Pushed to the limit: food abundance determines tag-induced harm in penguins

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Abstract

The energetic costs of animal movement change with body condition, although the consequences of this for foraging efficiency are rarely considered. We deployed externally attached devices to Magellanic penguins (Spheniscus magellanicus), known to increase the costs of swimming via increased drag in a consistent manner, and noted, however, that foraging behaviour and efficiency varied dramatically between years. We used our results to construct an energetics-based model and found that small increases in drag due to the attachment of externally attached tags predicted accelerating harm as prey availability decreased, which accorded with our observations. This explains earlier observations of differential breeding success in tagged versus untagged penguins in particular years, highlights the importance of understanding how animal body condition may affect population processes in general and advocates caution in interpretations of tag-derived data over variable environmental conditions.

Keywords: *animal welfare, body condition-dependent cost of transport, drag, energy expenditure, Magellanic penguin, Spheniscus magellanicus*

Introduction

Animals have to deal with environmental change, and are assumed to adopt appropriate behavioural strategies to cope with it (Sutherland 2006). Recognition of this underpins the large field of optimal foraging theory (Pyke 1984) where variation in prey abundance and accessibility is considered to modulate behaviour so that foragers maximise fitness (Stephens *et al* 2007). Indeed, efficient foraging should enhance breeding success, which explains why accessibility of food resources also interests population ecologists (eg Both *et al* 2006; Newton 2010). This putative link has led a growing number of researchers to use animal-attached tags to attempt to relate foraging effort and foraging success, traditionally difficult to quantify in wild animals (Stephens *et al* 2007), to reproductive success (Takahashi *et al* 2003), ultimately linking this back to environmental conditions (Weimerskirch *et al* 2005).

But animals also have to deal with natural changes in the efficiency of their movement over time as, for example, cyclical mass changes (Pond 1978) or external surface deterioration, in eg plumage (Wilson 1985) or the acquisition of epibionts by turtles (Frick *et al* 2000), necessitate varying power costs for travel (Witter & Cuthill 1993). The use of animal-attached tags may exacerbate this (Jepsen *et al* 2005) because external tags add mass and increase drag (White *et al* 2013). Energy models of movement indicate that it is

inappropriate to scale-up mass increases due to attached tags linearly with power costs in flying birds (Vandenabeele *et al* 2012) and that even empirically determined power cost increases for movement (Culik *et al* 1994; Methling *et al* 2011) may not scale linearly with foraging efficiency (Wilson *et al* 2004). This latter finding may indicate why, for example, a study by Saraux *et al* (2011) showed that the seemingly trivial addition of flipper bands to king penguins (*Aptenodytes patagonicus*) increased mortality over ten years by 16%. Interestingly, this study also indicated that birds were affected differentially between environmental conditions and years. Both banded and unbanded birds had good and poor breeding in years of high and low sea surface temperature (used as an index of prey availability), respectively, but the unbanded birds did markedly better in years with intermediate sea surface temperature.

The observation that animal-attached tag harm inter-relates with environmental variables and body condition raises important animal welfare issues. Almost 30 years ago, Wilson *et al* (1986) reported that tagging penguins affects performance, which highlighted both the welfare and the scientific implications of tagging and specifically related penguin performance to the size of tags. Clearly, however, the issue is not that simple because the harm caused by tags also co-varies with animal body condition and the particulars of the environment. Aside from the seminal work by

Saraux *et al* (2011), however, this topic has received very little attention and, to our knowledge, it has never been put into an energetic framework.

While conducting fieldwork on breeding Magellanic penguins (*Spheniscus magellanicus*) in Argentina during 2012, in a study seeking to document inter-annual variation in foraging areas and behaviours using animal-attached GPS-depth recorders, we noted that birds spent much longer at sea than usual. In addition, 2012 was a poor year for breeding, with many emaciated chicks in the colony. In an attempt to understand this, we used our logger-acquired data to construct a simple energetic model of energy expenditure versus energy gain for breeding Magellanic penguins based on tag data from 2012, the 'bad' year, and from 2008 and 2011, two 'normal' years. We describe this model below, which clarifies the mechanism by which variability of environmental conditions can lead to differential harmful effects of external tags, including those just used for identification (cf Saraux *et al* 2011) and point to the value of this approach in informing animal welfare decisions.

Materials and methods

Fieldwork was conducted during the early chick-rearing period between November and December 2008, 2011 and 2012 at the Punta Norte/San Lorenzo Magellanic penguin colony (42°04′S, 63°49′W). Twenty-four Magellanic penguins brooding small chicks were equipped with GPS loggers (GPS-TDlog, Earth and Ocean Technologies, Kiel, Germany) recording depth, latitude and longitude. The horizontal accuracy of the positional fixes (recorded at 1 Hz when the penguins were not underwater) was better than 5 m for 90% of fixes (GPS-TDlog Manual) while the depth data, recorded at 0.5 Hz, was accurate to 0.3 m. The tag measured 96 × 39 × 27 mm (length × width × height), comprising approximately 6.5% of the cross-sectional area of the bird, and had a mass of 75 g, which is *circa* 1.7% of the mean Magellanic penguin body mass.

Twenty-four foraging trips (nine from 2008, eight from 2011 and seven from 2012) conducted during the early chick-rearing period were analysed. Only two of these were incomplete, those belonging to the 2012 dataset since the foraging trips were so long that the tag batteries became exhausted. Foraging trips were divided into three distinctive behaviours which accorded to temporally distinct segments: travelling, resting and foraging. Travelling occurred during the outbound and inbound phases of the trip and was identified using criteria defined in Sala *et al* (2012a); resting, comprised all non-diving periods at sea exceeding 4 min while foraging accounted for the remaining time (Sala *et al* 2012a). For each foraging trip the following variables were calculated: (i) total time resting; (ii) the total time foraging; (iii) the total time travelling; (iv) the total foraging trip duration (the sum of the three variables defined above); (v) trip length, ie the total cumulative horizontal distance travelled between all positional fixes along the foraging track; and (vi) maximum distance reached from the colony. For the two cases from the 2012 season where the tag batteries were exhausted before birds returned to the colony,

we estimated the maximum distances from the colony (D_{max}) and the total distances travelled (D_{tot}) using the strong linear relationships between these two variables and trip duration (T_{dur}): $T_{dur} = 0.26\ D_{tot} - 6.2$ ($r^2 = 0.96$, $F_{1,6} = 133.3$; $P < 0.0001$) and $T_{dur} = 0.65\ D_{max} - 11.4$ ($r^2 = 0.55$, $F_{1,6} = 6.9$; $P = 0.048$) (see Sala *et al* 2012a).

In addition, since prey capture by Magellanic penguins is virtually always associated with an undulation in the depth profile over time (Simeone & Wilson 2003) because these birds capture their prey by lunging at them from underneath (Wilson *et al* 2010), we used the number of undulations in the depth profile during foraging dives as a linear proxy for prey capture success (for details, see Sala *et al* 2012b). We did this for each bird by dividing the total number of undulations occurring during the foraging trip by the foraging duration and thus derived a measure of prey capture rate. Since there were no differences between the studied variables between 2008 and 2011 (Mann-Whitney *U* tests; trip duration (h): $U = 19$, $P = 0.11$, trip length (km): $U = 23$, $P = 0.24$; maximum distance from the colony (km): $U = 26$, $P = 0.37$; prey capture rate (undulations per h): $U = 31$, $P = 0.67$), data from both breeding seasons were pooled and compared to the information obtained during 2012.

At the time of the study, all penguins had small chicks and pairs alternated shifts; one bird of the pair foraged at sea for a period while the mate brooded the chicks before roles switched (Williams 1995). In brief, the model assumed that penguins foraging at sea gained enough energy to cover all incurred energetic costs during both the time at sea and the preceding time on land (Wilson *et al* 2005). We varied both the rate of prey acquisition at sea (Sala *et al* 2012b) and the energetic cost of swimming due to an attached tag (Bannash *et al* 1994; Culik *et al* 1994) within credible limits and estimated the length of time that birds had to forage accordingly.

For the model, we divided the period at sea into our three activities: travelling, resting and foraging (see above). We determined the rate of energy expenditure for these different activities according to the amount of time spent swimming underwater and the amount of time spent resting between dives at the water surface for the three activities (Table 1). Birds on land brooding chicks were assumed to have energy expenditures equating to resting metabolic rates (Table 1) because they primarily sleep when brooding chicks and, since birds alternate duties, we assumed that the time spent at sea equalled that on land. Although penguin behaviour both at sea and on land is more complex than implied in our model, because they also sleep at sea during extended foraging trips and have to accumulate food for their chicks, our primary model does not deal with this because we wished the approach to be simple and generally applicable, rather than just be of use for penguins. We did, however, incorporate both extended resting and incorporation of food for the chicks in the *Discussion* which alludes to the specifics of penguins. As such, the outputs of our primary model should denote basic relevant trends with value for many tag-equipped species.

Table 1   Parameters used in model.

Behaviour	Parameter	Value	Reference
Literature data			
Swimming underwater	Power (W)	47.5	Luna-Jorquera & Culik (2000); Wilson *et al* (2011)
Resting at surface	Power (W)	23.8	Luna-Jorquera & Culik (2000)
Resting on land	Power (W)	15.2	Luna-Jorquera & Culik (2000)
Travelling	Dive duration (s)	30.7	Sala JE, Wilson RP, Frere E & Quintana F (unpublished data)
	Surface duration (s)	21.2	Sala JE, Wilson RP, Frere E & Quintana F (unpublished data)
	Energy to swim per dive (J)	950	Derived
	Energy to rest per dive (J)	71.4	Derived
	Mean power per dive (W)	44.4	Derived
Foraging	Dive duration (s)	79.4	Sala JE, Wilson RP, Frere E & Quintana F (unpublished data)
	Surface duration (s)	22.0	Sala JE, Wilson RP, Frere E & Quintana F (unpublished data)
	Energy to swim per dive (J)	3,800	Derived
	Energy to rest per dive (J)	523.6	Derived
	Mean power per dive (W)	42.4	Derived
Brood requirements	Food caught (g)	200	Wilson *et al* (1989)*
	Energy density of food caught (J g^{-1})	5,500	Ciancio *et al* (2007)

* Quantity reported brought back to 'small' chicks by congeneric African penguin (*Spheniscus demersus*) (150 g) scaled up linearly to equate with the proportionate difference in mass between African and Magellanic penguins using mass data in Williams (1995).

Table 2   Mean (± SD) values and range (minimum-maximum) characteristics of completed foraging trips performed by Magellanic penguins during the early chick-rearing period at Punta Norte colony, Península Valdés, Argentina.

| Parameter	2008 & 2011 (17)	2012 (7)	Mann-Witney *U* test	*P*-value
Trip length (km)	155.6 (± 48.40) [76.7–254.5]	277.5 (± 150.5) [114.7–499.2]	33.0	**0.0493**
Maximum distance from the colony (km)	48.5 (± 13.2) [20.1–71.6]	110.3 (± 60.3) [48.7–205.5]	16.0	**0.0031**
Trip duration (h)	28.9 (± 10.3) [15.0–49.4]	63.7 (± 40.2) [21.0–122.1]	31.0	**0.0377**
Total travel duration	8.3 (± 4.0) [2.9–17.2]	12.6 (± 5.5) [5.5–19.2]	30.0	**0.0327**
Total foraging duration (h)	13.8 (± 6.6) [7.1–27.7]	34.4 (± 24.8) [9.3–78.3]	24.0	**0.0327**
Total resting at-sea duration (h)	6.8 (± 3.9) [1.9–15.4]	16.6 (± 16.4) [1.2–40.3]	52.0	0.3283
Prey capture rate (undulations h^{-1})	27.5 (± 4.9) [18.5–35.1]	13.6 (± 5.4) [9.9–25.5]	6.5	**0.0004**

Data were derived from the GPS loggers. Significant statistical tests are shown in bold. Mann-Whitney *U* tests were used to compare between years (ie 2008 and 2011 vs 2012). Sample size (number of birds) per year is given in parentheses.

Results

During 2012 Magellanic penguins displayed very different foraging parameters (Table 2) compared to 2008 and 2011 (which were statistically indistinguishable from each other), exploiting regions farther from the colony (Figure 1) and spending more time at sea and more time consecrated to both travelling and foraging (Table 2). In addition, birds in 2012 had significantly lower rates of undulations in their dive profiles, being approximately half that of the normal years (Table 2), indicating that prey capture rates were similarly reduced (Sala *et al* 2012b).

Our model, which used values for rates of energy expenditure for diving and resting penguins and assumed that our birds were in steady state, balancing energy use during foraging and brooding cycles with energy gained during foraging, revealed that, for unequipped penguins, there was a critical limit in the acquisition of prey (expressed in terms of joules gained per second of foraging behaviour), lower than which birds could not balance energy expenditure with energy acquisition (Figure 2). Immediately above this threshold, foraging duration values were untenably high, but these decreased

Figure 1
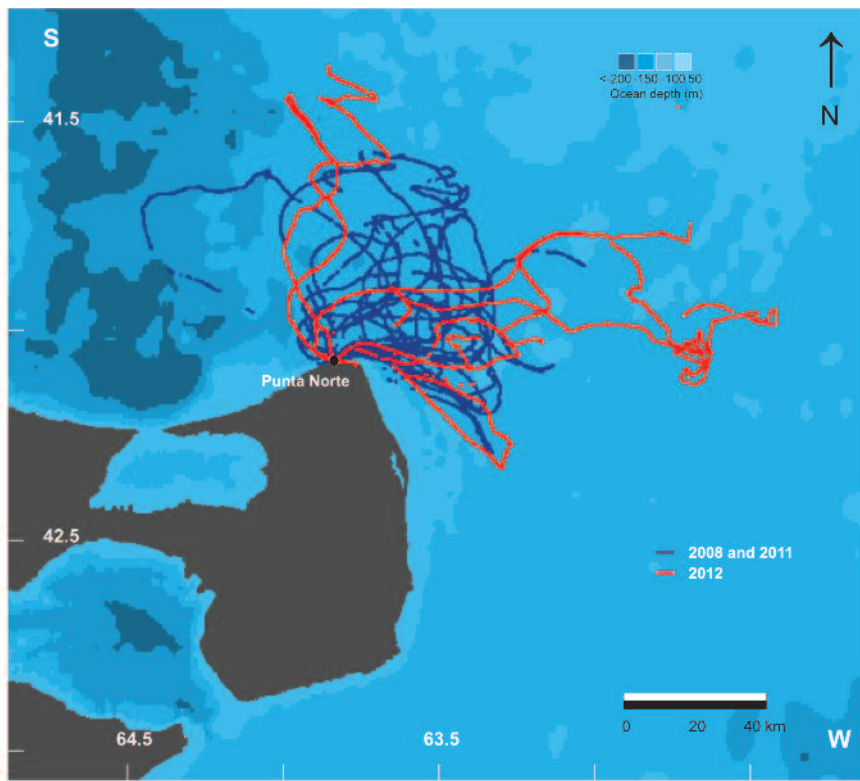
Area use by Magellanic penguins foraging from the Punta Norte colony during 2008 and 2011 (dark blue tracks) and during 2012 (red tracks).

Figure 2
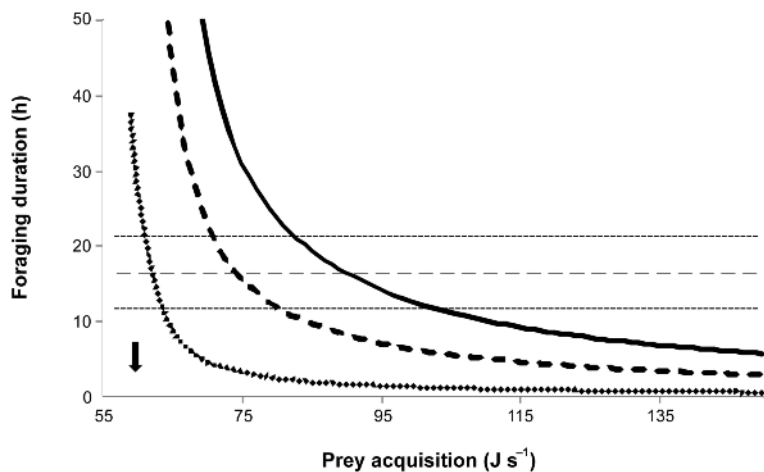
The predicted relationship between the time necessary for foraging (to balance energy expenditure with energy gain) and food abundance for untagged Magellanic penguins having to spend a total of 1 h (dotted line), 5 h (dashed line) and 10 h (black line) commuting to and from the foraging area. The point below which prey acquisition rates do not allow the birds to balance energy expenditure with gain, which is invariant of commuting duration, is shown by the arrow. The long ashed horizontal line shows the mean (± SD; short dashes) time spent foraging by Punta Norte birds during 2008 and 2011 (Table 2). For details see text.

approximately exponentially with increasing prey acquisition rates (Figure 2). Longer commuting durations did not change the critical limit in the prey acquisition rate but did increase the time that had to be spent in the foraging area, particularly where prey acquisition rates were close to the lower critical limit (Figure 2).

Varying the energy expended by swimming penguins by defined amounts, to simulate the effects of attached devices (Bannasch *et al* 1994; Culik *et al* 1994), did not result in a change in the form of the exponential decay of time spent in the foraging area although it did result in a

shift in the lower critical limit in prey acquisition rate together with a shift in the distribution to the right (Figure 3[a]). The change in the lower critical limit was a linear function of the percentage increased energy expended during underwater swimming (over that of an unequipped bird) (Figure 3[a]). Our model predicted that Magellanic penguins commuting for 5 h during a foraging trip at sea would have a lower critical limit in prey acquisition rate of 58.9 J s^{-1} while unequipped but that this would rise to 66.3 J s^{-1} if birds were equipped with devices increasing energy expenditure for swimming by 20%.

Figure 3
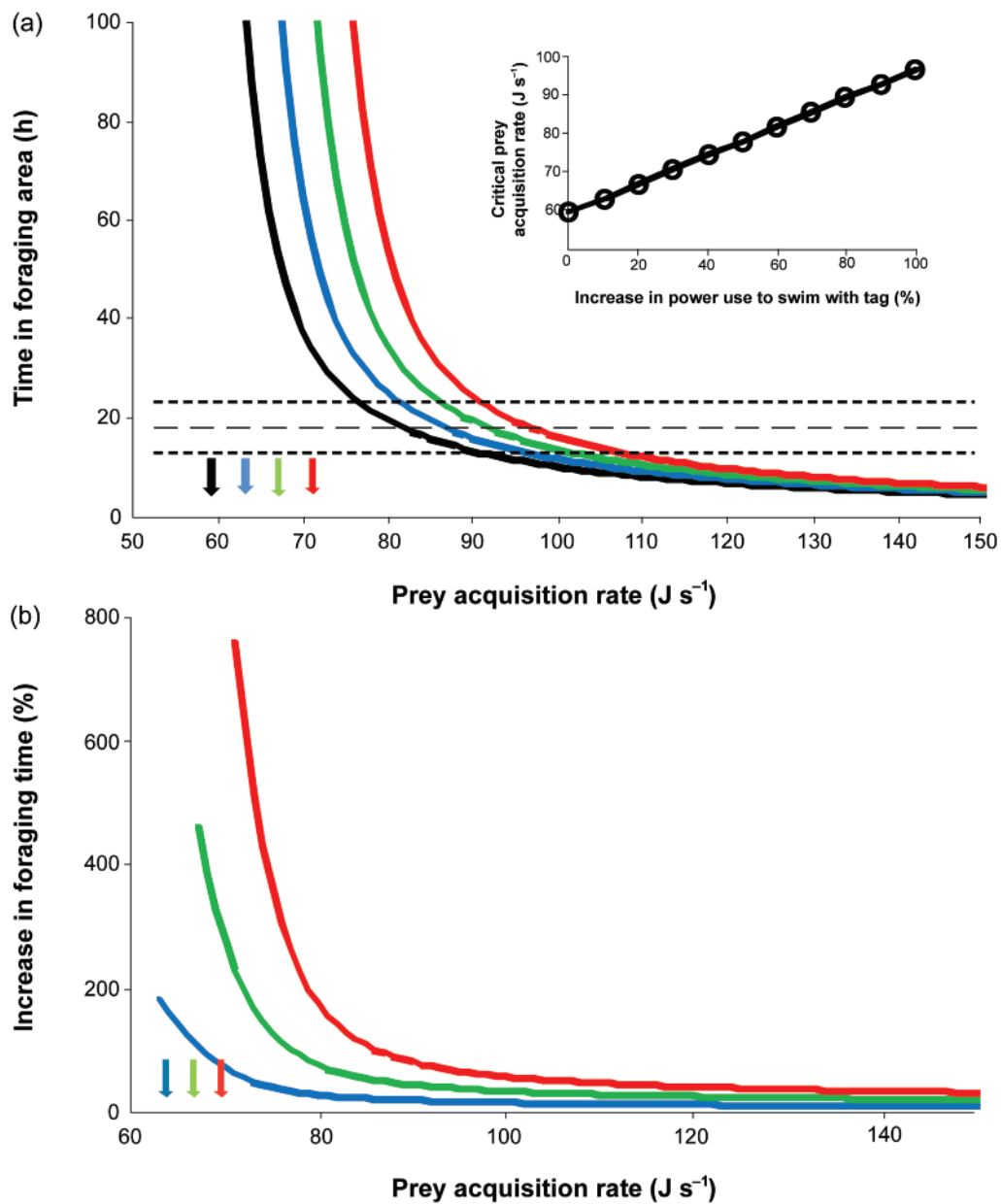
Showing (a) the time predicted necessary for Magellanic penguins to forage as a function of prey acquisition rate in order to balance energy expenditure with energy gain (assuming 8.3 h commuting between nesting and foraging area; Table 1). The long dashed horizontal line shows the 'normal' mean and the short dashed the standard deviation (see Table 1). The four lines depict birds carrying tags that impact them differentially; black line — an untagged bird, blue, green and red lines represent birds carrying tags that increase energy expenditure by 10, 20 and 30%, respectively. The points below which prey acquisition rates do not allow the birds to balance energy expenditure with gain are shown by correspondingly coloured arrows. These minimum prey acquisition values (y) are a linear function of device impact (expressed in terms of percentage increase in energy expenditure to swim underwater with a tag over that of swimming without a tag [x]) according to $y = 0.37x + 58.9$. (b) shows the data in (a) expressed as a percentage increase in time spent foraging over the norm (untagged birds) maintaining the same colour coding.

Importantly, the amount of time spent foraging by penguins equipped with such devices was still predicted to be double that of unequipped birds at prey acquisition rates of 78 J s⁻¹ and 50% longer at prey acquisition rates of 89 J s⁻¹ (Figure 3[b]). The greater the amount of energy spent by the penguin to swim with a tag above normal, the longer the time taken to balance energy needs (Figure 3[b]). By the time prey acquisition rates had increased to 200 J s⁻¹, tags causing 10, 20 and 30% greater energy expenditure during swimming were predicted to cause only a modest increase in foraging duration equating to 10, 20 and 31% longer than that of unequipped birds.

Discussion

Our results are based on a small sample of birds and over a relatively short time-period, but the levels of significance (Table 2) lend confidence to the conclusions regarding changes in foraging behaviour. In addition, our model is deliberately simplistic but provides a framework based on energetics, with which to examine expected changes in a central place foraging animal faced with a food supply varying both in distance from the central place and in abundance at the foraging site as well as, critically, examining how the cost of locomotion affects predicted foraging patterns. In this model, we did not include any food necessarily ingested for the chick by our foraging birds, nor did we incorporate extended periods of rest by birds at the foraging site, which presumably become more likely as birds spend longer at sea. However, as with the commuting distance, both of these simply equate to birds having to increase the rate of prey acquisition if foraging durations are held constant or increase the time necessarily spent foraging if prey acquisition rates are held constant (Figure 2). We note that the lower crucial rates, indicating periods where penguins are only just able to balance energy ingested with energy expended, represent conditions under which birds would not normally be operating. For instance, Sala *et al* (2012b) calculate prey acquisition rates for birds from Punta Norte to be 1,005 J s^{-1} underwater. To make these values comparable to ours (which refer to rates of energy acquisition for the whole foraging period rather than just the time spent underwater), we have to correct for the time spent at the surface, which would convert their Punta Norte values to 788 J s^{-1}, making them some 13 times higher than our critical values of 59 J s^{-1} (for untagged penguins). If we ignore device effects, for the moment, we can use our model, modified slightly to incorporate both the food assumed brought back to the brood (Table 1) and time spent at the surface resting for the 2012 birds (Table 2), to calculate a rate of food acquisition of 136 J s^{-1} for the 2012 season, less than 20% that given by Sala *et al* (2012b) for 'normal' years. Our model thus explains why we observed such extended foraging trips in terms of at-sea prey availability. Our findings are backed by two other metrics: (i) a halving of the rate of undulations, as a proxy for foraging success, during foraging in 2012 compared to 2008 and 2011 (Table 2); and (ii) figures released by the Ministerio de Agricultura, Ganadería y Pesca de la República Argentina (2012), which show mean (± SD) fishing fleet captures of anchovy, the main Magellanic penguin prey at Punta Norte (Scolaro *et al* 1999), for the region for 2009 to 2011 inclusive, to be 2,363 (± 400) tons while the equivalent figure for 2012 was 1,263 tons.

We recognise that this latter calculation is based on the swimming energetics of an untagged penguin but uses data from a tag-fitted model bird, and is weakened because we do not know the energetic effect of the tag nor do we know whether the prey acquisition rate is the same for tagged and untagged birds (we have assumed it to be the same (but see Wilson *et al* [2004]). It is unfortunate that we did not document the length of foraging trips of unequipped birds during our study since, by doing this, and assuming similar percentages of at-sea time allocated to foraging, resting and commuting, we could have iteratively determined the energetic cost of swimming with the device.

This modelling exercise demonstrates an advance that might allow researchers to make predictions as to how hard tagged animals are working compared to non-tagged animals and to correct for it, at least partially (Wilson 2011). Most importantly, the approach seems critical at times of poor food availability because it shows that increases in energy expenditure by animals carrying external tags do not necessarily equate to equivalent linear changes in foraging parameters. More specifically, variation in prey accessibility results in a differential harmful effect of the tag, demonstrating that even using standardised (eg fixed size) tags does not result in constant effects. This is particularly germane for studies seeking to compare variation in foraging behaviour over time, as exemplified in inter-annual studies (eg Sala *et al* 2012a), where tag use during poor foraging conditions will lead to an accelerated harm over that apparent during good foraging conditions. In our case the harm takes the form of the increased time spent at sea which will decrease chick provisioning rates (Ropert-Coudert *et al* 2004), reducing growth rates (eg Cooper 1977) and likely increasing mortality (Heezik & Davis 2008). This may explain why Dugger *et al* (2006) found that increased foraging duration in banded Adélie penguins (*Pygoscelis adeliae*) varied with year. Clearly, one immediate way of determining whether the effects of the tags are problematic in the field is to compare foraging trip length of unequipped animals to those of equipped animals. We did not do this during our study, however, realising the situation too late, and not wishing to deploy more tags under these difficult circumstances.

But the matter of deploying tags, or not, under poor circumstances raises ethical issues too, particularly with regard to whether we should be deploying tags on animals experiencing foraging difficulties in order to clarify those conditions. We suggest that this should be an important consideration for ethical bodies approving studies as well as for scientists in the field, suddenly faced with an unusual situation as we were. One approach to dealing with this problem is to use the Bateson's Decision Cube where animal suffering is judged against the importance of the research and the likelihood of benefit (McMahon *et al* 2012). A problem here is that there are different opinions as to the values ascribed to these various axes, not least because they are generally couched qualitatively. However, models of energy flux, such as the one posed here, have real worth in helping give hard values to some elements of the axes, such as in describing animal suffering in terms of energy expended to acquire food, and this must surely be a good first step in any attempt to decide between further scientific manipulation and a hands-off approach.

Acknowledgements

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