How much energy do African Penguins *Spheniscus demersus* extract from the sea?

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ABSTRACT

The primary objective of this project was to estimate the amount of energy African Penguins *Spheniscus demersus* expend to complete a successful breeding attempt, and thereby provide an estimate of the amount of fish required to do this. We undertook simultaneous logging of tracks and assessment of daily energy requirements on eight African Penguins. GPS loggers were used to determine the time spent at sea during a foraging trip and doubly labelled water experiments were undertaken to estimate the energy expended during a foraging trip. We estimated that the rate of energy expenditure on land during breeding was 361.6 kJ day^{-1} kg^{-1} and the rate at sea was 1491.2 kJ day^{-1} kg^{-1} in a two parameter model which explained 98.3% of the variance in energy expenditure. Under a set of assumptions relating to average behaviour, we estimated that the amount of Anchovy *Engraulis encrasicolus* required by two adults during the breeding period to raise a family of two chicks is 151.7 kg. Of this, 17.3 kg is fed to each chick, and each adult consumes 58.6 kg. The overall "efficiency" of breeding (the ratio of the mass of chicks produced and the total mass of food consumed during the entire breeding attempt) was estimated to be 3.73%. This analysis potentially provides us with a method that can be used to estimate the ratio between food availability on a daily basis and food requirements. The present results suggest that this ratio might be of the order 500–1000. To improve all these estimates, sample size needs to be increased.

INTRODUCTION

In the first years of the 21st century, populations of African Penguins *Spheniscus demersus* in the Western Cape were increasing (Underhill et al. 2006). They have subsequently collapsed (Crawford et al. 2011). During the second decade of the 21st century, the critical task for penguin biologists is to investigate, urgently and objectively, every possible explanation for this decrease. Once the reason or reasons for this decrease are understood, the next step is to develop and recommend mitigation measures which will first slow down the rate of decrease and then reverse it.

One possible explanation for the decrease is that it is related to food availability, both on a local scale (i.e. around breeding colonies) and on an ecosystem wide scale (e.g. Durant et al. 2010, Crawford et al. 2011). This project contributes to this possibility by estimating the amount of energy African Penguins expend to complete a successful breeding attempt, and thereby providing an estimate of the amount of fish required to do this. It also provides a rough estimate of the amount of fish required for the remainder of the year, outside the breeding season and including the annual moult period.

METHODS

The fieldwork methods are modelled on those of Navarro (2010). This involves the simultaneous use of techniques for tracking and assessing daily energy requirements. GPS loggers were used to determine the time spent at sea during a foraging trip, the distance travelled and other information that can be derived from knowledge of the tracks. Doubly labelled water experiments were undertaken to estimate the energy expended during a foraging trip. The use of GPS loggers on African Penguins was pioneered by Petersen et al. (2006), and details of the GPS logger fieldwork and data analysis procedures are available there. Nagy et al. (1984) undertook a doubly labelled water experiment using the radioactive isotope of hydrogen known as tritium, with atomic mass 3. This study used the stable isotope deuterium, with atomic mass 2. The Nagy et al. (1984) study was undertaken when energetics research based on doubly labelled water was still a novelty; there have subsequently been significant advances in understanding of appropriate fieldwork methods, the equipment used to determine concentrations of the stable isotopes has become vastly more accurate, and the equations used to generate the final results have been honed and improved to remove potential biases (Speakman 1997). Our energetics fieldwork and analysis procedures followed exactly the protocols used by Navarro (2010) in his parallel study of the Cape Gannet.

This is the first study to use both technologies simultaneously on African Penguins. The size of the sample of penguins on which both the GPS logger performed perfectly and the doubly labelled water (DLW) experiment was successful was eight. This limited the statistical data analysis options to the estimation of a maximum of two parameters. The GPS logger data were used to determine the two key contrasting components of behaviour from an energetics perspective: time on land and time at sea. These times were computed over the period that the DLW experiment was conducted. The experiments were performed on adult African Penguins feeding small- to medium-sized chicks.

Our aim was to estimate the total amount of energy expended during the breeding season for two parents to raise two chicks to fledging. Fortunately, the chick energetics of African Penguins was studied by Bouwhuis et al. (2007). Sandra Bouwhuis was an MSc student at the University of Groningen, the Netherlands, who undertook this chick energetics study as one of her two main thesis projects. She did her fieldwork on Robben Island in 2004. To do this she used a Gompertz growth coefficient of 0.0460, which was the median growth rate of 104 chicks which she measured until they fledged in 2004. This can be considered a “normal” year (Barham et al. 2008). The ADU gained extensive experience of studies of energetics using DLW through the supervision and co-supervision of PhD and MSc projects (Bakker 2004, Mullers 2004, Bouwhuis 2005, Tjørve 2006, Navarro 2010).

The additional energy requirements of African Penguins to prepare for moult and to recover from it were estimated by Waller (2011). These estimates were based on a 31% increase in mass prior to moult with the energetic value of these reserves estimated to be 30 kJ g^{-1}, a 47% mass loss during moult, and the energetic value of the protein to be regained after moult being 6 kJ g^{-1} (see Waller 2011 for details).

The small sample size limited the modelling we were able to do. We fitted the two-parameter model

Energy Expenditure = Time of Land × Rate on Land + Time at Sea × Rate at Sea

where the Energy Expenditure (kJ kg^{-1}) was estimated from the DLW experiment on the penguin, and the Time on Land (days) and Time at Sea (days) were estimated from the GPS logger tracking done simultaneously on the same penguin. The two unknowns, the Rate at Sea (kJ day^{-1} kg^{-1}) and the Rate on Land (kJ day^{-1} kg^{-1}), were estimated by the method of least squares from the birds for which both the DLW experiment and the GPS logger performed simultaneously. The calculations were done in programme R, using the linear regression model with the constant term omitted.

Our primary goal was to estimate the Family Energy Consumption (FEC, MJ) of a pair of adult African Penguins raising two chicks in a "normal" year:

FEC = 2×Adult Energy Consumption during breeding + 2×Chick Energy Consumption

To do this we used a 40-day incubation period with adults making foraging trips on alternative days, 25-day guard stage with foraging trips on alternative days, 50- day post-guard stage with daily foraging trips (Hockey et al. 2005). We used 11-hour foraging trips, an average adult mass 3.17 kg, and assimilation efficiency 0.76 (Cooper 1977, Nagy et al. 1986, Bouwhuis et al. 2007, Hockey et al. 2005).

RESULTS AND DISCUSSION

In the model

Energy Expenditure = Time on Land × Rate on Land + Time at Sea × Rate at Sea

We estimated the Rate on Land to be 361.6 kJ day^{-1} kg^{-1} (SE 110.2, t_5=3.28, P=0.0219) and the Rate at Sea to be 1491.2 kJ day^{-1} kg^{-1} (SE 393.6, t_5=3.778, P=0.0129). The model explained 98.3% of the variance in Energy Expenditure ($F_{2,5}$=208.1, P<0.001).

From these key values, we estimated the energy expenditure of two adults during a normal breeding year. As stated above, we assumed a 40-day incubation period with adults making foraging trips on alternative days, a 25-day guard stage with foraging trips on alternative days, a 50-day post-guard stage with daily foraging trips, 11-hour foraging trips, an average adult mass 3.17 kg, and an assimilation efficiency 0.76. The energy expenditure for both parents during the standard 115-day breeding period is estimated to be 790 MJ (i.e. 395 MJ per adult).

Bouwhuis et al. (2007) estimated the normal cost of raising a chick to be 116.5 MJ. Thus, for a pair of penguins the normal cost of raising a family of two chicks, from the start of incubation to fledging is estimated to be 1023 MJ (or 511.5 MJ per adult).

Assuming the entire diet during breeding to consist of Anchovy *Engraulis encrasicolus*, and the energetic value of Anchovy to be 6.74 kJ g^{-1} wet mass (Bachelor & Ross 1984), the amount of fish required to raise a family is 151.7 kg. Of this, 17.3 kg is fed to each chick, and each adult consumes 58.6 kg. Bouwhuis et al. (2007) estimated the fledging mass of chicks to be 2.83 kg. The overall "efficiency" of breeding is thus 3.73%; this is the ratio of the mass of chicks produced and the total mass of food consumed during the entire breeding attempt. The "efficiency" of chick growth is 16.4%; this is the ratio of mass of the chick and the total mass of food required to reach this mass.

In years of reduced food availability penguin chicks tend to grow more slowly, and the fledging period can be extended by 25 days to as long as 100 days. Rerunning the energetics calculations of Bouwhuis et al. (2007) with a Gompertz growth rate of 0.0302, results in a fledging period of 100 days, the total food requirements of a chick between hatching and fledging increases to 154.5 MJ, an increase of 33%. The maximum daily energy demand decreases from the value of 1787 kJ day^{-1} estimated by Bouwhuis et al (2007) to a recalculated value of 1615 kJ day^{-1}, a decrease of 10%. Thus extending the fledging has a cost of increasing the total amount of energy required by the chick by 33%, and reducing the maximum energy demand by 10%. Assuming that the extra 25 days of the fledging period is "post-guard", then the total energy consumption of the adult pair during the breeding period increases from 790 MJ to 973 MJ. Adding the energetic costs of rearing two chicks to fledging to this larger value, the energetic costs of a pair raising a family of two chicks in a year of reduced food availability is estimated to be 1282 MJ (equivalent to 190 kg of Anchovy).

These estimates for years of reduced food availability are based on the assumption that the average duration of feeding trips remains 11 hours. If these increase to 15 hours, then the total energy consumption of the adult pair increases to 1173 MJ, and the energetic costs of raising a family of two chicks further increases to 1482 MJ (220 kg Anchovy).

Returning to a normal breeding year, we can only make approximate estimates of energy requirements for the 240-day period outside of the breeding season. This is an absolute constraint, because the penguins are more-or-less continuously at sea, so DLW experiments are not possible. We assume that the moult duration on land is 21 days, and that the penguin is at sea for the remaining 229 days. During this at-sea period, no commuting is required, so the daily energy requirements are much less than the 1491 kJ day^{-1} kg^{-1} required at sea during the breeding period, but have to be substantially more than the 362 kJ day^{-1} kg^{-1} required per day on land, because of the energetic costs of heat production in cold water. For illustrative purposes, we have used a value of 895 kJ day^{-1} kg^{-1}, which is 60% of the estimated value during breeding. The energetic costs of 229 days at sea during the non-breeding, when no commuting is required, is thus estimated to be 854.6 MJ (= 229 days × 895 kJ day^{-1} kg^{-1} × 3.17 kg / 0.76 assimilation efficiency).

Likewise, during the 21-day period on land during moult, energy consumption must be larger than the value of 362 kJ day^{-1} kg^{-1} we estimated during incubation and brooding, because of the energetic costs of feather growth. This value is estimable using DLW methods. Unfortunately, none of the DLW experiments which we performed during moult produced meaningful results. We have assumed that the value is 50% higher, 542 kJ day^{-1} kg^{-1}. The energy expenditure of an adult of average mass of 3.17 kg during the 21-day moult period is thus provisionally estimated to be 36.1 MJ.

Waller (2011) estimated the additional energetic costs involved with increase in mass in preparation for moult and recovery of mass afterwards to be 29.2 MJ and 5.7 MJ respectively. The larger value for preparation is based on the fact that the reserves consist of both fat and protein, whereas the recovery involves mostly protein. The total cost of moult is thus estimated to be 71.0 MJ.

Thus the total energy costs outside the breeding season are estimated to be 926 MJ (855+71) per adult (137 kg Anchovy).

Thus finally, in a normal year the total energy requirements of one adult participating in the successful raising of two chicks is 1437 MJ $year^{-1}$ (=511+926) (or 213 kg Anchovy per year). The total annual energy requirements of pair of adult penguins successfully raising two chicks is thus estimated to be double this at 2874 MJ^{-1} (or 426 kg Anchovy per year). The analogous figure for a pair of Cape Gannets *Morus capensis* raising a single chick per year is 575 kg Anchovy per year (Navarro 2010); the cost of flight as a mode of transport is substantially higher than the cost of swimming.

The breeding colony at Dassen Island totalled 25 000 pairs in 2004. In order for each pair to have raised two chicks, they would have required a total of 3 793 tonnes of Anchovy (=151.7 kg × 25 000 pairs) over the 115 day breeding season. This represents an average of 33.0 tonnes day^{-1}. This would have had to be found within c. 20 km of the island. To put this figure in context, the Anchovy catch within this region averaged 9 047 tonnes $year^{-1}$ over the period 1998 to 2007 (DAFF pers. comm.).

The recruit spawner biomass survey (conducted in May each year, roughly the same time as the penguin colony census) averaged 172 000 tonnes of anchovy in this survey's Zone D (Cape Columbine to Cape Point) between 1998 and 2009 (the range was 2 200–516 000 tonnes). We treat the average as the biomass on a single day. In terms of the fact that the Anchovy are migrating south through Zone D, we envisage recruits entering Zone D at the north, and survivors (of fishing and predation by seabirds and seals) exiting at the south. Waller (2011) estimated that the average rate of southwards movement on Anchovy recruits must be of the magnitude of 2 km day^{-1}.

The length of Zone D is c. 250 km of coastline. If the anchovy were spread uniformly across this Zone (rather than in pulses), the density would be 688 tonnes km^{-1}. If all the Anchovy in a 40-km section of coastline adjacent to Dassen Island and symmetrically north and south of it were available to penguins, the estimated average biomass accessible daily is 27 250 t. At a rate of movement of 2km day^{-1}, Anchovy entering this section of coastline would be available to penguins for 20 days. Of the available biomass, 0.12% would be removed by penguins on a daily basis. From the inverse perspective, there is 834 times as much fish available as consumed. If the biomass of Anchovy were regarded as a standing stock, the penguins would remove 13.8% of it during the 115-day breeding season.

These calculations need to be seen as indicative, rather than as absolute. In particular, because of the enormous variability in the availability of fish, there might well be years when there is too little food. For example, if the Dassen Island penguin population of 2004 had encountered the year of minimum fish availability (2 200 tonnes), they would have had to remove 9.4% of the fish available each day. This is not sustainable, and breeding would have failed.

CONCLUSIONS AND RECOMMENDATIONS

The most valuable component of this analysis is probably not the fact that it provides us with an approach to estimate food requirements of breeding African Penguins, but that there is potential to estimate the ratio between food availability and food requirements. This is critical information for recommendations about the real food requirements of penguins. At present the results suggest that, on a daily basis, the total biomass of food around the island might need to be 500–1000 times larger than the biomass actually consumed by the population.

Another tentative conclusion of this analysis is that, in most years, food shortage during the breeding season, in itself, is not be the primary cause of the collapse of the penguin population. It is possible that the southward migration is pulsed so extremely that the gaps between shoals of Anchovy are so large that chicks starve during these periods. A hint of this is provided in the May 2005 recruit biomass survey: stratum D, Cape Columbine to Cape Point had only 2 200 tonnes of Anchovy; however stratum C, immediately to the north, was estimated to have had 297 000 tonnes of Anchovy at the same time, most of which would have passed through the penguin-accessibility zone around Dassen Island a month or two later.

Thus developing an understanding of the pattern of movement of Anchovy recruits seems to be critical to our understanding of the penguin collapse. The impact of fishing on the frequency and shape of the fish pulses is another aspect that needs to be studied. The ADU has already, to some extent, initiated this by undertaking GPS logging of penguins at the same time as small-scale and detailed surveys of fish around Robben and Dassen Islands takes place. These fish surveys are conducted by DAFF. There is a need to do these on a larger scale, with a larger number of GPS loggers deployed simultaneously with the fish surveys.

Although the fit of the fundamental model from which all our results are derived is excellent (98.3% of variance explained), it was based on a small sample of eight observations. Ideally the sample size should be increased, and preferably doubled.

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