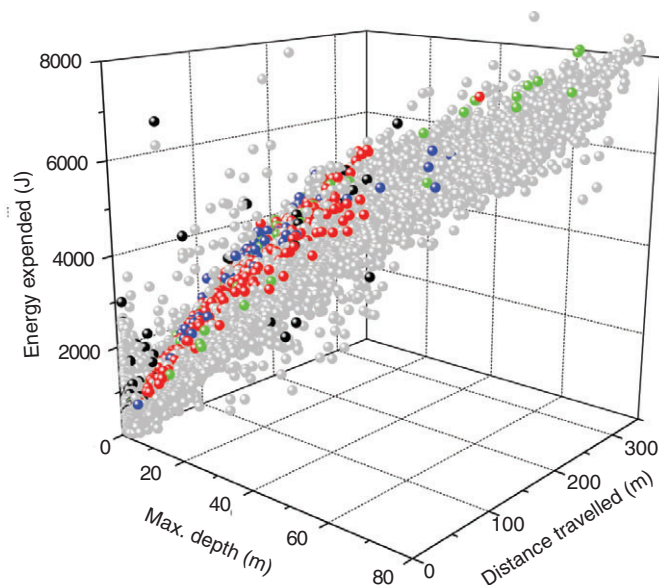


Fig. 4. Derived energy envelope showing the total energy used by Magellanic penguins (from four different colonies – grey circles) during single dives as a function of maximum depth reached and the total distance travelled during the course of the dive. Note that all points lie close to a well-defined three-dimensional envelope, with the envelope defining physical undertakings that cannot be accomplished using less energy than that shown. Examples of data from the different colonies are shown using 100 points selected at random from each site (see Fig. 3). Colour schemes as for Fig. 3.

propose that the precise conditions of prey encounter cause the birds to modify their diving behaviour, even individually (Fig. 5), which results in them using particular areas of the energy envelope in order to maximize their net harvesting rate. Certainly, Magellanic penguins from the four study sites feed on different prey (those from San Lorenzo feed primarily on anchovy (*Engraulis anchoita*), birds from Puerto Deseado on silverside (*Austroatherina* spp.) and squid (*Loligo* spp.), those from San Julian on a mixture of equal parts squid and sprat (*Sprattus fuegensis*), whereas birds from Cabo Virgenes feed primarily on sprat (Frere et al., 1996) [Wilson et al. (Wilson et al., 2005) and references therein]. None of the prey species is available at all sites (Frere et al., 1996; Scolaro et al., 1999) [Wilson et al. (Wilson et al., 2005) and references therein], and although data on prey ecology are scarce (Kaltenberg and Benoit-Bird, 2009) it is clear that the depth distribution of these various prey species is complex, depending, among other things, on time of day, size of fish and locality (e.g. Hansen and Madirolas, 1996; Hansen et al., 2001), and there is also considerable variation in depth utilization patterns according to species (www.fishbase.org). The complexity of prey ecology and paucity of data on the prey distribution in time and space means that we cannot explain why birds from the different colonies use different areas on the energy envelope. However, our simple model can clarify how different dive strategies best cater for varying densities of prey down the water column.

All other things being equal, moving animals should attempt to minimize their cost of transport (e.g. Culik et al., 1994) because this allows them to travel the maximum distance on minimum energy. This is generally applicable for penguins searching for prey because the likelihood of encountering prey is a function of the distance that they travel (Wilson, 1985; Wilson et al., 2004). However, because power requirements vary with swim angle during the descent, so too do costs of transport, and this needs to be equated with the profitability of different depths, which, in turn, depends on the vertical distribution of prey in the water column. In other words, for pelagic foragers such as penguins, swim angles during the descent can be shallower because prey can be searched for both horizontally and vertically. Otherwise, pelagic foragers might descend at an angle that minimizes the vertical cost of transport to a particular depth, whereupon a large part of the remaining dive duration could be spent swimming horizontally where transport costs down the water column are negated (see Eqn 4 and the second part of Eqn 7). However, this strategy minimizes the likelihood of encountering prey at any depth in the water column other than that chosen for the bottom phase. Swimming down at an angle that allows

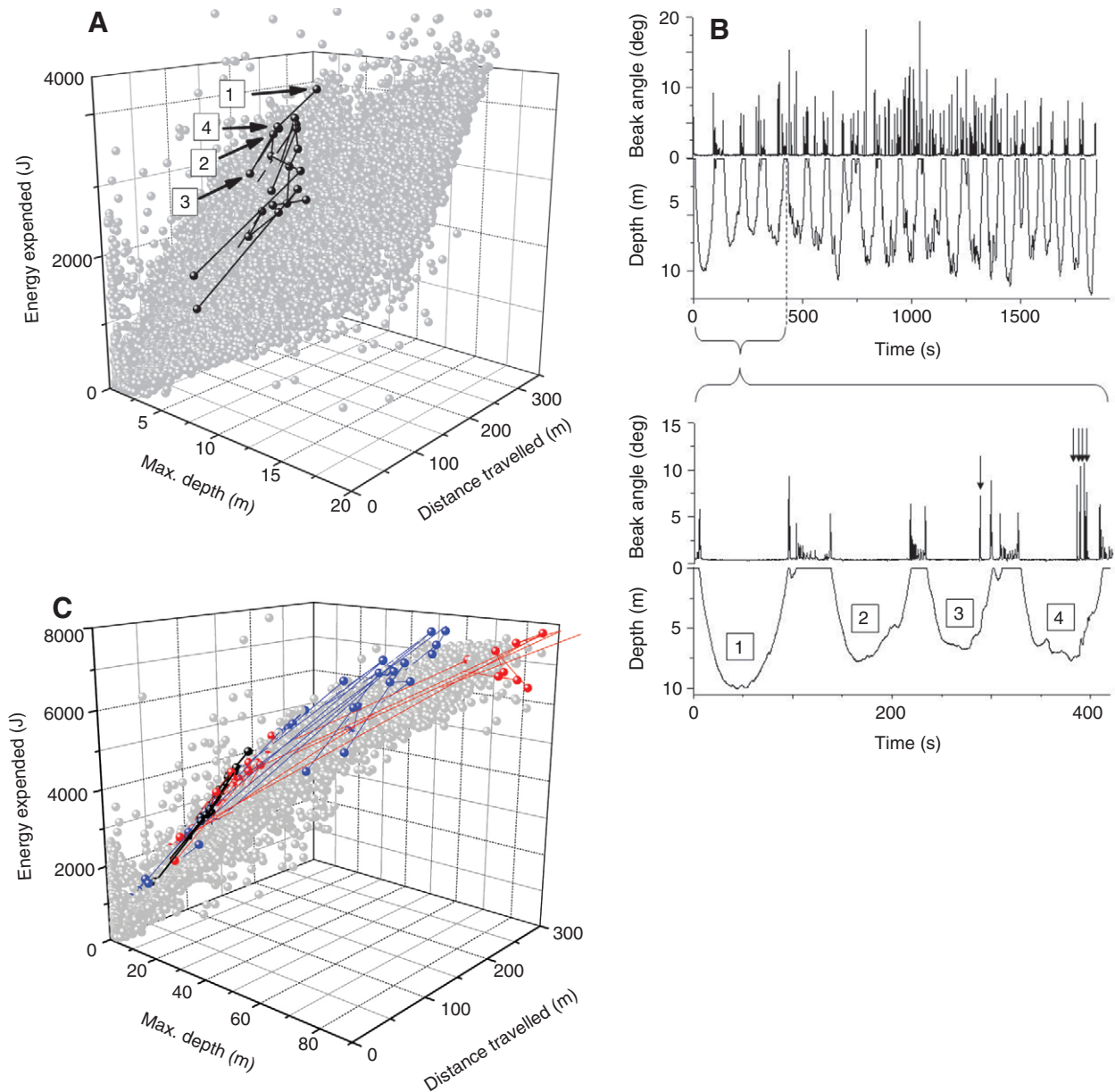


Fig. 5. (A) Expanded section of the derived energy envelope (with expended energy values between 2000 and 4000 J for the dive) highlighting the change in envelope area used by a single bird over the course of 22 consecutive dives (black spheres), all to a very similar depth (the first four dives are numbered for reference to B). B shows the detail in the depth profile and the beak opening angle for all 22 dives (upper traces), and an expanded view of the first four (lower figure). Note that the beak is opened while the bird is at the surface for breathing (cf. Wilson et al., 2003) and otherwise opened underwater for prey ingestion (arrows – one prey item is caught in dive 3 and 4 in dive 4). (C) The dives of the bird exemplified in B (black spheres) is shown on a more expansive section of the energy envelope in relation to a series of dives made by two other birds denoted by red and blue spheres, respectively, to show how individuals move over the energetic niche. Note that both latter birds have had 500 J added to their energy values for each dive in order to lift them out of the conglomeration of points making up the surface, for better visualization.

predators to cover both horizontal and vertical axes in their search for prey deals with this problem. The decision to search at particular swim angles implies that birds have information on the putative depth distribution of prey. The energetic consequences of swim angles during the descent on relative harvesting rate can be examined by allowing our model penguins to dive while acquiring prey at different rates according to depth. This approach (Fig. 7) shows better harvesting conditions if penguins dive at shallow swim angles for prey distributed near the surface, and at steep angles for deeper prey. This strategy is intuitive (although the complexities behind the

reasoning may not be obvious) and leads to a generalized solution for animals foraging in the pelagic zone using increasingly steep swim angles during the descent for dives directed at increasingly deeper depths (as has been noted in a great many studies (e.g. Wilson et al., 1996; Ropert-Coudert et al., 2001), but universally steeper swim angles during the descent for benthic-feeding diving birds [see Ribac et al. (Ribac et al., 2007) and references therein]).

The specific problem facing Magellanic penguins feeding primarily on pelagic prey is their assumed imperfect knowledge of the distribution of the prey within the water column. Indeed, there

Table 4. Values in the linear relationship ($y=ax+b$) between the rate of descent in any dive (y) and the number of prey caught in the preceding dive (x)

Bird	Depth range	a	b	r^2	F	P
1	29–34 m	0.098	0.97	0.77	14.8	<0.01
2	37–39 m	0.031	1.2	0.73	9.44	<0.05
3	15–16 m	0.04	1.02	0.49	5.43	<0.1
4	10–14 m	0.034	1.03	0.7	29.24	<0.001
5	17–19 m	0.054	1.11	0.67	23.51	<0.001

The relationship is based on: rate of descent (m s^{-1}) = a (prey ingested) + b , for Magellanic penguins diving serially within a narrow depth range. Thus, the example for bird 1, which dived to between 29 and 34 m, shows that rate of descent = 0.098 (number of prey ingested) + 0.97 .

is evidence to suggest that there is a complex ‘arms race’ between air-breathing, diving predators and pelagic prey that results in prey minimizing their chances of predation by being distributed within the water column in an unpredictable manner (cf. Wilson et al., 1993). We suggest that variation in the rates of descent of Magellanic penguins within and among colonies on the Argentine coast reflects the notion that birds attempt to ‘predict’ prey depth distributions, even though they have the capacity to modify their particular strategies based on information acquired during foraging. The latter would account for the observed higher rates of descent (steeper swim angles during the descent) in penguins that had previously encountered prey (Table 4; cf. Fig. 5), a pattern that has also been observed in Adélie penguins feeding on Antarctic krill (*Euphausia superba*) (Ropert-Coudert et al., 2001) and is probably what accounts for inter-dive variation within individual penguins (Fig. 5).

Sato et al. and Goldbogen et al. showed for penguins and whales, respectively, that swim angle can have a graded response with respect to patch quality and distribution (Sato et al., 2004; Goldbogen et al., 2008). The effect of swim angles during the descent, modulated by prey capture rate (Table 4), on net harvesting rate can be examined by applying the energy envelope model to data gathered from the IMASEN-equipped birds. Here, the gain in the number of prey items swallowed during the dive is divided by the energetic costs for descents to the foraging depths (defined in Table 4; Fig. 8). This ‘catch per unit effort’ (CPUE) for the angle-modulated dives

(a measure of foraging success) can be compared with the CPUE for dives with constant swim angles (determined from the relationship between swim angle during the descent and depth for the population of birds; Fig. 8). This approach shows that in all but one of the birds studied, Magellanic penguins would apparently increase their net gain by modulating swim angle during the descent according to prey ingestion rates (Fig. 8). Specifically, when birds have prior knowledge about the depth at which prey are located, they can increase their foraging efficiency by minimizing the vertical cost of transport (by increasing swim angle during the descent) and decreasing the time allocated to horizontal searching except at their projected foraging depth. This effective reduction in energy for the descent allows more time for exploitation at the allocated search

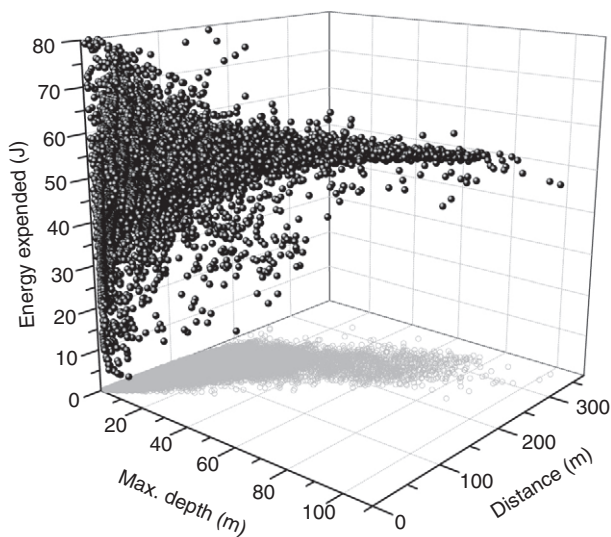


Fig. 6. Derived power envelope showing the mean power used by Magellanic penguins (from all colonies) during single dives as a function of maximum depth reached and the total distance travelled during the course of the dive.

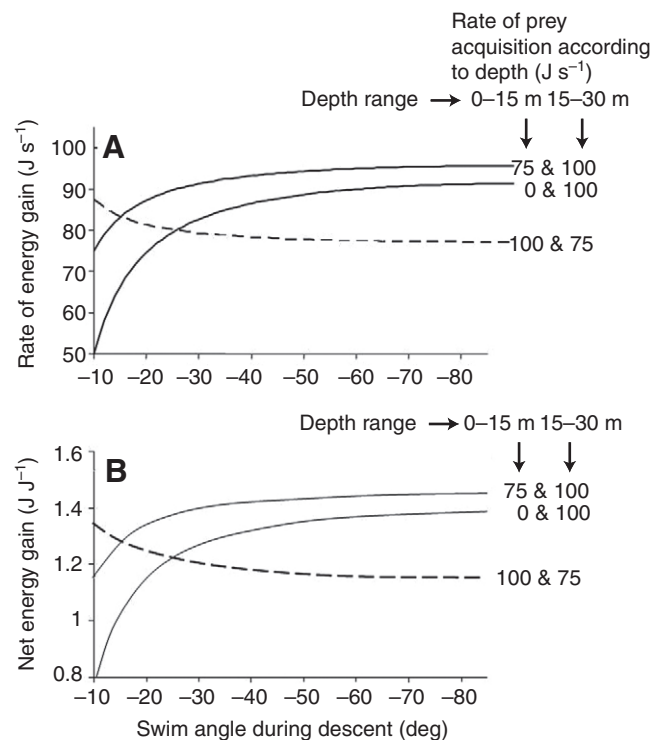


Fig. 7. (A) Rate of energy gain and (B) net energy gain as a function of descent angle calculated for a Magellanic penguin executing a dive to 30 m (for simplicity, the ascent is left out of the calculations) and encountering different prey densities in water depths of 0–15 m and 15–30 m. The dive duration is constant and corresponds to the time that it takes the bird to descend from 0 to 30 m at a 10 deg angle. Where steeper descent angles occur, the difference between maximum dive duration and descent duration is allocated to horizontal swimming along the bottom with overall energy expenditure calculated according to the model set out in the text. Prey density is expressed as a mean rate of energy gain (J s^{-1} , which equates with joules per unit distance because speed is held constant).

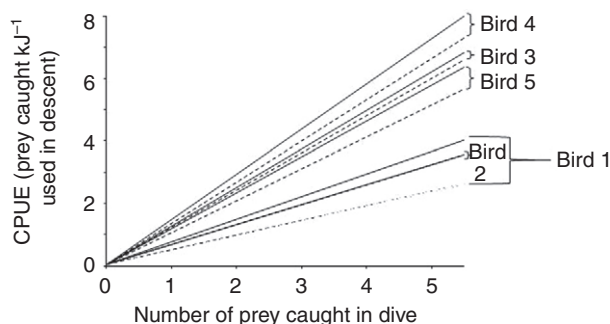


Fig. 8. The harvesting success [solid lines; expressed as catch per unit effort (CPUE; in prey items per kJ energy expended)] in Magellanic penguins as predicted using (1) a model of energy expended during the descent phase of dives (see text) and (2) data on how birds modulate descent rate according to the number of prey items they have caught in the preceding dive (Table 3). Note that this approach assumes that the number of prey caught in adjacent dives is equal (Wilson, 2003). The associated dashed lines show the harvesting success of penguins ingesting the same number of prey items but maintaining a constant descent rate irrespective of the number of prey ingested. For this case, the rate used is derived from that predicted by the general relationship between descent duration and maximum dive depth for Magellanic penguins at Cabo Virgenes (the site from which the data in Table 2 derive); descent rate = $(0.424 \text{ depth} + 6.1) / \text{depth}$ (cf. Fig. 2A).

depth but becomes more inappropriate as the likelihood that the prey will move out of the projected dive depth increases (see above). The dynamism of fish schools during exploitation by predators (e.g. Nottestad et al., 2002) is testimony to the complexity of the situation with which penguins have to deal.

Our treatise has examined how dive profile trajectories relate to the energy envelope, and how judicious dive strategies may maximize prey harvest rates in a pelagic marine predator. Selection of the behaviourally mediated dive trajectory determines the physical conditions (specifically hydrostatic pressure) to which each individual penguin is exposed. The case of the penguin is particularly well defined because the physical properties of the environment in which it operates change predictably with depth. Our three-dimensional energy envelope is overly simple because real energetic niches are multi-dimensional. For example, energy expenditure per dive (Fig. 4) will also vary with physical parameters such as temperature (Chappell et al., 2004; Porter and Kearney, 2009), and may be heavily impacted by swimming speed during the bottom phase for some species (e.g. Soto et al., 2008), the manoeuvres undertaken during prey pursuit (Weihs, 1981; Hughes and Kelly, 1996), and the accelerations and decelerations involved in catching agile and evasive prey (Soto et al., 2008) and during complex feeding mechanisms (Potvin et al., 2009). Other (also non-diving) animals may have energy expenditure affected by humidity (Marhold and Nagel, 1995), pressure (Lovvorn, 1999), salinity (Pechenik et al., 2000) and light intensity (Boshouwers and Nicaise, 1993), as well as by parameters that animals themselves can change such as speed of movement (Rubenson et al., 2004) and climb angle (Laursen et al., 2000). Our ability to integrate all relevant dimensions enables a better assessment of the consequences of any changes in the environment (both biotic and abiotic) to which organisms are exposed, and determine the extent to which the behavioural repertoire displayed in response to changing conditions may be optimal. Where such methods are used in measures of foraging success they can be equated with energy expenditure to assess efficiency (Bernays et al., 2004).

Elucidating species-specific n -dimensional energy niches is also important for immobile animals that react predictably to a temporally variable environment [e.g. resting metabolic rate in shellfish (Arifin and Bendell-Young, 2001)], and for mobile species that react by relocation that enables them to exploit less demanding areas of their power envelopes [e.g. desert animals seeking shade to lower their resting metabolic rate (Erbeling and Paarmann, 1985; Weathers et al., 2001)]. The consequences of this movement for subsequent physical environment-related energy expenditure makes modelling the system a challenge because of the difficulty in determining how behaviour and physiology interact. Ultimately though, the specific invariance of any species' energetic niche, which will become ever better defined as the number of dimensions increases, should give us a clear multi-dimensional envelope on which we can base more complex models of behaviour and life history strategies.

LIST OF SYMBOLS AND ABBREVIATIONS

A	cross-sectional area of the penguin
C_d	coefficient of drag
D	depth
F	thrust
g	gravitational constant
gV	upthrust
GLMM	general linear mixed effects model
P_i	power input;
P_o	power output
P_{total}	total mechanical power output
U	swimming speed
V_1	volume of air in the penguin at the surface
V_2	volume of air in the penguin at depth
W	mechanical work
γ	swim angle between the bird's trajectory and the sea surface
θ	dive angle
ρ	density of seawater
%DE	percentage deviance explained

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