

RESEARCH ARTICLE

Similar foraging energetics of two sympatric albatrosses despite contrasting life histories and wind-mediated foraging strategies

Caitlin E. Kroeger^{1,*}, Daniel E. Crocker², Rachael A. Orben³, David R. Thompson⁴, Leigh G. Torres⁵, Paul M. Sagar⁶, Lisa A. Sztukowski^{7,8}, Timothy Andriese⁹, Daniel P. Costa¹⁰ and Scott A. Shaffer⁹

ABSTRACT

Understanding the environmental and behavioral factors that influence how organisms maintain energy balance can inform us about their potential resiliency to rapid environmental changes. Flexibility in maintaining energy balance is particularly important to long-lived, central-place foraging seabirds that are constrained when locating food for offspring in a dynamic ocean environment. To understand the role of environmental interactions, behavioral flexibility and morphological constraints on energy balance, we used doubly labeled water to measure the at-sea daily energy expenditure (DEE) of two sympatrically breeding seabirds, Campbell (Thalassarche impavida) and grey-headed (Thalassarche chrysostoma) albatrosses. We found that species and sexes had similar foraging costs, but DEE varied between years for both species and sexes during early chick rearing in two consecutive seasons. For both species, greater DEE was positively associated with larger proportional mass gain, lower mean wind speeds during water take-offs, greater proportions of strong tailwinds ($>12 \text{ m s}^{-1}$), and younger chick age. Greater proportional mass gains were marginally more costly in male albatrosses that already have higher wing loading. DEE was higher during flights with a greater proportion of strong headwinds for grey-headed albatrosses only. Poleward winds are forecasted to intensify over the next century, which may increase DEE for grey-headed albatrosses that heavily use this region during early chick rearing. Female Campbell albatrosses may be negatively affected by forecasted slackening winds at lower latitudes due to an expected greater reliance on less energy efficient sit-and-wait foraging strategies. Behavioral plasticity associated with environmental variation may influence future population responses to climate change of both species.

KEY WORDS: Seabirds, Doubly labeled water, Field metabolic rate, Foraging behavior, Daily energy expenditure, GPS tracking, Life history

INTRODUCTION

Animals adjust their behavior to maintain homeostasis when energy costs become too great (Schneider, 2004), such as during extreme temperature or weather events (Wingfield, 2013). For example, Arabian oryx (*Oryx leucoryx*) shift to nocturnal foraging as environmental heat loads increase (Hetem et al., 2012) and little penguins (*Eudyptula minor*) increase dive frequency to locate dispersed prey after storm surges (Pelletier et al., 2012). However, if behavioral changes are energetically maladaptive (e.g. if increased dives do not increase foraging success; Berlincourt and Arnould, 2015), long-lived animals may favor self-maintenance over breeding, as predicted by life-history theory (Costa, 1991; Stearns, 1992), and populations may decline (Tuomainen and Candolin, 2011). Species with long-lived individuals depend on phenotypic (e.g. physiological or behavioral) plasticity to adjust to the rapid pace of climate change (Reed et al., 2011). Thus, studying behavioral strategies and environmental factors that can influence how individuals maintain energy balance may inform us about a population's short-term resiliency to rapid environmental changes.

Environmental factors can affect the energy balance of organisms in addition to intrinsic variability from factors such as breeding status or sex (Schneider, 2004; Wingfield et al., 2011). The problem of maintaining energy balance in a changing world is acutely relevant to breeding seabirds that face a multitude of climate-driven and human-induced environmental challenges (Croxxall et al., 2012; Daunt and Mitchell, 2013). Seabirds are central-place foragers, thus constrained by both time and distance when locating patchily distributed food during the energetically intensive breeding season (Ydenberg et al., 1994). Accordingly, when changes occur in the accessibility or abundance of resources, individuals can incur energy deficits that influence reproductive investment (Kitaysky et al., 2010; Suryan et al., 2006; Thorne et al., 2015; Weimerskirch, 2007). When individuals are near their energetic limits, extrinsic perturbations have a greater impact on energy balance and can affect reproductive success and survival (Elliott et al., 2014; Weiner, 1992). In some cases, however, external changes can be energetically beneficial. For example, wandering albatrosses (*Diomedea exulans*) showed improved energy intake and reproductive success from strengthening wind patterns that have reduced commute times to foraging habitat in the Southern Ocean (Weimerskirch et al., 2012).

The energetics of long-lived seabirds foraging at sea has been well studied, particularly in albatrosses that are well known for their energy-efficient soaring flight (Costa and Prince, 1987; Sachs et al., 2012; Shaffer et al., 2001a, 2004; Weimerskirch et al., 2000;

¹Department of Ocean Sciences, 1156 High Street, University of California at Santa Cruz, Santa Cruz, CA 95064, USA. ²Department of Biology, Sonoma State University, 1801 E Cotati Avenue, Rohnert Park, CA 94928, USA. ³Department of Fisheries and Wildlife, Oregon State University, 2030 SE Marine Science Drive, Newport, OR 97365, USA. ⁴National Institute of Water and Atmospheric Research Ltd (NIWA), 301 Evans Bay Parade, Hataitai, Wellington 6021, New Zealand.

⁵Department of Fisheries and Wildlife, Marine Mammal Institute, Oregon State University, 2030 SE Marine Science Drive, Newport, OR 97365, USA. ⁶National Institute of Water and Atmospheric Research Ltd (NIWA), 10 Kyle Street, Riccarton, Christchurch 8011, New Zealand. ⁷Marine Biology & Ecology Research Centre, Plymouth University, Plymouth PL4 8AA, UK. ⁸Department of Commonwealth of the Northern Mariana Islands, Department of Lands and Natural Resources, Division of Fish and Wildlife, PO Box 10007, Saipan, MP 96950. ⁹Department of Biological Sciences, San Jose State University, One Washington Square, San Jose, CA 95192, USA. ¹⁰Department of Ecology and Evolution, University of California Santa Cruz, Santa Cruz, CA 95062, USA.

*Present address: Farallon Institute, 101 H Street Suite Q, Petaluma, CA 94954, USA.

†Author for correspondence (ckroeger@faralloninstitute.org)

© C.E.K., 0000-0002-7797-4386; L.A.S., 0000-0002-1418-7211

Weimerskirch et al., 2005). However, few studies have integrated measures of daily energy expenditure (DEE) from related, sympatrically breeding species that exhibit contrasting foraging strategies and life histories across multiple breeding seasons (but see Antollos et al., 2017). Comparing the energetic cost of differing chick provisioning strategies from sister groups – and sexes within those groups – may highlight the relative efficiency of certain strategies. From this comparison of strategies, combined with examining energetic responses to environmental variability across years, we can improve our understanding of life-history patterns and which populations may be advantaged or disadvantaged when responding to forecasted environmental changes.

In this study, we measure the at-sea DEE of two congeneric seabird species with contrasting foraging strategies and life histories – the Campbell (*Thalassarche impavida*) and grey-headed (*Thalassarche chrysostoma*) albatrosses – during early chick rearing across 2 years. Campbell albatrosses are annually breeding neritic foragers with a population that steeply declined from 1996 to 1984 but showed an increasing trend until the last two decades (Sagar, 2014; Waugh et al., 1999c). Grey-headed albatrosses are biennially breeding oceanic foragers and the population on Campbell Island, New Zealand, has been in continuous decline since the 1940s, potentially as a result of environmental conditions (Waugh et al., 1999c). However, this decline has shown signs of stabilizing in the last two decades (Sagar, 2014). Our objective was to measure energetic costs of foraging across species, sexes and years, and to identify important behavioral and environmental factors that influence variations in DEE. We hypothesize that (1) the biennially breeding grey-headed albatrosses will have higher DEE, as high breeding costs are thought to cause a deferral of reproduction in favor of self-maintenance in the following year (Ryan et al., 2006), consistent with life-history theory, and (2) differences in DEE between years or sexes for both species are driven by environmental (e.g. wind speed or sea surface temperature) differences across years or foraging areas. This study illuminates the phenotypic plasticity of seabirds and identifies energetically expensive environmental conditions, enabling us to better anticipate population-level impacts of environmental changes.

MATERIALS AND METHODS

Ethics statement

Field research was carried out under the following approvals and permits: San Jose State University Institutional Animal Care and Use Committee Protocol no. 976 and New Zealand Wildlife Act Permit no. SO-26385-FAU. Blood samples were imported into the USA for analysis using permits issued by the United States Department of Agriculture Animal and Plant Health Inspection Service (USDA-APHIS; 119370).

Study species and site

Campbell albatrosses, *Thalassarche impavida* (Mathews 1912), and grey-headed albatrosses, *Thalassarche chrysostoma* (Forster 1785), were studied during the guard stage (early chick rearing) in December 2011 and 2012. Both species breed in adjoining colonies at Bull Rock located on the north cape of Campbell Island (52°S, 169°E), New Zealand Subantarctic territory. Pairs raise one chick per breeding season and, for 3 weeks post-hatch, mates alternate between foraging trips at sea and guarding the nest (Warham, 1990). Each season, up to 20 Campbell and 20 grey-headed albatrosses were sampled to measure DEE, foraging behavior and mass gain (Table 1).

Table 1. Sample sizes for each species and year to depict data usage

	Campbell albatrosses		Grey-headed albatrosses	
	2011	2012	2011	2012
Initial sample size	17	20	14	20
Missing tracks, only TBW estimated	0	1	2	0
Missing tracks, DEE estimated	1	3	0	0
DLW technique failure	5	1	2	4
Final sample size (male/female)	11 (6/5)	15 (8/7)	10 (7/3)	16 (11/5)

Individuals without tracks or final samples were still used to estimate total body water (TBW) and for predictive equations in the single-sample method. If tracking data were missing but departure and arrival times were recorded, individuals were still used for estimates of daily energy expenditure (DEE). Birds with doubly labeled water (DLW) technique failure were excluded from the estimation of TBW and DEE.

Field procedures

Nest attendance was monitored starting in late incubation to obtain pre-trip fasting durations. Mates were differentiated using non-toxic, temporary livestock paint sprayed on the breast feathers. After eggs hatched, an adult from each pair was captured just before departure to sea. A background blood sample was collected (0.5–1 ml) from a tarsal or brachial vein with a 22-gauge needle and 1 ml syringe then transferred into dry spray-coated lithium heparin blood collection tubes (BD Vacutainer plastic in 2011; BD Vacutainer glass in 2012). Doubly labeled water (DLW; 1.8 ml) containing 0.9% NaCl with 42.15 atom percent excess (APE) ^{18}O and 5.39 MBq g^{-1} ^3H (2011) or 43.70 APE ^{18}O and 5.91 MBq g^{-1} ^3H (2012) or 43.87 APE ^{18}O and 5.91 MBq g^{-1} ^3H (also 2012) was then injected intraperitoneally (2011) or intramuscularly (2012). Syringes containing DLW were weighed before and after injection on the same surface using a portable balance. Prior to each weight, the same empty syringe was weighed for calibration. Annually, a subset of six to eight birds from each species were contained for an equilibration period of 90 min (Shaffer et al., 2001b), after which a second blood sample was obtained for the calculation of total body water (TBW) (Nagy and Costa, 1980). This subset approach allowed us to use the single-sample method of determining TBW on the remaining birds to minimize disturbance and potential changes in natural behaviors (Schultner et al., 2010; Speakman, 1997).

After DLW injection, birds were weighed using a spring-loaded Pesola scale (to nearest 25 g). To calculate an index of body size for estimating body condition, the minimum bill depth, maximum bill length and tarsus length were measured with calipers to the nearest 0.02 mm, and a relaxed wing chord was measured using a wing chord ruler from the bend in the wrist to the tip of the primaries to the nearest 1 mm. To measure foraging behaviors, GPS devices [igot-U, GT-120 (2011) or GT-600 (2012), Mobile Action Technology Inc.], were secured to dorsal feathers with Tesa cloth tape. All devices were removed from their original plastic casing and waterproofed with heat-shrink tubing before deployment (total package mass <32 g with tape) and each recorded a position at 10 min (2011) or 5 min (2012) intervals. Once birds returned from foraging trips, they were captured and a final blood sample (final 1) was collected to measure isotope turnover (Lifson and McClintock, 1966). Birds were weighed to measure mass change and GPS devices were removed. For birds that remained on the nest for another 24–48 h guarding the chick, an additional mass measurement and a second final blood sample (final 2) were collected.

In December 2011, samples were packaged and stored in a cool location (approximately 10°C) until they could be frozen (−20°C) in

January 2012. The following year, blood samples were stored in a cooler with icepacks until they could be transported (within 1–6 days) to a solar-charged battery-powered freezer (-15°C , Waeco CF18 fridge/freezer). Samples were then stored at -80°C in January 2013. All samples were transported from New Zealand to the USA on dry-ice and subsequently stored at -80°C .

Estimates of energy expenditure

Laboratory analysis

Whole blood samples were used because samples could not be centrifuged before red blood cells lysed. A portion of each sample was distilled using a variation of the freeze-capture method (Ortiz et al., 1978) and the distillate was measured in triplicate in 7 ml EcoLite(+) scintillation cocktail (MP Biomedicals, Solon, OH, USA) with a scintillation spectrometer (Beckmann LS3801) to determine specific activity of the ^3H isotope. The specific activity of the ^{18}O isotope was measured by isotope-ratio mass spectrometry (Metabolic Solutions, Nashua, NH, USA).

Calculation of total body water, pool sizes and water flux

Total body water was calculated from the dilution space of the ^{18}O isotope using an equation from Nagy (1983; see their Appendix I) to account for changes in percentage of TBW across the foraging trip (Shaffer et al., 2006). This was compared against the dilution space from the ^3H isotope to assess the percentage of error (^3H typically overestimates the body water pool by about 4%; Nagy and Costa, 1980; Shaffer et al., 2006; Speakman, 1997). The plateau approach was also used to estimate the ^{18}O and ^3H dilution spaces of the isotopes with eqn 17.11 from Speakman (1997). The percent mass approach was used to estimate final 1 and final 2 TBW (Speakman, 1997). The dilution space ratio of each bird and the ratio of mean isotopic turnover rates of ^3H to ^{18}O were calculated to ensure reliable estimates of CO_2 production, and any birds that had dilution space ratios outside 0.97–1.1 or turnover rate ratios outside 0.5–0.9 were excluded from further energetics calculations (Table 1; Speakman, 1997). For single-sampled birds, the initial isotope enrichments and pool sizes were estimated from linear models derived from the two-sample birds using initial body mass and moles of injectate as predictors (Speakman, 1997). Water influx and efflux ($\text{ml kg}^{-1} \text{ day}^{-1}$) were calculated using eqns 4 and 6, respectively, from Nagy and Costa (1980).

Calculation of CO_2 production

CO_2 production ($\text{ml g}^{-1} \text{ h}^{-1}$) was calculated using a one-pool method: eqn 2 from Nagy (1980). Nagy's (1980) one-pool equation was used for analyses because this method adjusts for changes in water space and is potentially more accurate for species that have higher elimination rates, which is probable for seabirds foraging in the ocean and ingesting seawater with prey (Shaffer, 2011; Speakman and Hambly, 2016). This approach has also been used in other studies of albatross energetics (Antolos et al., 2017; Shaffer et al., 2001a, 2003), which facilitated comparison with this previous research. Nevertheless, results derived from Speakman's (1997) one-pool method are also reported. To account for periods of inactivity after release and before recapture (Costa and Prince, 1987; Shaffer et al., 2001a), all estimates of CO_2 production were corrected using on-nest CO_2 production derived from subtracting the CO_2 production calculated with final sample 2 from the CO_2 production calculated with final sample 1. The average on-nest CO_2 production for each species was applied in the following equation for the birds without final sample 2 to calculate at-sea CO_2 production: $(\text{total } \text{CO}_2 \text{ production} \times \text{total time} - \text{nest-only } \text{CO}_2 \times \text{total nest time}) / \text{total at-sea time}$. Total nest time was determined by

subtracting the GPS-determined at-sea time from the total time from injection to the final sample.

Calculation of daily energy expenditure

Production of CO_2 was converted to a measure of DEE (kJ day^{-1} ; Gessaman and Nagy, 1988). This was calculated using a conversion factor of 26.74 J ml^{-1} (grey-headed albatross) or 26.58 J ml^{-1} (Campbell albatross) (Adams et al., 1986; Costa and Prince, 1987). These constants were created based on the protein (P), lipid (L) and carbohydrate (C) composition of fecal DNA relative read abundance derived diet from breeding Campbell albatrosses consisting of approximately 40% fishes, 37% jellyfish, 22% crustacea and 1% cephalopod (McInnes et al., 2017), and a combination of stomach content and temperature-logger derived diets from grey-headed albatrosses consisting of approximately 72% squid, 25% jellyfish and 3% fish (Cattray et al., 2004a; Waugh et al., 1999b). The energy equivalents of CO_2 were approximated using the dry mass of nutrients per 100 g of diet (see equation for birds in appendix B of Gessaman and Nagy, 1988). The dry masses of nutrients from each dietary component were weighted by relative proportions in the species-specific diet, and then summed. The dry masses of P, L and C that were used, respectively, for each dietary component were: 53.3 g P, 37.1 g L and 5.2 g C for fish (Lenky et al., 2012); 57.9 g P, 32.9 g L and 0.7 g C for squid (Eder and Lewis, 2005); 16.5 g P, 0.5 g L and 0.9 g C for jellyfish (Doyle et al., 2007); and 8.2 g P, 14.0 g L and 3.5 g C for crustacea (Holland and Walker, 1975). Cost of flight was then calculated for each species following Costa and Prince (1987) as: $[\text{DEE}_{\text{at-sea}} - (\% \text{ trip on water} \times \text{mean DEE}_{\text{on-nest}})] / (1 - \% \text{ trip on water})$.

Sex determination

Bird sexes were identified from background blood samples by amplification of the sex chromosomes using polymerase chain reaction (PCR) methods described in Quintana et al. (2008) with minor modifications. The molecularly determined sexes matched 99% of observation-based estimates of sex when both adults of a pair were present and sexual size dimorphism was apparent; however, these observations are not likely to be more accurate than the molecular methods as copulation or egg-laying was not observed. For birds without background blood samples ($N=3$), sex was assigned with discriminant function analyses using post-foraging mass, minimum bill depth and wing chord morphometric data (Dechaume-Moncharmont et al., 2011). The Campbell albatross data were supplemented with molecularly sexed birds from a previous study ($N=37$; Sztukowski et al., 2017). Box's M -tests confirmed homogeneity of the variance-covariance matrices of the morphometric measurements for each species ('biotools'; da Silva et al., 2017). Discriminant function analysis correctly assigned the sex of Campbell albatrosses 79% of the time with a cut-off of 0.10 ($N=68$), and correctly assigned the sex of grey-headed albatrosses 87% of the time with a cut-off of 0.30 ($N=31$; regression equations in Kroeger et al., 2019).

Morphometrics

Wing loading

Wing traces were used from 10 random individuals of each species to calculate wing loading and wing aspect ratios (Pennycuik, 2008). Surface area of the wing was determined following the methods of Shaffer et al. (2001a), with the exception that the mean shoulder width (19.5 cm, $N=20$) of black-browed albatrosses, *Thalassarche melanophrys*, breeding on Kerguelen Island (49°S , 70°E) was used to estimate the root-box (S.A.S., unpublished data) as these data were

not collected for grey-headed and Campbell albatrosses from this study. In addition, mean masses of grey-headed and Campbell albatrosses were used to calculate wing loading.

Body condition

The body condition of birds from each species was determined after increasing the sample size with measurements from additional field seasons (Campbell albatross: $N=68$; grey-headed albatross: $N=121$). Morphometric measurements (minimum bill depth, maximum bill length and tarsus) were reduced with principle components analysis into a single body size index (Shaffer et al., 2001c) taken from the scores of the first principal component (PC1 explained 59% variance in Campbell albatrosses and 64% variance in grey-headed albatrosses; 'biotools'; da Silva et al., 2017). Body condition was calculated from the residuals of body mass on PC1 (i.e. size-corrected mass) as this index has been shown to be a better predictor of total lipids in Procellariiformes with high percentage body lipids (Jacobs et al., 2012).

Foraging behavior

Before calculating foraging trip metrics, raw GPS data were filtered to remove points that produced speeds $>150 \text{ km h}^{-1}$ and rediscritized at 10 min intervals ('adehabitatLT'; Calenge, 2006). A high cut-off speed was chosen based on the ability of albatrosses to gain fast ($>127 \text{ km h}^{-1}$), sustained travel speeds during storm events (Catry et al., 2004b). Points over land were identified (ArcGIS) to separate on-land and at-sea behaviors and were excluded from further analyses along with any points at the beginning of trips that overlapped with doubly labeled water equilibration periods. Foraging trip metrics (i.e. total trip duration, maximum range, total distance and mean ground speed) were then calculated. Density utilization maps were created after removing transit points (classification described below) to map foraging areas using a smoothing factor of 1.5% (33.9 km) and cell size of 0.2% (4.5 km) of the mean X and Y data spatial extents, allowing us to optimize visualization at any scale ('adehabitatHR'; Calenge, 2006; Fig. 1).

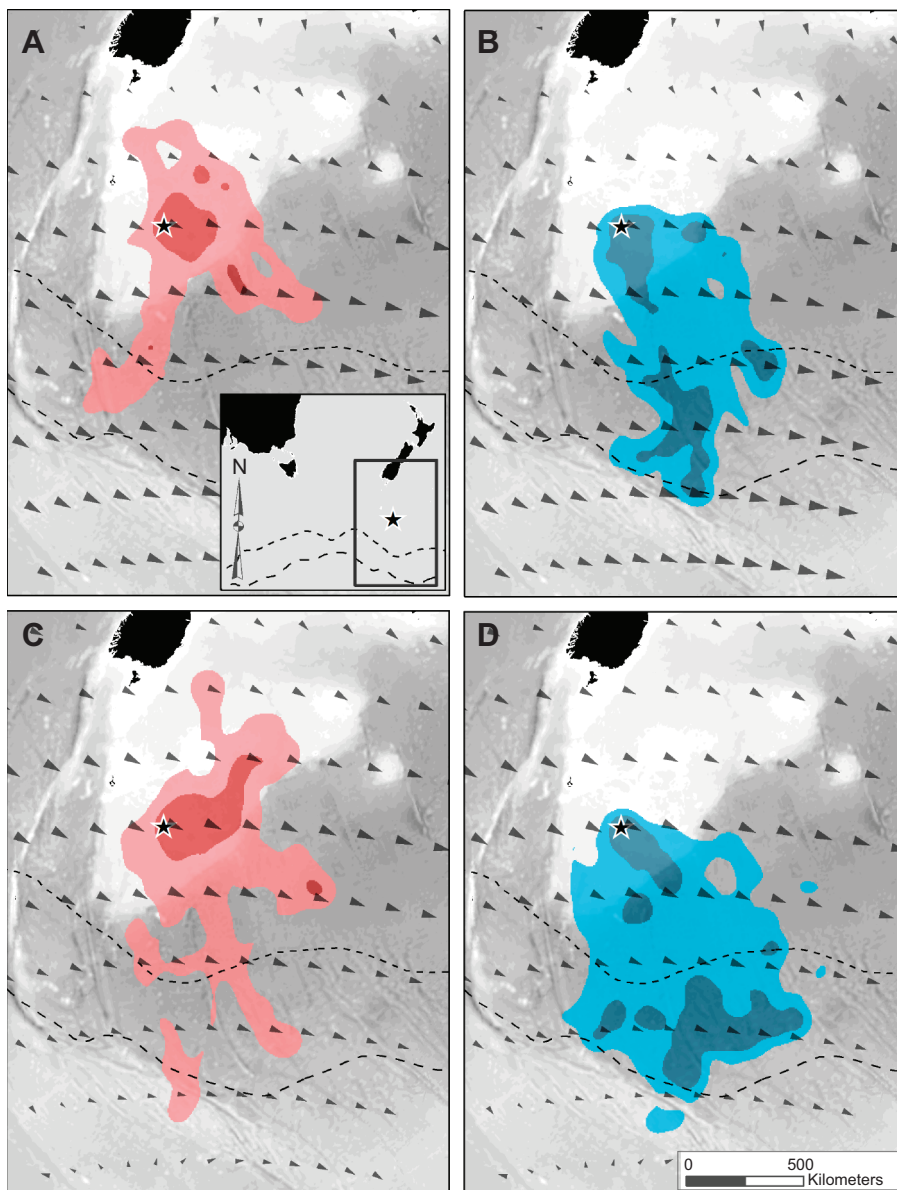


Fig. 1. Kernel density estimates depicting foraging patterns during the guard stage for Campbell and grey-headed albatrosses in 2011 and 2012. Campbell albatross density is shown in red; grey-headed albatross density shown in blue. Top panels: 2011; bottom panels: 2012. Arrowheads depict monthly (December) wind direction and speed, measured at 1000 mb atmospheric pressure from a base period of 1971 to 2000, with the size of the arrow head scaled to the magnitude of the wind speed. The dashed lines delineate the Subantarctic (upper) and Polar (lower) Fronts. The black star represents breeding colony on Campbell Island. Inset is provided for orientation on the globe. Map boundaries: 45°S to 65°S and 157.5°E to 172.5°W.

To classify behavioral states at sea, data points corresponding to area restricted search (ARS), rest and transit were identified using the residence space and time (RST) method with dynamically scaled radii as described by Torres et al. (2017). To correct potentially misidentified resting points, all points with speeds $<5 \text{ km h}^{-1}$ were assigned as rest. During the guard stage, albatrosses typically only rest on the water after landing for a feeding event because take-offs are energetically expensive (Shaffer et al., 2001a; Weimerskirch et al., 2000). The proportion of time spent on the water during a foraging trip was calculated using all rest locations divided by the total number of locations. The number of daily take-offs from the water, which we equated to foraging effort as defined by daily water landings, were calculated from the number of transitions from rest to ARS or transit divided by the length of the foraging trip in days. Foraging effort is relative rather than absolute because successive water landings can occur within 10 min intervals (Weimerskirch and Guionnet, 2002). Foraging success was determined by the proportion of mass gained relative to the birds' initial body mass.

Environmental metrics

Wind and sea surface temperature data extraction

Ocean surface wind vectors (meridional and zonal at 10 m altitude) and sea surface temperature (T_{SS}) were extracted at 31 km grid cell and 3 h resolution from the ERA5 climate re-analysis dataset along the albatross tracks. At the recorded mean maximum bird ground speed ($\sim 25 \text{ m s}^{-1}$) from this study, an albatross should have at least one point within gridded datasets.

Wind and sea surface temperature interactions

First, the bearing of each bird between consecutive locations was calculated ($a=6378137$, $f=1/298.26$; *bearing*, 'geosphere'; <https://CRAN.R-project.org/package=geosphere>). Bird ground speed was reduced to vector components and the bird air speed was then calculated as described by Shamoun-Baranes et al. (2007). The bearing of the wind towards each bird location was calculated in degrees as $180 \times (1 + \text{atan2}(u, v) / \pi)$, where u and v are wind components in the east and north direction, respectively. The bearing of the wind towards the bird relative to bird flight direction was then calculated as the wind bearing subtracted from the bird bearing with 360 added to values <0 . The angle of the wind on the bird was converted to a single side of the bird (0 to 180 deg) for assessment of wind effects from head to tail irrespective of the side of the bird, and the mean angle was calculated (*circular.mean*, 'circular'; <https://r-forge.r-project.org/projects/circular/>). The magnitude of flight compensation for the wind compared with drift was estimated for transit states as described by Tarroux et al. (2016).

The percentage of strong headwinds experienced during the trip was calculated as the proportion of winds $>12 \text{ m s}^{-1}$ and from 330 to 360 deg and 0 to 30 deg during flight (ARS and transit states). The percentage of strong tailwinds was similarly calculated, but for angles between 150 and 210 deg. The percentage of light winds was calculated using speeds less than 5 m s^{-1} at any angle. The percentage of crosswinds was calculated for all wind speeds at angles between 60 and 120 deg and 140 and 300 deg. Finally, the mean T_{SS} experienced was calculated from periods of contact with the water (i.e. rest).

Statistical analysis

Differences in energy expenditure, foraging behavior and environmental conditions between species and years were tested with three-way ANOVAs. Interaction terms were removed when not

significant and three-way ANOVAs were re-run to report F -statistics and P -values. Differences in the mean angle of the wind on the bird were tested separately for each term with circular ANOVAs ('circular'). For the linear ANOVAs, residuals were visually inspected for normality and heteroscedasticity. Where assumptions of normality were violated, variables were log transformed (DEE, water influx, initial body mass), Box-Cox power transformed (^{18}O percentage TBW, mean air flight speed, mean T_{SS} at rest; *boxcox*, 'MASS'; Venables and Ripley, 2002), or analysed using a gamma distribution (pre-trip fasting, post-trip nest time; 'gamlss'; Rigby and Stasinopoulos, 2005). In the case of proportion variables with high zero frequency (percentage light winds, percentage strong head/tailwinds), a compound Poisson-gamma distribution was used ('tweedie'; Dunn and Smyth, 2008). Welch's two-sample t -tests were used to compare body condition indices across years for each species, and paired t -tests were used to assess changes in body condition after foraging. Power analysis was used to determine the difference in DEE between species that would be significant ($P=0.05$) at 80% power (*pwr.2p2n.test*, 'pwr'; <https://CRAN.R-project.org/package=pwr>).

DEE (kJ day^{-1}) was regressed on: foraging metrics (foraging duration, daily distance, maximum range, daily take-offs, percentage rest on water, mean flight air speed), environmental metrics (mean wind speed at take-off, percentage light winds, percentage strong headwinds, percentage strong tailwinds, percentage crosswinds, mean wind bearing on bird, wind-drift compensation magnitude, mean T_{SS}) and morphometrics (body condition before and after foraging, percentage body mass gain) with species, year and sex as factors (lm , base R 3.3). Highly correlated variables and variables with variance inflation factors (VIF) >4 were removed backwards stepwise from a base linear model (*vif*, 'car'; Fox and Weisberg, 2011). The number of daily landings and percentage light wind were negatively correlated with mean take-off wind speed; thus, the former two were removed. Body condition after foraging, daily distance, maximum range, mean wind speed and mean flight air speed were also removed. The remaining variables were placed into a global model that was automatically subset to generate a list of models (*dredge*, 'MuMIn'; <https://CRAN.R-project.org/package=MumIn>). A model was selected from the list using *model.avg* on a subset with ΔAIC less than 2. After selecting the most important variables, continuous and binary interactions were tested. A model was selected based on lowest AICc scores and greatest weights. A second model was run with the addition of chick age, time on nest before departure and duration of previous foraging trip, and these results are presented separately from the first model due to sample size reduction ($N=52$ to $N=47$). Any variables identified as important in the second model were tested in the first, and vice versa, and the AIC scores and weights were evaluated again to refine the final models. Residuals from each model were visually assessed to meet assumptions of normality and homoscedasticity. All analyses were run in R 3.1.0 and R 3.3.3 (<https://www.R-project.org/>) unless stated otherwise. R packages are delimited with apostrophes and functions are italicized.

RESULTS

Final sample sizes for each species by field season and sex are provided in Table 1. Mean chick age during initial sampling was 2.6 days older in grey-headed albatross compared with Campbell albatross (Table S1). Time fasting on the nest before trips was equivalent across species, sex and years (Table S1). Time on the nest after foraging before capture was also equivalent across species, sex and years (Table S1).

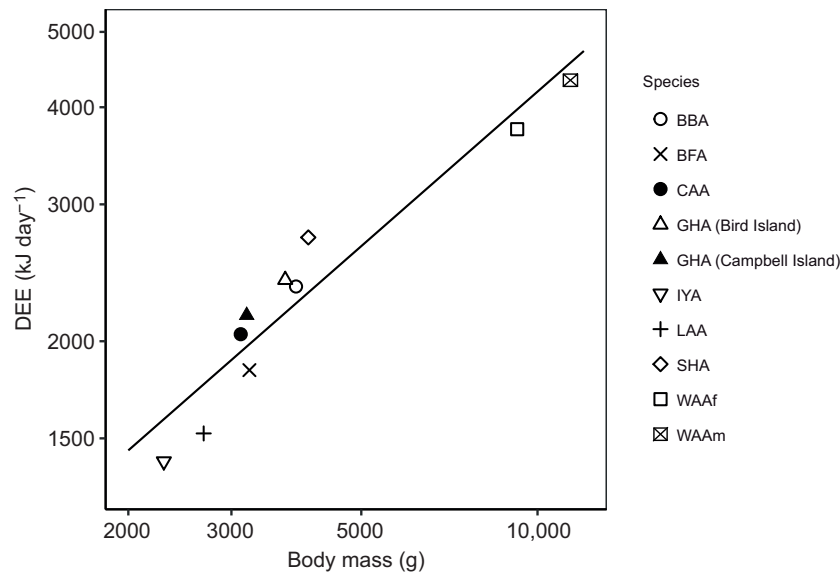


Fig. 2. Updated allometric relationship between body mass and daily energy expenditure for albatross species on logarithmic scale. Regression line includes: black-browed (*Thalassarche melanophrys*, BBA), black-footed (*Phoebastria nigripes*, BFA), Campbell (*Thalassarche impavida*, CAA), grey-headed (*Thalassarche chrysostoma*, GHA Bird Island and GHA Campbell Island), Indian yellow-nosed (*Thalassarche carteri*, IYA), Laysan (*Phoebastria immutabilis*, LAA) and shy albatrosses (*Thalassarche cauta*, SHA), and female and male wandering albatrosses (*Diomedea exulans*, WAAf and WAAm; see appendix A in Shaffer, 2011 and Antolos et al., 2017). The allometric equation is $DEE = 0.98 + 0.66 \times \text{body mass}$.

Total body water, water flux and energy expenditure

The effect of species on TBW varied by year and sex, with highest estimated total body water in male grey-headed albatrosses in 2012 (60%) and the lowest estimated in female Campbell albatrosses in 2012 (50%; Table S1). Moreover, male grey-headed albatrosses had 8% lower TBW in 2011 compared with 2012 (Table S1). These TBW values are consistent with previously reported ranges in *Thalassarche* albatrosses (Antolos et al., 2017; Costa and Prince, 1987; Shaffer et al., 2004). Water influx rate was higher in grey-headed albatrosses by 32% (63 ml day^{-1}) in 2012 compared with 2011, and by 26% (54 ml day^{-1}) compared with Campbell albatrosses in 2012 (Table S1). There were no significant differences in water influx rate between years in Campbell albatrosses, between species in 2011, or between sexes (Table S1).

The mean DEE of both species were above the regression line for the allometric equation for smaller albatrosses (Fig. 2; adjusted from Antolos et al., 2017): mean DEE was $2039 \pm 571 \text{ kJ day}^{-1}$ ($655 \pm 172 \text{ kJ kg}^{-1} \text{ day}^{-1}$) for Campbell albatrosses and $2163 \pm 672 \text{ kJ day}^{-1}$ ($684 \pm 223 \text{ kJ kg}^{-1} \text{ day}^{-1}$) for grey-headed albatrosses. Mean DEE was 29% higher for Campbell albatrosses in 2011 compared with 2012 and 23% higher for grey-headed albatrosses in 2011 compared with 2012, but was similar between species and sex (Table S1). Power analysis determined that a difference of $491 \text{ kJ kg}^{-1} \text{ day}^{-1}$ would have been required to detect a significant difference between species at 80% power. The power to detect the observed difference was low at 0.11; however, a logistically challenging sample size of 340 individuals from each group would have been required. Campbell and grey-headed albatross field metabolic rates (FMR) at sea were both 2.2 times greater than their estimated basal metabolic rates (BMR; Ellis and Gabrielsen, 2002; Fig. 3) and, respectively, 2.1 and 2.2 times greater than FMR on the nest.

Morphometrics

Grey-headed albatrosses had greater wing loading than Campbell albatrosses (118 versus 109 N m^{-2} ; $t = -2.7$, d.f. = 12.4, $P = 0.019$). Likewise, estimated mean aspect ratio of grey-headed albatrosses was higher than Campbell albatrosses (14.3 versus 13.5 ; $t = -3.6$, d.f. = 11.9, $P = 0.004$).

Within both Campbell albatrosses and grey-headed albatrosses, pre-foraging and post-foraging body condition (size-corrected mass) did not differ across years ($P > 0.05$). Post-foraging body

condition was greater than pre-foraging condition only in Campbell albatrosses in 2011 ($t = -4.0$, d.f. = 10, $P = 0.003$).

Foraging behaviors

Campbell albatross foraging was primarily concentrated over the Campbell Plateau northeast of Campbell Island in both years, with some foraging extending over deeper waters southward towards the Subantarctic Front (Fig. 1A,B). The maximum range for individuals was similar across years, but Campbell albatrosses – particularly females – traveled less daily distance in 2011 with slower airspeeds

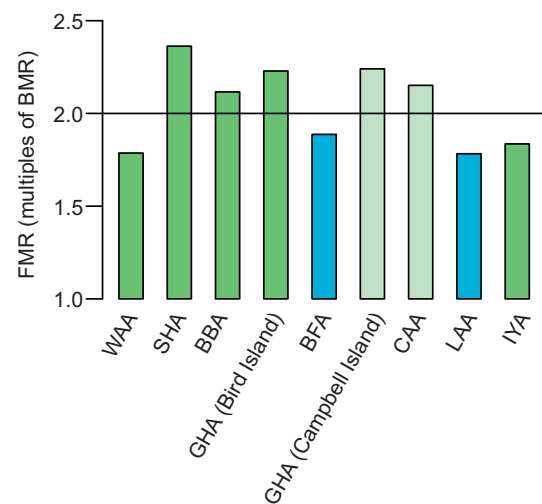


Fig. 3. Relative differences in energy expenditure across albatross species based on expressing field metabolic rate as a multiple of basal metabolic rate. FMR, field metabolic rate; BMR, basal metabolic rate. The horizontal line at 2BMR represents the mean ratio across species. Bars are ordered by body mass from largest to smallest. Blue bars represent albatrosses breeding in the North Pacific and green bars represent those breeding in the Southern Ocean. Light green bars represent albatrosses from this study. The figure includes: wandering (*Diomedea exulans*, WAA), shy (*T. cauta*, SHA), black-browed (*T. melanophrys*, BBA), grey-headed (*T. chrysostoma*, GHA from Bird Island and Campbell Island), black-footed (*P. nigripes*, BFA), Campbell (*T. impavida*, CAA), Laysan (*P. immutabilis*, LAA), and Indian yellow-nosed albatrosses (*T. carteri*, IYA; see Appendix A; Shaffer, 2011 and Antolos et al., 2017).

than in 2012 (Table S2). Additionally, in 2011 Campbell albatrosses performed 45% more daily water take-offs and spent a greater percentage of their foraging trip on the water (48 versus 25% in 2012; Table S2) and gained less mass as a proportion of their pre-trip body mass (1.8 versus 10% in 2012; Table S1). Moreover, females spent 30% more time on the water than males in 2011, despite a similar number of take-offs and proportional mass gain (Tables S1 and S2).

Grey-headed albatross foraging was concentrated southeast near the shelf of the Campbell Plateau and between the Subantarctic and Polar Fronts (Fig. 1C,D). The maximum range for individuals was similar between years, but grey-headed albatrosses traveled shorter daily distances in 2011 with slower air speeds (Table S2). In 2011, only slightly more daily water take-offs were detected, and birds spent a greater percentage of their foraging trip on the water (34% versus 19%; Table S2). Proportional mass gain was also lower for grey-headed albatross in 2011 (11% versus 18% of pre-trip body mass; Table S1). In contrast to Campbell albatrosses, female grey-headed albatrosses spent less time on the water and had the fastest air speeds compared with males, despite similar take-offs and proportional mass gain (Tables S1 and S2).

For both species and years, males had further maximum ranges and longer foraging trips than females (Table S2). In both years, grey-headed albatrosses exhibited greater trip duration, daily distance, maximum range, air speed and proportional mass gain compared with Campbell albatrosses (Tables S1 and S2). In 2011, Campbell albatrosses performed significantly more daily water take-offs than grey-headed albatrosses and spent a larger portion of their foraging trips on the water (Table S2).

Environmental metrics

Mean wind speeds encountered by Campbell and grey-headed albatrosses were, respectively, 2.2 and 1.3 m s⁻¹ higher in 2012 compared with 2011. Female grey-headed albatrosses encountered greater mean wind speeds than female Campbell albatrosses (2.3 m s⁻¹ higher average), but windspeeds experienced by males did not differ between species (Table S3). Correspondingly, wind speeds during water take-offs were lowest for female Campbell albatrosses in 2011 and highest for female grey-headed albatrosses in 2012 (Table S3). There were no significant differences in the proportions of strong headwinds experienced across species, sex or

year. However, female Campbell albatrosses experienced almost zero strong tailwinds, while female grey-headed albatrosses experienced the greatest, although the amount was minimal at 2% (Table S3). The mean proportion of light winds experienced varied between species depending on year and sex: female Campbell albatrosses experienced twice the mean amount of light winds during flight of all individuals during 2012 (9.1%), while male Campbell albatrosses experienced almost no light winds during flight (0.4%; Table S3). The mean proportion of crosswinds in flight was lowest for female Campbell albatrosses at only 18% in 2011 compared with roughly 48% for female grey-headed albatrosses in 2011 (Table S3).

The mean bearing of the wind on birds during flight was consistent between species, sexes and years, with birds primarily experiencing crosswinds (Table S3). No significant differences or interactions between species, sex and year were found in the magnitude of compensation for the wind during transit (Table S2).

Mean T_{SS} encountered by birds on the water was lower for grey-headed albatrosses by about 2°C (Table S3). Mean T_{SS} at rest for all individuals ranged from 3.2 to 9.4°C; however, female Campbell albatrosses did not travel to waters below 4°C, unlike male Campbell albatrosses.

Factors influencing daily energy expenditure

Linear models were tested to identify factors that influenced DEE, and two final models are presented. Model 1 has a larger sample size ($N=52$) but does not include chick age. When chick age was included in Model 2, the sample size was reduced ($N=47$). In Model 2, younger chicks were associated with greater DEE in adults (Table 2). Year had the largest effect in both models, with higher DEE in 2011 (Table 2), although this effect was largely influenced by male albatrosses in 2011 (Fig. 4A). There were no significant interactions of year with any other variable. Mass gain positively affected DEE in both models, with males marginally expending more energy to achieve higher proportional mass gain than females in Model 2 (Fig. 4B). Species had no main effect on DEE, but the effect of the proportion of high headwinds on DEE depended on species, with a positive relationship observed only in grey-headed albatrosses (Table 2; Fig. 4C). Species also interacted with mean take-off wind speed in Model 1 (Table 2). In this model, mean take-off wind speed did not significantly affect DEE in Campbell

Table 2. Linear model assessing factors influencing DEE during early chick rearing

	Model 1 ($N=52$)		Model 2 ($N=47$)	
	Standardized β	Centered β coefficient	Standardized β	Centered β coefficient
Year	-0.74 [¶]	-919 (-1182, -655) [¶]	-1.08 [‡]	-1380 (-1640, -1120) [¶]
Sex	-0.44 [‡]	-547 (-871, -224) [‡]	-0.38 [‡]	-784 (-1070, -501) [‡]
Species	-0.62	-71.3 (-281, 138)	-0.35 [‡]	-39.3 (-221, 142)
Chick age	n.a.	n.a.	-0.50 [¶]	-63.5 (-83.4, -43.5) [¶]
Mass gain (%)	0.42 [§]	26.0 (14.3, 37.6) [§]	0.66 [¶]	41.5 (27.4, 55.6) [¶]
High headwind in flight (%)	-0.29 [‡]	-106 (-182, -29.7) [*]	0.06	24.7 (-46.9, 96.3)
High tailwind in flight (%)	—	—	0.33 [§]	122 (58.1, 186) [§]
Mean wind speed at take-off	0.09	27.2 (-46.7, 101)	-0.36 [§]	-106 (-158, -53.7) [§]
Year: sex	0.42 [‡]	597 (208, 987) [‡]	0.56 [§]	825 (467, 1180) [§]
Mass gain (%): sex	—	—	-0.38 [*]	-25.1 (-44.1, -6.21) [*]
High headwind in flight (%): species	0.80 [¶]	430 (299, 561) [¶]	0.52 [¶]	282 (167, 397) [¶]
Mean wind speed at take-off: species	-1.30 [‡]	-157 (-259, -55.2) [‡]	—	—
Intercept	0.00 [¶]	2770 (2530, 3020) [¶]	0.00 [¶]	3080 (2860, 3310) [¶]
R^2 (adjusted R^2)	0.59 (0.49)		0.78 (0.72)	
Residual standard error	429		338	
F statistic	5.96 (d.f.=10, 41) [¶]		11.5 (d.f.=11, 35) [¶]	

The dependent variable was DEE (kJ day⁻¹). Model 85% confidence intervals are given in parentheses. * $P<0.1$; [‡] $P<0.05$; [§] $P<0.01$; [¶] $P<0.001$. n.a., not applicable.

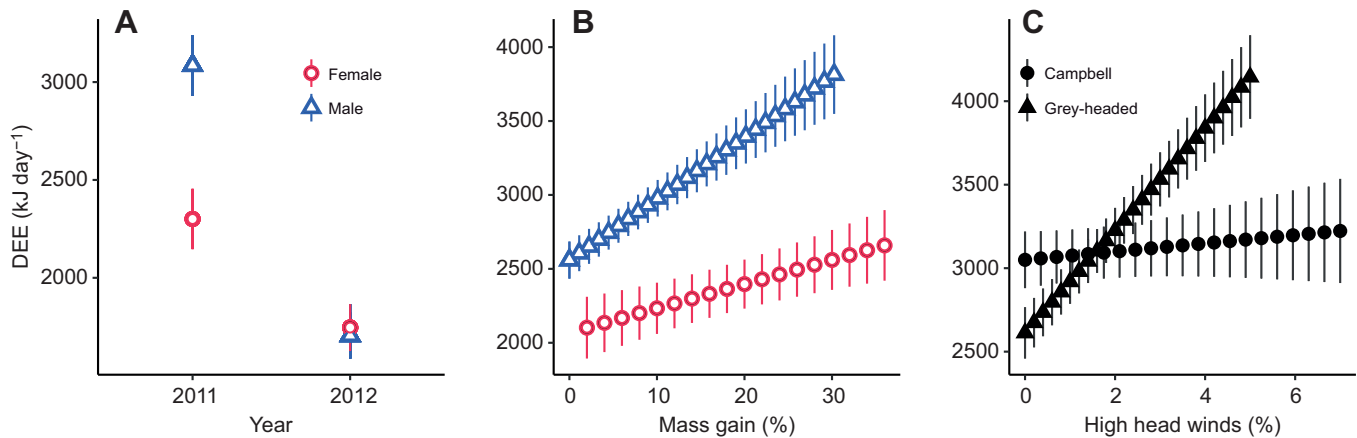


Fig. 4. Interaction plot depicting predicted daily energy expenditure regressed against year by sex, mass gain as a percentage of pre-foraging body mass by sex and the proportion of high headwinds during foraging by species. DEE was fitted from the Model 2 (Table 2) function using (A) grey-headed albatrosses, (B) grey-headed albatrosses in 2011 or (C) males in 2011 and the means of the remaining independent variables in the model (predict function, R 3.3). The trend in plot C is representative of each year and species as these factors did not differ in slope, only intercept. Likewise, the trend in plot B is representative of each sex and year as slopes did not differ; however, the intercept for males was lower than females for both species in 2012 (and both intercepts in 2012 were lower than 2011). Bars represent standard error of the fit.

albatrosses (estimate=27.3, s.e.=50.4, $t=0.54$, $P=0.59$; ‘interactions’ package, R 3.3) but, relative to Campbell albatrosses, DEE was higher at low take-off wind speeds and lower at high take-off windspeeds for grey-headed albatrosses (Fig. 5). Finally, the proportion of high tailwinds positively influenced DEE in Model 2 (Table 2).

DISCUSSION

Campbell and grey-headed albatrosses exhibited similar DEE while foraging during the guard-stage, including when physiological, behavioral and environmental conditions were considered. This

outcome was unexpected based on the contrasting life-history patterns of these species, as biennial instead of annual breeding is suggested to result from the need to recover body condition after higher breeding costs resulting from time and energy deficits (Jouventin and Dobson, 2002; Ryan et al., 2006). We note that it is possible that a difference (>491 kJ day $^{-1}$) was not detected due to our low sample size. However, significant annual differences in DEE were detected at this sampling magnitude. Biennially breeding grey-headed albatrosses also had greater wing loading due to both morphological differences and greater proportional mass gains at sea, which we expected to contribute to higher foraging costs in lower wind fields. However, these birds are probably aided by the use of favorable wind fields associated with their preferred foraging location along the Antarctic Circumpolar Current (Fig. 1; Wakefield et al., 2009; Weimerskirch et al., 2000), including high wind speeds at take-off that influenced lower DEE. Male albatrosses of both species expended more energy to achieve high proportional mass gain compared with females with similar proportional mass gains. Again, this result is consistent with greater wing loading in male albatrosses (Phillips et al., 2004; Shaffer et al., 2001c). However, we found that males had higher DEE in 2011 when their mass gain was lower than that observed in 2012. DEE was higher in 2011 overall (for both species and sexes), consistent with more daily take-offs and lower take-off wind speeds during foraging. High headwinds and tailwinds both increased DEE, but greater proportions of high headwinds had a greater effect on DEE in grey-headed albatrosses despite similar proportions experienced by both species. Finally, grey-headed albatross parents had older chicks when sampled pre-trip, and parents with older chicks expended less energy while foraging, but the cost associated with achieving higher mass gains (e.g. greater food loads) may explain why DEE was not lower than observed for Campbell albatrosses.

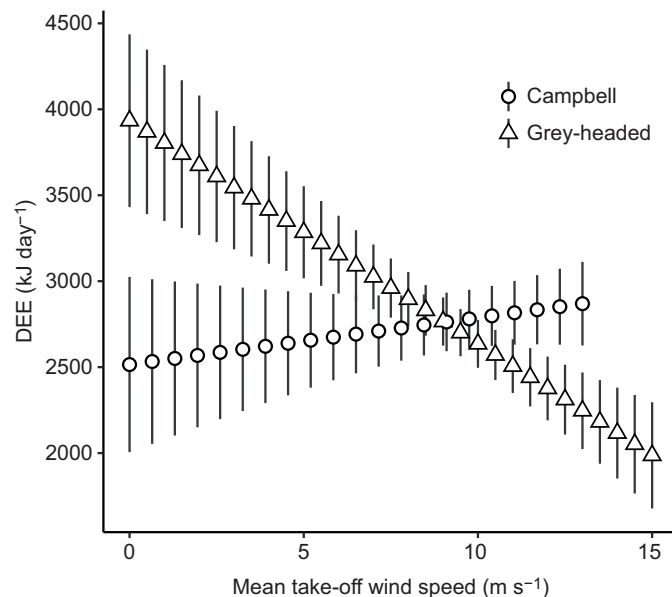


Fig. 5. Interaction plot depicting predicted daily energy expenditure regressed against mean take-off wind speed by species. Daily energy expenditure (DEE) was fitted from the Model 1 (Table 2) function using male albatrosses in 2011 and the means of the remaining independent variables in the model (predict function, R 3.3). The trend is representative of each sex and year as these factors did not differ in slope, only intercept. Bars represent standard error of the fit.

Species differences in daily energy expenditure

Campbell and grey-headed albatrosses had similar energy expenditures at sea compared with other *Thalassarche* species relative to both body size and BMR (with the exception of the much smaller Indian yellow-nosed albatross, *Thalassarche carteri*, which appear to be even more economical; Figs 2 and 3). Campbell and

grey-headed albatrosses had similar absolute and mass-corrected DEE during guard-stage foraging trips due to similarities in mean body mass. Both species had smaller mean body mass and lower absolute DEE at sea than late chick-rearing grey-headed albatrosses from Bird Island (Costa and Prince, 1987) and incubation-stage black-browed albatrosses from Kerguelen Island (Shaffer et al., 2004). These differences in mass and absolute DEE could be a result of breeding stage (Shaffer et al., 2003); however, incubating Campbell albatrosses (Kroeger et al., 2019) are still 24% smaller in mass than incubating black-browed albatrosses (Shaffer et al., 2004), and grey-headed albatrosses on Campbell Island are known to be smaller than conspecifics elsewhere (Waugh et al., 1999a). Moreover, grey-headed albatrosses from Bird Island and black-browed albatrosses have more energy-dense diets than the respective Campbell Island species (Clarke and Prince, 1980; McInnes et al., 2017; Waugh et al., 1999b; Xavier et al., 2003), which should produce larger individuals with greater energy requirements. The absolute energy requirements of black-browed albatrosses may contribute to their near-absence from breeding on Campbell Island relative to the endemic Campbell albatross (ACAP, 2009), especially if black-browed albatrosses do not raise young as successfully on lower energy income. This could be tested by measuring DEE from guard-stage black-browed albatrosses breeding on Campbell Island for a more direct comparison, if a sufficient sample size could be found.

The similar guard-stage costs of Campbell albatrosses and grey-headed albatrosses on Campbell Island were inconsistent with our predictions based on their differing life histories and foraging strategies. Biennial breeding is thought to result, in part, from higher breeding costs associated with traveling further distances to forage, which extends the breeding season and leaves little time to recover body reserves before breeding again (Dobson and Jouventin, 2010; Jouventin and Dobson, 2002). Indeed, grey-headed albatrosses travel further distances during the guard stage, but breeding duration for this species overlaps with the annually breeding Campbell albatrosses (chick rearing lasts approximately 116–152 versus 130 days, respectively (ACAP, 2010; Moore and Moffat, 1990) and is shorter than other annual breeders (Jouventin and Dobson, 2002). Therefore, similar foraging costs during the guard stage suggest that poorer food quality or higher energy deficits incurred during other breeding stages (e.g. incubation or late chick-rearing) or post-breeding may affect the breeding frequency of grey-headed albatrosses (Crossin et al., 2013). Grey-headed albatrosses in 2012 were leaner (higher total body water in males) and also had higher water influx than Campbell albatrosses, suggesting prey with lower energy density (e.g. greater proportions of salps). Grey-headed albatrosses primarily forage on squid that contain four to six times less calcium and less energy than the krill and fish (Clarke and Prince, 1980) typically consumed by annual breeders (Hedd and Gales, 2001; Waugh et al., 1999b). However, grey-headed albatross chicks grow at faster rates and fledge at greater body mass than Campbell albatross chicks (Moore and Moffat, 1990). Grey-headed albatross parents forage in predictable, strong westerly winds that probably offset wing loading and reduce the cost of larger food loads that may compensate for lower quality (Table S1; Weimerskirch et al., 2012). A greater allocation of energy to chicks rather than self-maintenance, however, may necessitate a longer self-recovery period or influence feather molt timing, which could interfere with breeding frequency (Edwards, 2008; McNamara and Houston, 2008). Additionally, calcium limitation within the adult could delay egg production and lead to biennial breeding (Edwards, 2008; McNamara and Houston, 2008).

Morphology and foraging success

Higher lipid reserves in guard-stage Campbell albatrosses relative to grey-headed albatrosses could be associated with wing loading differences (this study and Warham, 1977), where lower wing loading in Campbell albatrosses allows for accessing more energy-dense prey in lighter winds further north during the incubation stage (Furness and Bryant, 1996; Louzao et al., 2014; Sztukowski, 2015; Wakefield et al., 2009). The proportion of light winds experienced varied by species, sex and year, but female Campbell albatrosses generally experienced the greatest proportion of lighter winds. Their DEE, however, was less affected by light winds at take-off, perhaps because lower wing loading reduced effort relative to male Campbell albatrosses and grey-headed albatrosses under these conditions. Campbell albatrosses also have lower aspect ratios that increases maneuverability in lighter winds and may aid in foraging efficiency (Pennycuik, 2008; Phillips et al., 2004; Rayner, 1988). We were unable to directly test the effect of wing loading because we did not have wing measurements from individuals that were sampled for energy expenditure. However, differences in wing loading between species probably has a functional significance (e.g. flight costs) given that wing morphologies are believed to restrict the breeding ranges of other albatross species (Suryan et al., 2008).

The DEE of both Campbell and grey-headed albatrosses is higher relative to body mass compared with other albatross species (Fig. 3), as expected from Southern Ocean species that forage in more productive waters than North Pacific albatrosses (Antolos et al., 2017; Shaffer, 2011). Species that can gain more energy should be willing to expend more energy (Jodice et al., 2006). However, individuals that gain more mass relative to their body size will also expend more energy due to increased wing loading unless foraging in stronger winds where heavier loads increase flight stabilization and costs can be offset (Pennycuik, 1982; Warham, 1977). Indeed, grey-headed albatrosses recovered a higher proportion of their pre-foraging body mass – as might be expected from this species that consistently traveled further distances to the windy and nutrient-rich Subantarctic Front – yet they did not expend more energy than Campbell albatrosses. Within species and years, albatrosses with higher proportional mass gain exhibited greater DEE, especially males, suggesting that structurally smaller females with lower wing loading can gain more proportional mass at less cost in similar wind conditions. Given within-year effects of mass gain, it is notable that both species gained significantly more proportional mass in 2012 when DEE was lower. Foraging behaviors, wind interactions or factors not measured, such as preferred prey abundance, are likely important drivers of yearly differences in foraging efficiency.

Foraging behaviors

Individuals that took off from the water in higher wind speeds expended less energy, consistent with the effect of take-offs on energy expenditure observed in other albatrosses (Sakamoto et al., 2013; Shaffer et al., 2001a; Weimerskirch et al., 2000). When take-off wind speeds were lower, individuals performed more water landings, spent more time resting on the water, had lower foraging success and expended more energy (Tables S1 and S2). Gaining less mass with more water landings and performing more landings in energetically expensive wind speeds are somewhat counterintuitive because birds should limit landings to when food is located to conserve time and energy during chick rearing (Shaffer et al., 2001a; Weimerskirch et al., 2000). In 2011, Campbell albatrosses that had the highest mean take-off rates also spent a greater proportion of their total trip on the water, possibly because certain prey types required more surface time to exploit before resuming aerial searching (Weimerskirch, 2007;

Weimerskirch and Pinaud, 2007). These individuals may have consumed smaller or less energy-dense prey types such as jellyfish (McInnes et al., 2017) and employed a sit-and-wait strategy to conserve energy while optimizing net energy gain (Connors et al., 2015; Louzao et al., 2014). In 2011, albatrosses may have employed this strategy if lower wind speeds reduced in-flight search efficiency and take-off efficiency (Spear and Ainley, 1997; Wakefield et al., 2009; Weimerskirch et al., 2000). Furthermore, when take-off wind speeds were higher, individuals may have spent less time on the water during feeding events, which could have led to under-represented landing frequencies given the sampling interval (10 min) of the GPS loggers in this study. Thus, mean wind speed at take-off may be a more reliable predictor of DEE than the number of take-offs when sampling intervals are potentially greater than landing intervals.

Environmental interactions

In addition to the effects of proportional mass gain and take-off wind speed, DEE was also affected by the proportion of strong headwinds during flight ($>12 \text{ m s}^{-1}$). Strong headwinds can offset flight direction and potentially force more energetically expensive corrective maneuvering (Louzao et al., 2014; Tarroux et al., 2016; Wakefield et al., 2009), particularly in species with higher wing aspect ratios like grey-headed albatrosses. Grey-headed albatrosses also encountered higher mean wind speeds than Campbell albatrosses (Table S3), so the proportion of strong headwinds encountered should be costlier. Albatrosses are known to use looping flight paths while transiting to foraging destinations (Weimerskirch et al., 2000) – keeping the wind at low-cost angles – but time and space constraints during early chick-rearing can limit the use of efficient flight strategies (Kroeger, 2019). Accordingly, DEE was higher when the proportion of strong headwinds was higher for grey-headed albatrosses compared with Campbell albatrosses under the same model conditions. Furthermore, although the consequences of strong tailwinds on soaring seabirds has received less attention (but see Alerstam et al., 2019; Spear and Ainley, 1997) and most cost models do not include this effect (Felicísimo et al., 2008; Louzao et al., 2014; Raymond et al., 2010), we found that a greater proportion of strong tailwinds was also energetically costly for both species. This cost may result from light wing loads while transiting from the nest to foraging grounds that are primarily downwind (Fig. 1), as this transit occurred when strong tailwinds could be most destabilizing to flight due to reduced body mass (Alerstam et al., 2019).

The influence of chick age

Although the sample size decreased when chick age was considered, DEE was found to be lower in parents rearing older chicks. Sampling occurred at roughly the same duration after a foraging trip, but those with larger chicks were probably able to offload more food to their chick before recapture, weighing and re-sampling (Huin et al., 2000). Partially, or even fully, digested food in the forestomach may not fully equilibrate with total body water (Ricklefs et al., 1986). Thus, it is conceivable that body water pool sizes were over-estimated relative to the concentration of isotopes in the blood at the time of weighing. This effect would inflate the estimates of metabolic rate in adults with younger chicks. However, in 2012, individuals that were more successful foragers and probably retained more stomach contents at the time of re-sampling (Huin et al., 2000) had lower DEE that year. Hence it is more likely that as chicks age, food delivery is less frequent, allowing parents to use more energy-efficient foraging strategies to obtain food and maintain homeostasis (Weimerskirch and Lys, 2000; Weimerskirch et al., 2003).

Implications and future directions

Overall, we were able to link a suite of behavioral, morphometric and environmental measures to variations in DEE in two sympatric southern albatross species. Although grey-headed albatrosses had greater foraging success and similar energy expenditure to Campbell albatrosses, their primary prey source and guard-stage body reserves indicate that grey-headed albatrosses may incur greater self-maintenance costs consistent with their life history as biennial breeders. Future changes in prey availability are thus an important consideration for future modeling efforts as climate change is expected to affect productivity in the Southern Ocean (Constable et al., 2014). In addition, wind fields are projected to weaken towards lower latitudes while becoming stronger towards higher latitudes (Lovenduski and Gruber, 2005; Thompson and Wallace, 2000), which may reduce foraging opportunities for some species (this study) while enhancing opportunities for others (Weimerskirch et al., 2012). A decrease in wind strength in lower latitudes where Campbell albatrosses range (Lovenduski and Gruber, 2005) could entail more individuals using a less energetically efficient sit-and-wait strategy. In contrast, an increase in wind strength at higher latitudes where grey-headed albatrosses range (Lovenduski and Gruber, 2005) could increase flight costs. Understanding the factors that influence the DEE of animals, such as changing wind fields, is essential for assessing the vulnerability of species in the face of climate change. This information is also crucial for management efforts, especially as species less tolerant to environmental perturbations may require management to reduce more remediable stressors (Cooke et al., 2013).

Acknowledgements

We thank the New Zealand Department of Conservation for permitting this project and providing logistical support; Henk Haazen and crew for providing safe transportation to and from Campbell Island; Joy Sagar for field assistance; Kyle Morrison, Ray Bucheit and Rob Dunn for field support; Jen Jelincic for laboratory analysis assistance; Jonathan Felis for geographic information system mapping; and Rachel Holser for providing thoughtful feedback on initial drafts of the manuscript. We also thank Jeff Pentel and the numerous people listed in the funding section for their generous financial donations that made this work possible.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: C.E.K., D.E.C., D.P.C., S.A.S.; Methodology: C.E.K.; Formal analysis: C.E.K., D.E.C., S.A.S.; Investigation: C.E.K., D.E.C., R.A.O., P.M.S., L.A.S., T.A.; Resources: D.E.C., D.R.T., L.G.T., P.M.S., L.A.S., T.A., S.A.S.; Writing - original draft: C.E.K.; Writing - review & editing: D.E.C., R.A.O., D.R.T., L.G.T., P.M.S., L.A.S., D.P.C., S.A.S.; Visualization: C.E.K.; Supervision: S.A.S.; Project administration: D.R.T., L.G.T.; Funding acquisition: D.R.T., L.G.T., P.M.S.

Funding

This work was supported by the New Zealand Ministry of Business, Innovation and Employment (contract CO1X0905); MARES program (grant FPA 2011-0016); American Ornithologists' Union; Earl H. and Ethel M. Myers Oceanographic and Marine Biology Trust; Jim Brown Award; San José State University Graduate Student Research Award; and crowd-source funding from Experiment.com (individual donors: Jeff Pentel, Wayne Sentman, Jill Marketos Milburn, Laura Wagner, Mark Kroeger, David Thompson, Sadie Birdfeather, Jen Jelincic, Amy Lush, Paul Richard Wagner, Lucius Bono, Scott Shaffer, Beth Flint, Anita Phagan, Cassie Marketos, Anne Cassell, Dan Saltman, Sandra Machado, Herma Van Gerner, Annie Schmidt, Renee Murphy Shaffer, Heather Day, Corey Clatterbuck, Emily Nichols, Susy Alarcon Arriaga, Cleo Small, Devon O'Meara, Mary Moskal, Wynter Skye Standish, Rachael Orben, Hannah Madden, Oscar Jasklowski and Cindy Wu).

Supplementary information

Supplementary information available online at <https://jeb.biologists.org/lookup/doi/10.1242/jeb.228585.supplemental>

References

- ACAP (2009). ACAP Species Assessment: Black-browed Albatross *Thalassarche melanophris*. Agreement on the Conservation of Albatrosses and Petrels. 1-22.
- ACAP (2010). ACAP Species Assessment: Grey-headed Albatross *Thalassarche chrysostoma*. Agreement on the Conservation of Albatrosses and Petrels. 1-18.
- Adams, A. N. J., Brown, C. R. and Nagy, K. A. (1986). Energy expenditure of free-ranging wandering albatrosses *Diomedea exulans*. *Physiol. Zool.* **59**, 583-591. doi:10.1086/physzool.59.6.30158606
- Alerstam, T., Bäckman, J. and Evans, T. J. (2019). Optimal central place foraging flights in relation to wind. *J. Ornithol.* **160**, 1065-1076. doi:10.1007/s10336-019-01677-4
- Antolos, M., Shaffer, S. A., Weimerskirch, H., Tremblay, Y. and Costa, D. P. (2017). Foraging behavior and energetics of albatrosses in contrasting breeding environments. *Front. Mar. Sci.* **4**, 1-12. doi:10.3389/fmars.2017.00414
- Berlincourt, M. and Arnould, J. P. Y. (2015). Influence of environmental conditions on foraging behaviour and its consequences on reproductive performance in little penguins. *Mar. Biol.* **162**, 1485-1501. doi:10.1007/s00227-015-2685-x
- Calenge, C. (2006). The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Model.* **197**, 516-519. doi:10.1016/j.ecolmodel.2006.03.017
- Catry, P., Phillips, R. A., Phalan, B., Silk, J. R. D. and Croxall, J. P. (2004a). Foraging strategies of grey-headed albatrosses *Thalassarche chrysostoma*: integration of movements, activity and feeding events. *Mar. Ecol. Prog. Ser.* **280**, 261-273. doi:10.3354/meps280261
- Catry, P., Phillips, R. A. and Croxall, J. P. (2004b). Sustained fast travel by a gray-headed albatross (*Thalassarche chrysostoma*) riding an Antarctic storm. *Auk* **121**, 1208-1213. doi:10.1642/0004-8038(2004)121[1208:SFTBAG]2.0.CO;2
- Clarke, A. and Prince, P. A. (1980). Chemical composition and calorific value of food fed to mollymauk chicks *Diomedea melanophris* and *D. chrysostoma* at Bird Island, South Georgia. *Ibis (Lond 1859)* **122**, 488-494. doi:10.1111/j.1474-919X.1980.tb00903.x
- Connors, M. G., Hazen, E. L., Costa, D. P. and Shaffer, S. A. (2015). Shadowed by scale: subtle behavioral niche partitioning in two sympatric, tropical breeding albatross species. *Mov. Ecol.* **3**, 1-20. doi:10.1186/s40462-015-0060-7
- Constable, A. J., Melbourne-Thomas, J., Corney, S. P., Arrigo, K. R., Barbraud, C., Barnes, D. K. A., Bindoff, N. L., Boyd, P. W., Brandt, A., Costa, D. P. et al. (2014). Climate change and Southern Ocean ecosystems. I. How changes in physical habitats directly affect marine biota. *Glob. Chang. Biol.* **20**, 3004-3025. doi:10.1111/gcb.12623
- Cooke, S. J., Sack, L., Franklin, C. E., Farrell, A. P., Beardall, J., Wikelski, M. and Chown, S. L. (2013). What is conservation physiology? Perspectives on an increasingly integrated and essential science. *Conserv. Physiol.* **1**, 1-23. doi:10.1111/j.1474-919X.1980.tb00903.x
- Costa, D. P. (1991). Reproductive and foraging energetics of high latitude penguins, albatrosses and pinnipeds: implications for life history patterns. *Am. Zool.* **31**, 111-130. doi:10.1093/icb/31.1.111
- Costa, D. P. and Prince, P. A. (1987). Foraging energetics of grey-headed albatrosses *Diomedea chrysostoma* at Bird Island, South Georgia. *Ibis (Lond 1859)* **129**, 149-158. doi:10.1111/j.1474-919X.1987.tb03196.x
- Crossin, G. T., Phillips, R. A., Wynne-edwards, K. E. and Williams, T. D. (2013). Postmigratory body condition and ovarian steroid production predict breeding decisions by female gray-headed albatrosses. *Physiol. Biochem. Zool.* **86**, 761-768. doi:10.1086/673755
- Croxall, J. P., Butchart, S. H. M., Lascelles, B., Stattersfield, A. J., Sullivan, B., Symes, A. and Taylor, P. (2012). Seabird conservation status, threats and priority actions: a global assessment. *Bird Conserv. Int.* **22**, 1-34. doi:10.1017/S0959270912000020
- da Silva, A. R., Malafaia, G. and Menezes, I. P. P. (2017). biotools: an R function to predict spatial gene diversity via an individual-based approach. *Genet. Mol. Res.* **16**, gmr16029655.
- Daunt, F. and Mitchell, I. (2013). Impacts of climate change on seabirds. *MCCIP Sci. Rev.* **2013**, 125-133.
- Dechaume-Moncharmont, F., Monceau, K. and Cezilly, F. (2011). Sexing birds using discriminant function analysis: a critical appraisal. *Auk* **128**, 78-86. doi:10.1525/auk.2011.10129
- Dobson, F. S. and Jouventin, P. (2010). The trade-off of reproduction and survival in slow-breeding seabirds. *Can. J. Zool.* **88**, 889-899. doi:10.1139/Z10-054
- Doyle, T. K., Houghton, J. D. R., Mcdevitt, R., Davenport, J. and Hays, G. C. (2007). The energy density of jellyfish: Estimates from bomb-calorimetry and proximate composition. *J. Exp. Mar. Biol. Ecol.* **343**, 239-252. doi:10.1016/j.jembe.2006.12.010
- Dunn, P. K. and Smyth, G. K. (2008). Evaluation of Tweedie exponential dispersion models using Fourier inversion. *Stat. Comput.* **18**, 73-86. doi:10.1007/s11222-007-9039-6
- Eder, E. B. and Lewis, M. N. (2005). Proximate composition and energetic value of demersal and pelagic prey species from the SW Atlantic Ocean. *MEPS* **291**, 43-52. doi:10.3354/meps291043
- Edwards, A. E. (2008). Large-scale variation in flight feather molt as a mechanism enabling biennial breeding in albatrosses. *J. Avian Biol.* **39**, 144-151. doi:10.1111/j.2007.0908-8857.04139.x
- Elliott, K. H., Le Vaillant, M., Kato, A., Gaston, A. J., Ropert-Coudert, Y., Hare, J. F., Speakman, J. R. and Croll, D. (2014). Age-related variation in energy expenditure in a long-lived bird within the envelope of an energy ceiling. *J. Anim. Ecol.* **83**, 136-146. doi:10.1111/1365-2656.12126
- Ellis, H. I. and Gabrielsen, G. W. (2002). Energetics of free-ranging seabirds. In *Biology of Marine Birds*, pp. 359-407, EA Schreiber and J Burger.
- Felicesimo, A. M., Munoz, J. and González-Solís, J. (2008). Ocean surface winds drive dynamics of transoceanic aerial movements. *PLoS ONE* **3**, 1-7. doi:10.1371/journal.pone.0002928
- Fox, J. and Weisberg, S. (2011). *An {R} Companion to Applied Regression*, 2nd edn. Thousand Oaks, CA: Sage.
- Furness, R. W. and Bryant, D. M. (1996). Effect of wind on field metabolic rates of breeding northern fulmars. *Ecology* **77**, 1181-1188. doi:10.2307/2265587
- Gessaman, J. A. and Nagy, K. A. (1988). Energy metabolism: errors in gas-exchange conversion factors. *Physiol. Zool.* **61**, 507-513. doi:10.1086/physzool.61.6.30156159
- Hedd, A. and Gales, R. (2001). The diet of shy albatrosses (*Thalassarche cauta*) at Albatross Island, Tasmania. *J. Zool.* **253**, 69-90. doi:10.1017/S0952836901000073
- Hetem, R. S., Strauss, W. M., Fick, L. G., Maloney, S. K., Meyer, L. C. R., Shobrak, M., Fuller, A. and Mitchell, D. (2012). Activity re-assignment and microclimate selection of free-living Arabian oryx: responses that could minimise the effects of climate change on homeostasis? *Zoology* **115**, 411-416. doi:10.1016/j.zool.2012.04.005
- Holland, D. L. and Walker, G. (1975). The biochemical composition of the cypris larva of the barnacle *Balanus balanoides*. *ICES J. Mar. Sci.* **36**, 162-165. doi:10.1093/icesjms/36.2.162
- Huin, N., Prince, P. and Briggs, D. R. (2000). Chick provisioning rates and growth in black-browed albatross *Diomedea melanophris* and grey-headed albatross *D. chrysostoma* at Bird Island, South Georgia. *Ibis (Lond 1859)* **136**, 50-71. doi:10.1111/j.1474-919X.1994.tb08131.x
- Jacobs, S. R., Elliott, K., Guigueno, M. F., Gaston, A. J., Redman, P., Speakman, J. R. and Weber, J. M. (2012). Determining seabird body condition using nonlethal measures. *Physiol. Biochem. Zool.* **85**, 85-95. doi:10.1086/663832
- Jodice, P. G. R., Roby, D. D., Suryan, R. M., Irons, D. B., Turco, K. R., Brown, E. D., Thedinga, J. F. and Visser, G. H. (2006). Increased energy expenditure by a seabird in response to higher food abundance. *Mar. Ecol. Prog. Ser.* **306**, 283-293. doi:10.3354/meps306283
- Jouventin, P. and Dobson, F. S. (2002). Why breed every other year? The case of albatrosses. *Proc. R. Soc. Lond. B* **269**, 1955-1961. doi:10.1098/rspb.2002.2080
- Kitaysky, A. S., Piatt, J. F., Hatch, S. A., Kittaikaia, E. V., Benowitz-Fredericks, Z. M., Shultz, M. T. and Wingfield, J. C. (2010). Food availability and population processes: severity of nutritional stress during reproduction predicts survival of long-lived seabirds. *Funct. Ecol.* **24**, 625-637. doi:10.1111/j.1365-2435.2009.01679.x
- Kroeger, C. E. (2019). *Stress hormones, foraging energetics, and wind-use patterns in two sympatrically breeding southern albatrosses* (Doctoral dissertation, UC Santa Cruz).
- Kroeger, C., Crocker, D. E., Thompson, D. R., Torres, L. G., Sagar, P. M. and Shaffer, S. A. (2019). Variation in corticosterone levels in two species of breeding albatrosses with divergent life histories: responses to body condition and drivers of foraging behavior. *Physiol. Biochem. Zool.* **92**, 223-238. doi:10.1086/702656
- Lenky, C., Eisert, R., Oftedal, O. T. and Metcalf, V. (2012). Proximate composition and energy density of nototheniid and myctophid fish in McMurdo Sound and the Ross Sea, Antarctica. *Polar Biol.* **35**, 717-724. doi:10.1007/s00300-011-1116-9
- Lifson, N. and McClintock, R. (1966). Theory of use of the turnover rates of body water for measuring energy and material balance. *J. Theor. Biol.* **12**, 46-74. doi:10.1016/0022-5193(66)90185-8
- Louza, M., Wiegand, T., Bartumeus, F. and Weimerskirch, H. (2014). Coupling instantaneous energy-budget models and behavioural mode analysis to estimate optimal foraging strategy: an example with wandering albatrosses. *Mov. Ecol.* **2**, 8. doi:10.1186/2051-3933-2-8
- Lovenduski, N. S. and Gruber, N. (2005). Impact of the southern annular mode on Southern Ocean circulation and biology. *Geophys. Res. Lett.* **32**, 1-4. doi:10.1029/2005GL022727
- McInnes, J. C., Deagle, B. E., Catry, P., Jarman, S. N., Lea, R. A. M., Raymond, B., Phillips, R. A., Stanworth, A., Thompson, D. R., Crist, H. W. et al. (2017). High occurrence of jellyfish predation by black-browed and Campbell albatross identified by DNA metabarcoding. *Mol. Ecol.* **26**, 4831-4845. doi:10.1111/mec.14245
- McNamara, J. M. and Houston, A. I. (2008). Optimal annual routines: behaviour in the context of physiology and ecology. *Phil. Trans. R. Soc. B* **363**, 301-319. doi:10.1098/rstb.2007.2141
- Moore, P. J. and Moffat, R. D. (1990). Mollymawks on Campbell Island. *Sci. Res. Intern. Rep.* **59**, 1-44.
- Nagy, K. A. (1980). CO₂ production in animals: analysis of potential errors in the doubly labeled water method. *Am. J. Physiol.* **238**, 466-473. doi:10.1152/ajpregu.1980.238.5.R466
- Nagy, K. A. (1983). The doubly labeled water (³H¹⁸O) method: a guide to its use. Los Angeles, CA: University of California Publ. No. 12-1417.

- Nagy, K. A. and Costa, D. P. (1980). Water flux in animals: analysis of potential errors in the tritiated water method. *Am. J. Physiol.* **238**, R454-R465. doi:10.1152/ajpregu.1980.238.5.R454
- Ortiz, C. L., Costa, D. P. and Le Boeuf, B. J. (1978). Water and energy flux in elephant seal pups fasting under natural conditions. *Physiol. Zool.* **51**, 166-178. doi:10.1086/physzool.51.2.30157864
- Pelletier, L., Kato, A., Chiaradia, A. and Ropert-Coudert, Y. (2012). Can thermoclines be a cue to prey distribution for marine top predators? A case study with little penguins. *PLoS ONE* **7**, e31768. doi:10.1371/journal.pone.0031768
- Pennycuik, C. J. (1982). The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity. *Phil. Trans. R. Soc. Lond. B* **300**, 75-106. doi:10.1098/rstb.1982.0158
- Pennycuik, C. J. (2008). *Modelling the Flying Bird*. Elsevier.
- Phillips, R. A., Silk, J. R. D., Phalan, B., Cattr, P. and Croxall, J. P. (2004). Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proc. R. Soc. B Biol. Sci.* **271**, 1283-1291. doi:10.1098/rspb.2004.2718
- Quintana, F., Lopez, G. C. and Somoza, G. (2008). A cheap and quick method for DNA-based sexing of birds. *Waterbirds* **31**, 485-488.
- Raymond, B., Shaffer, S. A., Sokolov, S., Woehler, E. J., Costa, D. P., Einoder, L., Hindell, M., Hosie, G., Pinkerton, M., Sagar, P. M. et al. (2010). Shearwater foraging in the Southern Ocean: the roles of prey availability and winds. *PLoS ONE* **5**, e10960.
- Rayner, J. M. V. (1988). Form and function in avian flight. *Curr. Ornithol.* **5**, 1-66.
- Reed, T. E., Schindler, D. E. and Waples, R. S. (2011). Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. *Conserv. Biol.* **25**, 56-63. doi:10.1111/j.1523-1739.2010.01552.x
- Ricklefs, R. E., Roby, D. D. and Williams, J. B. (1986). Daily expenditure by adult Leach's storm-petrels during the nesting cycle. *Physiol. Zool.* **59**, 649-660. doi:10.1086/physzool.59.6.30158612
- Rigby, R. A. and Stasinopoulos, D. M. (2005). Generalized additive models for location, scale and shape. *Appl. Statist.* **54**, 507-554.
- Ryan, P. G., Phillips, R. A., Nel, D. C. and Wood, A. G. (2006). Breeding frequency in grey-headed albatrosses *Thalassarche chrysostoma*. *Ibis* **149**, 45-52. doi:10.1111/j.1474-919X.2006.00594.x
- Sachs, G., Traugott, J., Nesterova, A. P., Omo, G. D., Ku, F., Heidrich, W., Vysotski, A. L. and Bonadonna, F. (2012). Flying at no mechanical energy cost: disclosing the secret of wandering albatrosses. *PLoS ONE* **7**, e41449. doi:10.1371/journal.pone.0041449
- Sagar, P. (2014). Population estimates and trends of Campbell and grey-headed albatrosses at Campbell Island: Campbell and grey-headed albatross population estimates. *Prepared for the Department of Conservation* 1-28.
- Sakamoto, K. Q., Takahashi, A., Iwata, T., Yamamoto, T., Yamamoto, M. and Trathan, P. N. (2013). Heart rate and estimated energy expenditure of flapping and gliding in black-browed albatrosses. *J. Exp. Biol.* **216**, 3175-3182. doi:10.1242/jeb.079905
- Schneider, J. E. (2004). Energy balance and reproduction. *Physiol. Behav.* **81**, 289-317. doi:10.1016/j.physbeh.2004.02.007
- Schultner, J., Welcker, J., Speakman, J. R., Nordøy, E. S. and Gabrielsen, G. W. (2010). Application of the two-sample doubly labelled water method alters behaviour and affects estimates of energy expenditure in black-legged kittiwakes. *J. Exp. Biol.* **213**, 2958-2966. doi:10.1242/jeb.043414
- Shaffer, S. A. (2011). A review of seabird energetics using the doubly labeled water method. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **158**, 315-322. doi:10.1016/j.cbpa.2010.07.012
- Shaffer, S. A., Costa, D. P. and Weimerskirch, H. (2001a). Behavioural factors affecting foraging effort of breeding wandering albatrosses. *J. Anim. Ecol.* **70**, 864-874. doi:10.1046/j.0021-8790.2001.00548.x
- Shaffer, S. A., Costa, D. P. and Weimerskirch, H. (2001b). Comparison of methods for evaluating energy expenditure of incubating wandering albatrosses. *Physiol. Biochem. Zool.* **74**, 823-831. doi:10.1086/323650
- Shaffer, S. A., Weimerskirch, H. and Costa, D. P. (2001c). Functional significance of sexual dimorphism in wandering albatrosses, *Diomedea exulans*. *Funct. Ecol.* **15**, 203-210. doi:10.1046/j.1365-2435.2001.00514.x
- Shaffer, S. A., Costa, D. P. and Weimerskirch, H. (2003). Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. *Funct. Ecol.* **17**, 66-74. doi:10.1046/j.1365-2435.2003.00705.x
- Shaffer, S. A., Costa, D. P. and Weimerskirch, H. (2004). Field metabolic rates of black-browed albatrosses *Thalassarche melanophrys* during the incubation stage. *J. Avian Biol.* **35**, 551-558. doi:10.1111/j.0908-8857.2004.03264.x
- Shaffer, S. A., Gabrielsen, G. W., Verreault, J. and Costa, D. P. (2006). Validation of water flux and body composition in glaucous gulls (*Larus hyperboreus*). **79**, 836-845.
- Shamoun-Baranes, J., Loon, E., Van, Liechti, F. and Bouten, W. (2007). Analyzing the effect of wind on flight: pitfalls and solutions. *J. Exp. Biol.* **210**, 82-90. doi:10.1242/jeb.02612
- Speakman, J. R. (1997). *Doubly Labelled Water: Theory and Practice*. Chapman & Hall.
- Speakman, J. R. and Hambly, C. (2016). Using doubly-labelled water to measure free-living energy expenditure: some old things to remember and some new things to consider. *Comp. Biochem. Physiol. A* **202**, 3-9. doi:10.1016/j.cbpa.2016.03.017
- Spear, L. B. and Ainley, D. G. (1997). Flight behaviour of seabirds in relation to wind direction and wing morphology. *Ibis (Lond 1859)* **139**, 221-233. doi:10.1111/j.1474-919X.1997.tb04620.x
- Stearns, S. C. (1992). *The Evolution of Life Histories*. London: Oxford University Press.
- Suryan, R. M., Anderson, D. J., Shaffer, S. A., Roby, D. D., Tremblay, Y., Costa, D. P., Sievert, P. R., Sato, F., Ozaki, K., Balogh, G. R. et al. (2008). Wind, waves and wing loading: morphological specialization may limit range expansion of endangered albatrosses. *PLoS ONE* **3**, e4016. doi:10.1371/journal.pone.0004016
- Suryan, R. M., Irons, D. B., Brown, E. D., Jodice, P. G. R. and Roby, D. D. (2006). Site-specific effects on productivity of an upper trophic-level marine predator: bottom-up, top-down, and mismatch effects on reproduction in a colonial seabird. *Prog. Oceanogr.* **68**, 303-328. doi:10.1016/j.pcean.2006.02.006
- Sztukowski, L. A. (2015). Foraging ecology of the Campbell albatross: individual specialisation and fishery interactions. *PhD thesis*, Plymouth University and Université Pierre et Marie Curie.
- Sztukowski, L. A., van Toor, M. L., Weimerskirch, H., Thompson, D. R., Torres, L. G., Sagar, P. M., Cotton, P. A. and Votier, S. C. (2017). Tracking reveals limited interactions between Campbell albatross and fisheries during the breeding season. *J. Ornithol.* **158**, 725-735. doi:10.1007/s10336-016-1425-4
- Tarroux, A., Weimerskirch, H., Wang, S. H., Bromwich, D. H., Cherel, Y., Kato, A., Ropert-Coudert, Y., Varpe, Ø., Yoccoz, N. G. and Descamps, S. (2016). Flexible flight response to challenging wind conditions in a commuting Antarctic seabird: do you catch the drift? *Anim. Behav.* **113**, 99-112. doi:10.1016/j.anbehav.2015.12.021
- Thompson, D. W. J. and Wallace, J. M. (2000). Annular modes in the extratropical circulation. Part II: Trends. *J. Clim.* **13**, 1018-1036. doi:10.1175/1520-0442(2000)013<1018:AMITEC>2.0.CO;2
- Thorne, L. H., Hazen, E. L., Bograd, S. J., Foley, D. G., Conners, M. G., Kappes, M. A., Kim, H. M., Costa, D. P., Tremblay, Y. and Shaffer, S. A. (2015). Foraging behavior links climate variability and reproduction in North Pacific albatrosses. *Mov. Ecol.* **3**, 27. doi:10.1186/s40462-015-0050-9
- Torres, L. G., Orben, R. A., Tolkova, I. and Thompson, D. R. (2017). Classification of animal movement behavior through residence in space and time. *PLoS ONE* **12**, e0168513. doi:10.1371/journal.pone.0168513
- Tuomainen, U. and Candolin, U. (2011). Behavioural responses to human-induced environmental change. *Biol. Rev.* **86**, 640-657. doi:10.1111/j.1469-185X.2010.00164.x
- Venables, W. N. and Ripley, B. D. (2002). *Modern Applied Statistics with S*, 4th edn. Springer, New York.
- Wakefield, E. D., Phillips, R. A., Matthiopoulos, J., Fukuda, A., Higuchi, H., Marshall, G. J. and Trathan, P. N. (2009). Wind field and sex constrain the flight speeds of central-place foraging albatrosses. *Ecol. Monogr.* **79**, 663-679. doi:10.1890/07-2111.1
- Warham, J. (1977). Wing loadings, wing shapes, and flight capabilities of Procellariiformes. *New Zeal J. Zool.* **4**, 73-83. doi:10.1080/03014223.1977.9517938
- Warham, J. (1990). *The Petrels: Their Ecology and Breeding Systems*. A&C Black.
- Waugh, S. M., Prince, P. A. and Weimerskirch, H. (1999a). Geographical variation in morphometry of black-browed and grey-headed albatrosses from four sites. *Polar Biol.* **22**, 189-194. doi:10.1007/s0030000050409
- Waugh, S. M., Weimerskirch, H., Cherel, Y., Shankar, U., Prince, P. A. and Sagar, P. M. (1999b). Exploitation of the marine environment by two sympatric albatrosses in the Pacific Southern Ocean. *Mar. Ecol. Prog. Ser.* **177**, 243-254. doi:10.3354/meps177243
- Waugh, S. M., Weimerskirch, H., Moore, P. J. and Sagar, P. M. (1999c). Population dynamics of black-browed and grey-headed albatrosses *Diomedea melanophrys* and *D. chrysostoma* at Campbell Island, New Zealand, 1942-96. *Ibis (Lond 1859)* **141**, 216-225. doi:10.1111/j.1474-919X.1999.tb07544.x
- Weimerskirch, H., and 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. doi:10.1007/s003000000144
- Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep Res. Part II Top Stud. Oceanogr* **54**, 211-223. doi:10.1016/j.dsr2.2006.11.013
- Weimerskirch, H. and Guionnet, T. (2002). Comparative activity pattern during foraging of four albatross species. *Ibis (Lond 1859)* **144**, 40-50. doi:10.1046/j.0019-1019.2001.00021.x
- Weimerskirch, H. and Pinaud, D. (2007). Does prey capture induce area-restricted search? A fine-scale study using GPS in a marine predator, the wandering albatross. *Am. Nat.* **170**, 734-743. doi:10.1086/522059
- Weimerskirch, H., Ancel, A., Caloin, M., Zahariev, A., Spaggiari, J., Kersten, M. and Chastel, O. (2003). Foraging efficiency and adjustment of energy expenditure in a pelagic seabird provisioning its chick. *J. Anim. Ecol.* **72**, 500-508. doi:10.1046/j.1365-2656.2002.00720.x
- Weimerskirch, H., Gault, A. and Cherel, Y. (2005). Prey distribution and patchiness: factors in foraging success and efficiency of wandering albatrosses. *Ecology* **86**, 2611-2622. doi:10.1890/04-1866
- Weimerskirch, H., Guionnet, T., Martin, J., Shaffer, S. A. and Costa, D. P. (2000). Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proc. R. Soc. B* **267**, 1869-1874. doi:10.1098/rspb.2000.1223

- Weimerskirch, H., Louzao, M. and Delord, K.** (2012). Changes in wind pattern alter albatross distribution and life- history traits. *Science* **335**, 211-214. doi:10.1126/science.1210270
- Weiner, J.** (1992). Physiological limits to sustainable energy budgets in birds and mammals: ecological implications. *Trends Ecol. Evol.* **7**, 384-388. doi:10.1016/0169-5347(92)90009-Z
- Wingfield, J. C.** (2013). Ecological processes and the ecology of stress: the impacts of abiotic environmental factors. *Funct. Ecol.* **27**, 37-44. doi:10.1111/1365-2435.12039
- Wingfield, J. C., Kelley, J. P. and Angelier, F.** (2011). What are extreme environmental conditions and how do organisms cope with them? *Curr. Zool.* **57**, 363-374. doi:10.1093/czoolo/57.3.363
- Xavier, J. C., Croxall, J. P. and Reid, K.** (2003). Interannual variation in the diets of two albatross species breeding at South Georgia: implications for breeding performance. *Ibis (Lond 1859)* **145**, 593-610. doi:10.1046/j.1474-919X.2003.00196.x
- Ydenberg, R. C., Welham, C. V. J., Schmid-Hempel, R., Schmid-Hempel, P. and Beauchamp, G.** (1994). Time and energy constraints and the relationships between currencies in foraging theory. *Behav. Ecol.* **5**, 28-34. doi:10.1093/beheco/5.1.28