Title
Annual energy budget and food requirements of breeding wandering albatrosses (Diomedea exulans)

Journal
Polar Biology, 27(4)

ISSN
0722-4060

Author
Shaffer, Scott A

Publication Date
2004-03-01

Peer reviewed

Short Note

Polar Biology (2004) 27: 253-256.

Annual Energy Budget And Food Requirements Of Breeding Wandering Albatrosses (*Diomedea exulans*)

SCOTT A. SHAFFER

Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California 95060, U.S.A.

Dr. Scott A. Shaffer
Department of Ecology and Evolutionary Biology
University of California Santa Cruz
100 Shaffer Road
Santa Cruz, CA 95060-5730 USA
Tel: 1.831.459.2691
Fax: 1.831.459.3383
E-mail: shaffer@biology.ucsc.edu

Abstract

Energy budgets form an integral part of our understanding of animal energetics, particularly when presented in the context of reproduction. In this paper, I created a time-energy budget for a breeding pair of wandering albatrosses (*Diomedea exulans*) to estimate the annual breeding costs and food requirements of the population at Possession Island, Crozet Archipelago. For a breeding cycle that lasts 356 days on average, a pair uses 2,733 MJ to raise a single chick to fledging. This estimate is 1.21 × higher than previously calculated for wandering albatrosses breeding at Marion Island. Unlike the current analysis, the previous study assumed that foraging costs were constant across all stages of the breeding cycle. Recent evidence shows that foraging costs vary during breeding for wandering albatrosses at Crozet and is probably true for all populations. Incubation costs have also been shown to be substantially lower than previously determined. Nonetheless, if a wandering albatross pair at Crozet uses a total of 2,733 MJ to breed, they would need to consume at least 1.7 kg bird^{-1} day^{-1} of fresh food on average to balance their own energy requirements and to provision a single chick for approximately 278 days. At this rate of food consumption, the breeding population at Crozet would consume approximately 340 metric tonnes of fresh food per breeding season.

Keywords: breeding, Crozet, *Diomedea exulans*, energy expenditure, food consumption, time-energy budget, Wandering albatross

Introduction

Pelagic seabirds (i.e. albatrosses and petrels) generally represent the extreme in avian breeding ecology because they exhibit prolonged breeding cycles, slow natal development, and low annual reproductive output (Lack 1968; Ricklefs 1990). These extreme life history characteristics are thought to have evolved from a variety of reasons such as the limitation of energy resources in the pelagic environment (Lack 1968; Ashmole 1971), or possibly physiological restraint exhibited by adults when breeding (reviewed in Hamer et al. 2002). Consequently, the level of energy used by parents for breeding activities and the associated food requirements to carry out these activities, has a significant impact on the success or failure of reproduction (e.g. Chastel et al. 1995; Tveraa et al. 1998; Weimerskirch 1999). The construction of time-energy budgets can therefore provide a useful tool for modeling the constraints that affect breeding performance in these birds as well as many other organisms. Food consumption can also be estimated from energy budget models (e.g. Furness 1978) and from direct measures of metabolism (Nagy et al. 1984; Gabrielsen et al. 1987; Nagy 1987). Overall, these estimates may be critical for evaluating how individuals or populations respond to variability in the supply and demand of energy resources (Nagy 1989), and they may provide information about the role that seabirds play as top predators in the marine environment.

The development of time-energy budgets depends on our ability to partition the cost of specific activities in relation to how animals function within their environment. Thus, as measurements of energy expenditure and related activity patterns are obtained, the accuracy of energy budget models can be improved. As an example, Adams et al. (1986) previously estimated the breeding costs of wandering albatrosses (*Diomedea exulans*) to be 2,263 MJ per pair per year (discounting the costs of the pre-egg laying stage). This energy budget was based on foraging costs of adult albatrosses measured during the chick-rearing period only, and thus assumed that foraging costs were constant across all reproductive stages (i.e. incubation, chick-brooding, and chick-rearing). More recently however, Shaffer et al. (2003) determined that foraging costs of wandering albatrosses were 10% higher during chick-brooding than during incubation. Other studies on wandering albatrosses (Salamolard and Weimerskirch 1993; Weimerskirch et al. 1997b; Weimerskirch and Lys 2000) have also shown that parents regulate energy flow to the nest throughout reproduction suggesting that energy expenditures of adults vary between reproductive stages. Lastly, the energetic costs at the nest during incubation in wandering albatrosses were shown to be 1.8 × lower than previously measured (Shaffer et al. 2001b). Given these more recent observations in breeding effort and overall performance, I constructed a time-energy budget for wandering albatrosses to re-evaluate the annual breeding cost and food requirements of this species. The results of the new energy budget predict that annual breeding costs of wandering albatrosses are 21% higher and food requirements are nearly 50% greater than previously reported.

Methods

Time-energy budgets were created for a pair of wandering albatrosses breeding on Possession Island (46°S, 52°E), Crozet Archipelago, southwestern Indian Ocean (hereafter called Crozet). Because wandering albatrosses are sexually size dimorphic (males are ~ 20% heavier; Tickell 1968; Shaffer et al. 2001c), time and energy of activities within each stage of breeding were totaled separately for each sex, and then combined for the pair. During breeding, wandering albatrosses undergo three stages which can be defined as: 1) egg incubation stage, 2) chick-brooding stage where either adult broods (and guards) a young chick at the nest, and 3) chick-rearing stage where an older chick is left alone at the nest while both adults forage at sea (Tickell

1968). Foraging costs during the incubation and chick-brooding stages were obtained from Shaffer et al. (2001a; 2003) and egg incubation costs were from Shaffer et al. (2001b). The cost of adults to brood a chick has not been measured directly, so I assumed that it was at least equivalent to the cost of incubation (Shaffer et al. 2001b). This assumption is reasonable because Bevan et al. (1995) observed no statistical difference in cost to adult Black-browed albatrosses (*Thalassarche melanophrys*) when incubating an egg or brooding a chick. The foraging costs of adults rearing chicks have not been measured at Crozet. However, Weimerskirch and Lys (2000) determined that wandering albatrosses rearing chicks alternate between long trips like those performed during incubation and short trips like those performed during chick-brooding. On average, males spend 59% of their time conducting short trips, whereas females spend 44% of their time conducting short trips, and time at the nest for either parent to provision a chick is less than 12 hours (Weimerskirch and Lys 2000). Therefore, I estimated the energetic cost of the chick-rearing period by assuming that the cost per day of adults foraging on long or short trips was equivalent to those measured during incubation or brooding stages, multiplied by the percentage of time each adult spent conducting either type of foraging trip. These costs were then amortized over a 246-day period, which is the average duration of the chick-rearing stage (Tickell 1968). Details of total costs and durations for each stage are summarized in Table 1.

Results and Discussion

If both wandering albatross parents provision their chick until it fledges (~356 days post laying; Tickell 1968), the combined total cost of breeding for the pair would be approximately 2,733 MJ (Table 1). This equates to average energy expenditures of 4,130 kJ day^{-1} for a 10.35 kg male and 3,548 kJ day^{-1} for an 8.25 kg female over the entire breeding cycle. The main difference in cost between male and female wandering albatrosses is attributed to sexual size dimorphism in this species and not to differences in parental effort (Shaffer et al. 2003). The annual breeding cost of 2,733 MJ for a wandering albatross couple is 1.21 × higher than previously estimated for wandering albatrosses breeding at Marion Island (46°S, 37°E), southwestern Indian Ocean (Adams et al. 1986). Several factors may explain the difference in breeding cost between the two estimates. Primarily, Adams et al. (1986) assumed that average energy expenditures of foraging adults were constant across incubation, chick-brooding, and chick-rearing though it was only measured during chick-rearing. A recent study showed that foraging costs of breeding adults were more variable (10% higher during chick-brooding compared to incubation) between reproductive stages at Crozet (Shaffer et al. 2003). Furthermore, other studies that examined breeding performance of wandering albatrosses at Crozet show that parental effort and body condition vary throughout breeding (Salamolard and Weimerskirch 1993; Weimerskirch et al. 1997b; Weimerskirch and Lys 2000). Thus at Crozet and probably other breeding locations (e.g. Kerguelen, Macquarie, Marion, Auckland, and South Georgia Islands), foraging costs of wandering albatrosses are not constant throughout the breeding cycle. This conclusion is also supported by similar research on other seabird species (e.g. Obst et al. 1987; Bevan et al. 1995; Bech et al. 2002).

The cost of incubation for wandering albatrosses breeding at Crozet has also been shown to be significantly lower (1.8 ×; Shaffer et al. 2001b) than measurements collected from adults at Marion Island (Brown and Adams 1984). The main difference in cost can be attributed to measurement technique (respirometry *vs*. doubly labeled water) and the duration over which energy expenditures were measured (Shaffer et al. 2001b). Thus, for a 78 day incubation period, the combined total cost for both adults would be 123 MJ (Table 1) compared to an estimate of 201 MJ reported earlier by Adams et al. (1986).

The difference in total breeding costs of wandering albatrosses at Crozet and Marion Islands could also be attributed to intrinsic variation between populations. However, the breeding populations at Crozet and Marion Islands are probably quite similar because both islands occur at the same latitude and are closer to each other (~1,200 km) than they are to other islands. Furthermore some immigration and emigration of albatrosses between each island has previously occurred (Weimerskirch et al. 1997a), and the foraging ranges of each population are well within that of the other (Weimerskirch et al. 1993; 1994). Therefore it seems unlikely that intrinsic differences could account for the discrepancies in breeding costs that I calculated compared to that reported earlier by Adams et al. (1986).

When evaluating the total energetic costs to adult wandering albatrosses during each stage in the breeding cycle, it is clear that chick-rearing is the most costly part of reproduction because it requires 246 days or 77% of the total duration of the breeding cycle (Fig. 1). However, even when the costs to adults are averaged over a daily basis (e.g. 2103×10^3 kJ ÷ [246 days × 2 adults] from Table 1), energy demand is higher during the chick-rearing stage compared to that of the brooding and incubation stages (Fig. 1). One factor that may contribute to the high cost of chick-rearing is that wandering albatrosses provision their chicks throughout the Antarctic winter when food is thought to be less plentiful and weather conditions are more extreme (Salamolard and Weimerskirch 1993). Nevertheless, wandering albatross adults compensate for the high cost of chick-rearing by regulating energy flow between themselves and their chicks using two foraging modes (i.e. alternating between short and long foraging trips; Weimerskirch et al. 1997b). Furthermore, adults have a large "safety margin" of energy reserves due to their body size (Weimerskirch and Lys 2000), which can buffer the impact of high energy demand and presumed low food availability during chick-rearing.

If the total annual energy budget of breeding wandering albatrosses is 2,733 MJ per pair, then a couple would need to consume 809 kg of food to satisfy the energy requirements of all activities (i.e. $2{,}733 \times 10^3$ kJ ÷ 3.38 kJ g^{-1}, assuming metabolizable energy yield is 3.38 kJ g^{-1} fresh mass; Adams et al. 1986). Chicks receive an additional 180-195 kg of food during the chick-rearing period (Weimerskirch and Lys 2000), so total food consumption of a wandering albatross pair breeding on Crozet would be ~1000 kg per breeding season. Considering that parents spend about 300 days at sea (356 days total – [39 days during incubation + 12 to 20 days during brooding]; see Table 1), the average daily food consumption of both adults over the entire breeding season would be about 3.4 kg day^{-1} per pair, or 1.7 kg day^{-1} per bird. This quantity of food slightly underestimates the rate of food consumption on single foraging trips as determined directly by stomach temperature sensors (2.1 ± 1.0 kg day^{-1} per bird; Weimerskirch et al. 1994), but it seems more reasonable than a rate of 1.1 kg day^{-1} per bird determined by Adams et al. (1986).

Finally, one of the major benefits of developing a time-energy budget is the ability to not only estimate food consumption for a breeding pair (above), but also to extrapolate food consumption for a breeding population. Possession Island in the Crozet Archipelago has an annual breeding population of 340 wandering albatross pairs (Weimerskirch et al. 1997a). Therefore, if a breeding pair consumes 1000 kg per season, the entire breeding population on Possession Island would consume approximately 340 metric tonnes of fresh food per breeding season.

Acknowledgements

I thank H. Weimerskirch, D. P. Costa, and two referees for providing comments on earlier drafts of the manuscript. Logistical and financial support came from the National Geographic Society (Grant No. 6346-98), National Science Foundation (awards INT-9873760 and IBN-9972651), and the Office of Naval Research (Award No. N00014-00-l-0880).

References

Adams NJ, Brown CR, Nagy, KA (1986) Energy expenditure of free-ranging Wandering albatrosses *Diomedea exulans*. Physiol Zool 59: 583-591

Ashmole NP (1971) Seabird ecology and the marine environment. In: Farner DS and King JR (eds) Avian Biology. Academic Press, New York, pp 223-286

Bech C, Langseth I, Moe B, Fyhn M, Gabrielsen GW (2002) The energy economy of the arctic-breeding Kittiwake (*Rissa tridactyla*): a review. Comp Biochem Physiol 133A: 765-770

Bevan RM, Butler PJ, Woakes AJ, Prince PA (1995) The energy expenditure of free-ranging black-browed albatrosses. Phil Trans R Soc Lon B 350: 119-131

Brown CR, Adams NJ (1984) Basal metabolic rate and energy expenditure during incubation in the wandering albatross (*Diomedea exulans*). Condor 86: 182-186

Chastel O, Weimerskirch H, Jouventin P (1995) Body condition and seabird reproductive performance: a study of three petrel species. Ecology 76: 2240-2246

Furness RW (1978) Energy requirements of seabird communities: a bioenergetics model. J Anim Ecol 47: 39-53

Gabrielsen GW, Mehlum F, Nagy KA (1987) Daily energy expenditure and energy utilization of free-ranging Black-legged kittiwakes. Condor 89: 126-132

Hamer KC, Schreiber EA, Burger J (2002) Breeding biology, life histories, and life history-environment interactions in seabirds. In: Schreiber EA, Burger J (eds) Biology of Marine Birds. CRC Press, Boca Raton, pp 217-261

Lack D (1968) Ecological adaptations for breeding in birds. Methuen & Co, London

Nagy KA (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol Monogr 57: 111-128

Nagy KA (1989) Field bioenergetics: accuracy of models and methods. Physiol Zool 62: 237-252

Nagy KA, Siegfried WR, Wilson RP (1984) Energy utilization by free-ranging Jackass penguins, *Spheniscus demersus*. Ecology 65: 1648-1655

Obst BS, Nagy KA, Ricklefs RE (1987) Energy utilization by Wilson's storm-petrel (*Oceanites oceanicus*). Physiol Zool 60: 200-210

Ricklefs RE (1990) Seabird life histories and the marine environment: some speculations. Col Waterbirds 13: 1-6

Salamolard M, Weimerskirch H (1993) Relationship between foraging effort and energy requirement throughout the breeding season in the wandering albatross. Funct Ecol 7: 643-652

Shaffer SA, Costa DP, Weimerskirch H (2001a) Behavioural factors affecting foraging effort of breeding wandering albatrosses. J Anim Ecol 70: 864-874

Shaffer SA, Costa DP, Weimerskirch H (2001b) Comparison of methods to evaluate energy expenditure of incubating wandering albatrosses. Physiol Biochem Zool 74: 823-831

Shaffer SA, Weimerskirch H, Costa DP (2001c) Functional significance of sexual dimorphism in wandering albatrosses, *Diomedea exulans*. Funct Ecol 15: 203-210

Shaffer SA, Costa DP, Weimerskirch H, (2003) Foraging effort in relation to the constraints on reproduction in free-ranging albatrosses. Funct Ecol 17: 66-74

Tickell WLN (1968) The biology of the great albatrosses, *Diomedea exulans* and *Diomedea epomophora*. Ant Res Ser 12: 1-55

Tveraa T, Saether B-E, Aanes R, Erikstad KE (1998) Body mass and parental decisions in the Antarctic petrel *Thalassoica antarctica*: how long should the parents guard the chick? Behav Ecol Sociobiol 43: 73-79

Weimerskirch H (1999) The role of body condition on breeding and foraging decisions in albatrosses and petrels. In: Adams NJ, Slotow RH (eds) Proceedings of the 22nd International Ornithological Congress. Bird Life South Africa, Durban, pp 1178-1189

Weimerskirch H, Brothers N, Jouventin P (1997a) Population dynamics of wandering albatross *Diomedea exulans* and Amsterdam Albatross *D. amsterdamensis* in the Indian Ocean and their relationships with longline fisheries: conservation implications. Biol Conserv 79: 257-270

Weimerskirch H, Cherel Y, Cuenot-Chaillet F, Ridoux V (1997b) Alternative foraging strategies and resource allocation by male and female wandering albatross. Ecology 78: 2051-2063

Weimerskirch H, Doncaster CP, Cuenot-Chaillet F (1994) Pelagic seabirds and the marine environment: foraging patterns of wandering albatrosses in relation to prey availability and distribution. Proc Roy Soc Lond B 255: 91-97

Weimerskirch H, Lys P (2000) Seasonal changes in the provisioning behaviour and mass of male and female wandering albatrosses in relation to the growth of their chick. Polar Biol 23: 733-744

Weimerskirch H, Salamolard M, Sarrazin F, Jouventin P (1993) Foraging strategy of Wandering albatrosses through the breeding season: A study using satellite telemetry. Auk 110: 325-342

Table 1 Time-energy budgets of breeding wandering albatrosses on Possession Island, Crozet Archipelago. The time and cost of feeding a chick at the nest during the chick-rearing period was assumed to be negligible because adults remain at the nest for less than one day on average (Weimerskirch and Lys 2000). Daily energy expenditure (DEE) is presented in kilojoules (kJ) and total energy expenditure (TEE) is presented in Megajoules (MJ). The body masses given are the average body masses of adult male and female wandering albatrosses (Shaffer et al. 2001a; 2003).

Reproductive Stage and Activity		Male (10.35 kg)	Female (8.25 kg)	Totals Per Pair
INCUBATION				
On Nest	Time (days)	39	39	78
	DEE (kJ day^{-1})	1,749	1,394	3,143
	TEE (MJ)	68.2	54.4	123
At Sea	Time (days)	39	39	78
	DEE (kJ day^{-1})	4,333	3,748	8,081
	TEE (MJ)	169	146	315
Totals	Time (days)	78	78	156
	TEE (MJ)	237	201	438
CHICK-BROODING				
On Nest	Time (days)	20	12	32
	DEE (kJ day^{-1})	1,749	1,394	3,143
	TEE (MJ)	35.0	16.7	51.7
At Sea	Time (days)	12	20	32
	DEE (kJ day^{-1})	4,844	4,127	8,971
	TEE (MJ)	58.1	82.5	141
Totals	Time (days)	32	32	64
	TEE (MJ)	93.0	99.0	192
CHICK-REARING				
At Sea (Short trips)	Time (days)	145	109	254
	DEE (kJ day^{-1})	4,844	4,127	8,971
	TEE (MJ)	702	450	1,152
At Sea (Long trips)	Time (days)	101	137	238
	DEE (kJ day^{-1})	4,333	3,748	8,081
	TEE (MJ)	438	513	951
Totals	Time (days)	246	246	492
	TEE (MJ)	1,140	963	2,103
TOTALS FOR BREEDING	Time (days)	356	356	712
	TEE (MJ)	1,470	1,263	2,733

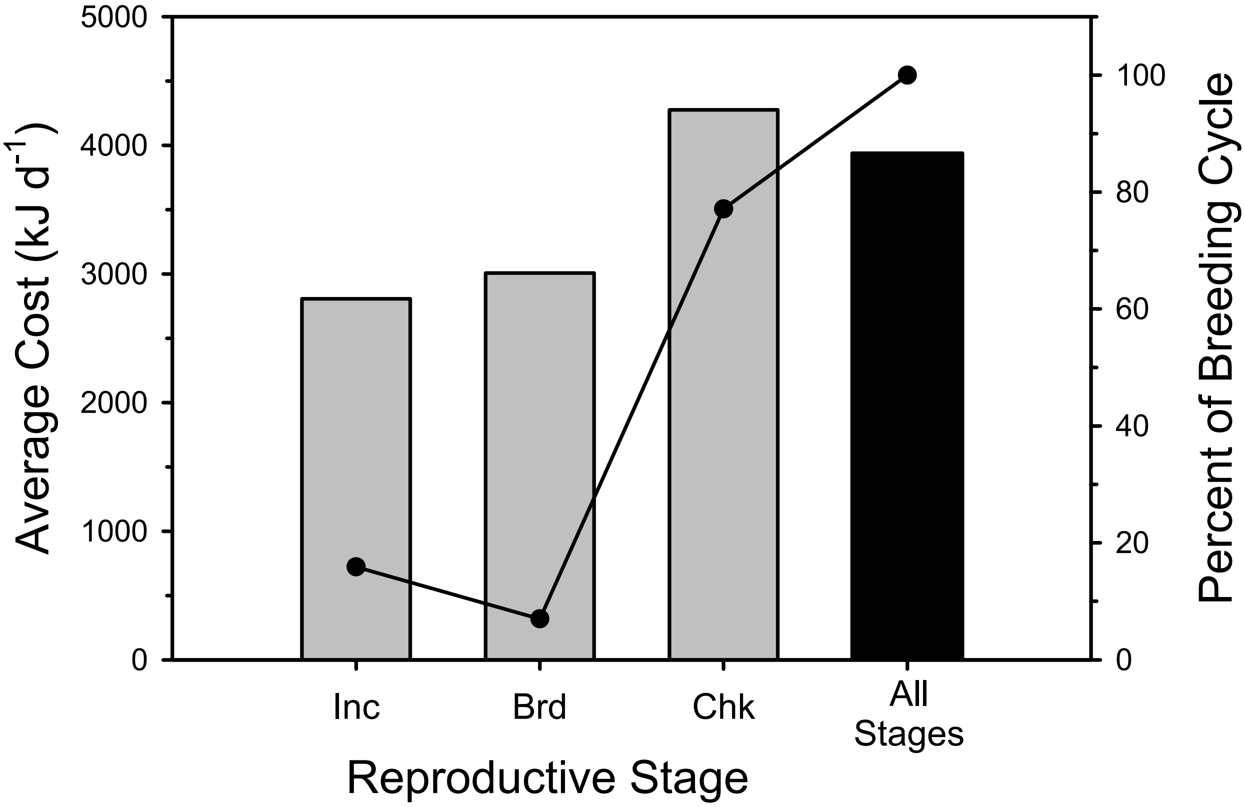

Fig. 1 The average cost per day and proportion of the total cycle duration for each breeding stage in wandering albatrosses at Crozet. The average cost for each stage (gray bars) and all stages combined (black bar) includes both time at sea and time on the nest for a breeding pair (see Table 1 and text for details). The breeding cycle includes the incubation (Inc), chick-brooding (Brd), and chick-rearing (Chk) stages.