Title

Stress hormones, foraging energetics, and wind-use patterns in two sympatrically breeding southern albatrosses

Author

Kroeger, Caitlin Elizabeth

Publication Date

2019

UNIVERSITY OF CALIFORNIA
SANTA CRUZ

STRESS HORMONES, FORAGING ENERGETICS, AND WIND-USE PATTERNS IN TWO SYMPATRICALLY BREEDING SOUTHERN ALBATROSSES

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

OCEAN SCIENCES

by

Caitlin E. Kroeger

September 2019

The Dissertation of Caitlin E. Kroeger is approved:

Dr. Scott A. Shaffer, chair

Professor Christopher A. Edwards

Professor Daniel P. Costa

Dr. Daniel E. Crocker

Quentin Williams
Vice Provost and Dean of Graduate Studies

Table of Contents

List of Figures

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

List of Tables

CHAPTER 2

CHAPTER 3

CHAPTER 4

Dissertation Abstract

Stress hormones, foraging energetics, and wind-use patterns in two sympatrically breeding southern albatrosses

by
Caitlin E. Kroeger

The modulation of energy balance through physiological or behavioral adjustments (i.e., allostasis) allows organisms to cope with unexpected challenges, ensuring reproductive success and survival. However, energetic challenges can be exacerbated during critical life stages such as breeding, when more resources are needed to feed offspring. Amphibious marine organisms like seabirds already face a unique challenge of finding patchily distributed ephemeral prey within a vast, dynamic ocean and delivering prey to hungry chicks at land-based nests. With the depletion of ozone and rising sea temperatures, atmospheric and oceanographic disruptions are escalating, affecting the distribution of prey in addition to altering windscapes that seabirds, like the glider-shaped albatrosses, rely on for traveling. Metabolic stress hormones in seabirds can be used to indicate adverse changes within the environment; however, the functional role of stress hormones is confounded by factors such as species, life history, or breeding stage. In chapter 2, I used structural equation models to improve our understanding of the role of corticosterone, a stress hormone, as a mediator of energy balance in two sympatric breeding albatrosses during incubation and early-chick-rearing stages. Campbell (*Thalassarche impavida*) and grey-headed albatrosses (*T. chrysostoma*) are annual and biennial breeders, respectively, that occupy differing prey niches. By measuring foraging behavior, mass change, and hormone levels, I found that corticosterone concentrations before and after foraging trips were similar between species and across stages, potentially because of behavioral flexibility or different corticosterone functional roles across stages. However, when parents were provisioning small chicks during the guard stage, the former were more sensitive to changes in energy balance, suggesting that hormone concentrations elicited during this stage are indicative of foraging conditions. Also, pre-trip corticosterone may determine foraging destination in incubation-stage Campbell albatrosses, but it remains unclear if this mediates foraging success. In chapter 3, I examined the role of environmental interactions, behavioral flexibility, and morphological constraints on energy balance during early chick-rearing using the doubly labelled water method to estimate the daily energy expenditure (DEE) of GPS tracked individuals. In both species, greater DEE was associated with greater foraging success, lower mean wind speeds during water take-offs, a greater proportion of strong tailwinds (> 12 ms^{-1}), and younger chick age. Greater foraging success was marginally costlier in male albatrosses of both species and DEE was higher in grey-headed albatrosses when they experienced a greater proportion of strong headwinds. Climate models predict wind speeds will weaken in the foraging range of female Campbell albatrosses and intensify in the range of grey-headed and male Campbell albatrosses, thus breeding costs may increase for both species. In chapter 4, I used a flight cost function to show that mean flight costs were greater during the incubation stage for grey-headed albatrosses, which may interrupt breeding cycles. I then used reanalyzed wind data in combination with bird-borne GPS tracking data to score the cost of flight path trajectory choices and to calculate vector correlation coefficients to evaluate wind-use consistency. Greater wind-use consistency resulted in lower mean flight costs and greater foraging success for both species, but Campbell albatrosses that use low-wind regions had the greatest wind-use consistency. Males of both species gained less mass than females when making similar cost choices during incubation stage transit. Chick-rearing individuals of both species traded greater cost choices for greater foraging success during outbound transit. Overall, foraging strategy, mediated by hormones and morphology, revealed energetic vulnerabilities with respect to species, sex, and breeding stage.

Acknowledgements

The text of this dissertation includes a reprint of the following previously published material with permission from the University of Chicago Press and the co-authors:

Kroeger, C., Crocker, D. E., Thompson, D. R., Torres, L. G., Sagar, P., & 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. Physiological and Biochemical Zoology 92:223-238.

Scott Shaffer supervised the research which forms the basis for the dissertation. Daniel Crocker provided laboratory and analytical guidance. David Thompson, Leigh Torres, and Paul Sagar provided logistical support for the fieldwork. All co-authors for Chapter 2 provided edits and comments during the preparation of the manuscript. Lisa Sztukowski and Rachael Orben provided critical field assistance, field advice, and edits for Chapter 3. David Thompson, Leigh Torres, and Paul Sagar provided edits for Chapter 3. Daniel Costa provided advice for Chapter 3. Abram Fleishman provided coding assistance and advice for Chapter 4. I, Caitlin Kroeger, conceived these studies and drafted all parts of the manuscripts in Chapters 2, 3, and 4.

This compilation of work would not have been possible without all the support I have received over the years – I am grateful for all of it – but first, I would like to thank my committee. Thank you, Scott Shaffer, for setting me up with this opportunity, investing in me, being my advocate, taking my satellite-phone calls from the field, helping me through this entire process, and constantly assuring me that everything will turn out fine. It’s not easy to advise someone from the other side of the Santa Cruz mountains, so thank you checking in and making trips over Hwy 17 for meetings. Dan Crocker, thank you for letting me use your lab space and equipment at SSU, for walking me through laboratory procedures, for answering very many questions, for all your guidance through my first publication, and for so many thoughtful contributions to my work. Your kindness and generosity with your time has been tremendous. I will always be in awe of you and your brain – you are an inspirational mentor and scientist. Dan Costa, thank you for welcoming me into your lab all these years, for your enthusiasm toward my work, and for your willingness to sit down with me to impart your wisdom regarding metabolic studies. It's an honor to be a part of your legacy. Also, thank you for laughing when I photoshopped dinosaurs into an old photo of you. Chris Edwards, you somehow made courses that I dreaded turn out to be some of the most enjoyable learning experiences of my academic career. I appreciate that you always guided me toward the answers without giving them away – you helped me grow as a critical thinker and problem solver. I know most of my research is outside of your wheelhouse, so thank you for agreeing to be part of this committee and fully engaging in your role when called upon.

Thank you to the National Institute of Water and Atmospheric Research, who made the expedition to Campbell Island possible with funding from the New Zealand Ministry of Business, Innovation and Employment. Thank you to David Thompson, Leigh Torres, and Paul Sagar for securing the funding that made all of this megafauna research possible and for your help along the way. David and Leigh provided so much logistical support getting me to the field and back and making sure I had everything I needed to survive and succeed. I am sure I'm only aware of the very tip of the iceberg that is all the work that they put into this. Paul introduced me to Campbell Island and the birds and taught me how to properly hike in gale-force winds. He and his wife, Joy, made all the hard work getting the field camp up and running a humorous and memorable experience. Thank you to Henk Haazen and his crews for safely sailing us to and from the island and for the amazing pancake breakfasts. Thank you to Lisa Sztukowski, Rachael Orben, Ray Bucheit, and Allyson Larned for suffering long hours through the rain and cold to help me catch birds. Thank you to Kyle Morrison, Ray Bucheit, and Rob Dunn for carrying absurdly heavy food loads to Bull Rock. Thank you to

Luis Huckstadt and Kyle Morrison for the personal deliveries of my samples from New Zealand. I also thank the New Zealand Department of Conservation for permitting this project and providing logistical support.

A very special thank you to Tim Andriese at SJSU who spent many hours in the lab meticulously processing the DNA of my birds to determine their sex. Thank you to Marm Kilpatrick at UCSC for jump-starting me with lessons in R and statistics. A huge thank you to the many people and institutions who funded this research. First, through Experiment.com, the following people donated toward laboratory expenses: 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, Elizabeth 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. I also received funding from the Jim Brown Award, Friends of Long Marine Lab Student Research & Education Award, American Ornithologist’s Union, Dr. Earl H. Myers & Ethel M. Myers Oceanographic and Marine Biology Trust, ARCS Scholarship Foundation, UCSC President’s Dissertation-Year Fellowship, and a GSR from the Ocean Sciences Department. I must also thank Lezlie Ward and Rondi Robison, the Ocean Science Department managers (past and present) for making sure everything ran smoothly from the moment I began this PhD and for always looking out for me. They were there to make sure I didn’t drop the ball and enthusiastically supported my ideas for the department. They are two of the most genuinely kind humans I have ever met and work so hard to make sure their students get the emotional, logistical, and financial support they need.

From the beginning, I started this project with the support of a bright-eyed and slightly bewildered cohort of fresh graduate students at SJSU. Thank you, Stacy Moskal, Emma Kelsey, Corey Clatterbuck, and Jen Jelincic for weaving a long-lasting support network. I can't think of a better group of brilliant and caring women in science to have started this journey with. And Cat Yi – you were a such bright light – none of us will ever forget you. Also, thank you to Jerry Smith for believing in me and telling me I could go on to do great things. At UCSC, I had the great fortune to become immersed in yet another cohort of outstanding, supportive people. Thank you, Kimberley Mayfield, Michelle Drake, Jessie Zupcic, Anna Lowe, Wilson Sauthoff, Dianna Baetscher, and Danielle Glynn for making my transition to Santa Cruz less jarring after living with birds for 4 months. Kim, your strength, success, and unstoppable momentum despite everything life throws at you has been powerfully inspiring. Michelle, thank you for being there to talk, whiteboard, dance, sing, cry, hug, and laugh it all out – hearing your laugh can turn the worst day into the best day. Jessie, thanks for being the little sister I never knew I wanted. Anna, thank you for challenging me to see the world a little differently. Thank you to the UCSCers outside of my cohort who helped me maintain my sanity through this process including: Omar Hamdani (those coffee conversations were vital), Kyle Broach (thanks for the hallway tango and the acapella sound track), Stephan Bitterwolf (you are reliable and reliably hilarious). Emily Brault, Regina Radan, Cori Gibble, Britt Henke – thank you for helping me decompress when needed. Ryan Driscoll, Rachel Clark, and Hope Ianiri, thank you for your support through the very end.

Thank you to my fellow seabirders and colleagues – you are a rare and wildly delightful flock. Melinda Conners, Rachael Orben, Morgan Gilmour, and Abram Fleishman, thanks for the comradery, uncontrollable giggles, navigational advice for grad school, field adventures, help with coding, and generally sharing your curiosity over these feathered creatures. Thank you to Jon Felis for the never-ending maps, the good-natured banter, and tolerating all those olive pits. Thank you to Emma for that last-minute escape to Lehua Island and to Jessie Beck and Ryan Carle for the occasional escapes to Año Nuevo Island.

And thank you to the Costa Lab for taking in yet another seabird gal. Luis Huckstadt, you deserve and award for putting up with my shenanigans and sass for the last 6 years. Thank you for your constant willingness to provide scientific advice and help at all hours of the day. You have been the best big brother, and yes, it HAS been a pleasure for me. Theresa Keates, thank you for being one of the most thoughtful humans on earth and always demonstrating genuine acts of kindness. And Rachel Holser, thank you for the many edits; words of advice; always leaving the door open; providing hugs, food, tea, and computer backups; for never judging and for simply being there to listen. You have been the most steadfast, calming, magical omega force in my life and I would be lost without you.

Thank to my friends and family who have been my unwavering cheerleaders from afar, who have unconditionally loved me through long absences in communication, and whom helped recharge my spirits when visits were possible: Sarah Howard, Cassie Marketos, Madeleine Rose, Heather Day, Erin Pickett, Jennapher Teunissen van Manen, Abby Lawson, Maggie Murray, Sadie Birdfeather, Mark Kroeger, Karin Holser, Mama Holser and many more. Thank you to the friends who have been here in Santa Cruz to pry me away from my work. Most of you have been named but a special thanks to Lenny Backus and Abram Fleishman for all the belays and leading the scary stuff. Thank you to my tango family, my pottery family, and my horse family – but especially the Lingemanns. John and Nancy, this world is a better place because you are in it. Scott Elkins, you took care of me and my family through some of the worst of times, thank you. Sadie Birdfeather, my other mom, thank you for all that you do to reduce stress from my life and for working so hard to take care of our family. I appreciate and love you very much. Will Bohle, thank you for the endless supply of chips, pizza, and ice cream as I finished this thing. I'm not sure if this means you love me or are hoping to collect on my life insurance after my arteries clog, but either way you have the key to my heart. And thank you for bringing Taki into our lives. Now that this is all done, let's go climb some mountains together. Finally, Tobi. You were the keeper of my sanity during so many long hours at the computer and the perfect distraction - you were my best friend and made me laugh constantly and your snuggles and purrs were always perfectly timed. I miss you daily.

To anyone else whom I've forgotten to thank who has providing guidance, advice, laughter, or kindness throughout this endeavor, you are in my heart, just currently not in my head because albatrosses are very big birds and take up a lot of space. Which reminds me, I owe the biggest thanks to the birds who didn't sign up for this but tolerated it all very well.

Grey-headed (left) and Campbell albatross (right) on Campbell Island.
Photo by Rachael Orben.

***

"But I don't want to go among mad people," Alice remarked.
"Oh, you can't help that," said the Cat: "we're all mad here. I'm mad. You're mad."
"How do you know I'm mad?" said Alice.
"You must be," said the Cat, "or you wouldn't have come here."
— Lewis Carroll, Alice in Wonderland

Dedication

This dissertation is dedicated to my family and my chosen family, but especially to

***

Ned Kroeger

Dad, I wish you were here to see how it all turned out. Your love of birds certainly foreshadowed this whole journey. You gave me everything I needed to navigate this world: you were, and will always be, my compass in life. Thank you for showing me how to practice patience, kindness, and compassion.

***

Maggie Murray

Mom, you have always supported my dreams since the day you told me I could be anything I wanted when I grew up (turns out I couldn't become a My Little Pony, but this is an acceptable alternative). Thank you for teaching me courage, perseverance, and how to live life a full of wonder and adventure.

***

Jeff Pentel

You are my guardian angel (the rarest of birds) and without you, I absolutely could not have made it this far. Thank you for the sharing the secret of the albatross and the constant joy and magic you bring to my life.

***

and to the albatrosses

This is, literally, all for you.

Chapter 1

Introduction

Organisms living in dynamic environments must be able to respond behaviorally and physiologically to changing conditions (Yoshimura and Clark 1991; McNamara 1998; Ghalambor et al. 2007; Canale and Henry 2010). Marine ecosystems are ideal for examining the interface between a dynamic environment and the flexibility of its inhabitants. Oceans are highly productive, but resource distribution and abundance vary in both space and time, favoring life history traits that can tolerate fluctuations with minimal impact to populations (Clarke 1988; Russell et al. 1992; Weimerskirch et al. 1994; Sims et al. 2006). Long-lived organisms often exhibit physiological and behavioral plasticity, allowing them to adjust to stochastic environmental changes that they will likely encounter during their lifetime (Canale and Henry 2010). However, with mounting anthropogenic and climate-induced changes to the marine environment, in addition to natural variation, there is growing concern over the ability of marine species to cope with new environmental extremes (Parmesan 2006; Grémillet and Charmantier 2010; Hoegh-Guldberg and Bruno 2010; Somero 2010; Doney et al. 2012; Daunt and Mitchell 2013).

Amphibious marine vertebrates spend the majority of their lives interacting with the ocean but are accessible to researchers during breeding seasons on land. Moreover, many amphibious marine vertebrates are central place foragers while breeding: they go out to sea to gather food or replenish energy stores in order to feed or nurse their land-based offspring (Costa 1991). If parents are unable to find sufficient prey within a short period of time, their offspring are less likely to survive and recruit to the breeding population (Suryan et al. 2006; Durant et al. 2007; Sandvik et al. 2012). While foraging at sea, these animals encounter and adjust to numerous stressors – including competition, shifting prey distributions, changes in oceanographic features linked to food – all of which are exacerbated by climate changes and thus impact foraging behaviors and energy consumption (Ainley et al. 2006; Bost et al. 2009; Weeks et al. 2013; Thorne et al. 2015). Marine vertebrates can exhibit a variety of physiological and behavioral responses to environmental changes. During low production El Niño years, sea lions adjust behaviorally to altered food distributions by shifting their foraging range (Weise et al. 2006). Under similar El Niño conditions, marine iguanas employ a starkly different response to the energetic stress associated with poor foraging conditions: they shrink in body size, reabsorbing both soft tissue and bone to reduce energy demands (Wikelski and Thom 2000). Kittiwakes buffer against environmental variability during the energetically demanding breeding period by adjusting hormone levels in order to maintain parental behavior and stimulate foraging effort (Chastel et al. 2005). The various conditions that organisms experience can alter energy available for self-maintenance and reproductive investment, thus the ability to respond ultimately influences adaptation (Rickleffs 1990).

Seabirds are amphibious central place foragers that breed along coastlines or offshore islands and interact extensively with the marine environment while foraging at sea. Many seabirds are also at an extreme end of the life history spectrum, with long lifespans and low annual fecundity as a result of the time and energy required to locate patchily distributed prey at or below the surface of the ocean (Lack 1968; Ricklefs 1990; Weimerskirch 2007). Pelagic species like albatrosses (family Diomedeidae) are some of the most extreme examples, as they delay maturity for up to 13 years, have low annual reproductive rates of one chick every year or two, and are exceptionally long-lived, thus reproducing well beyond the age of most humans (Warham 1990; Tickell 2000; Froy et al. 2013). Albatrosses are highly adapted to exploit wind energy in flight, allowing them to travel vast distances across the ocean at remarkably low energy costs in order to locate food for chicks (Adams et al. 1986; Costa and Prince 1987; Weimerskirch et al. 2000; Shaffer et al. 2001; Sachs et al. 2012). However, if adults are faced with additive environmental stressors and competition at sea, they may choose their own survival over reproductive investment in a given year, especially when there are more opportunities to breed over their lifetime (Rickleffs 1990; Dobson and Jouventin 2010). The sensitivity and flexibility of physiological and behavioral responses from these birds, especially during periods of peak energy demand when caring for offspring, is still not well understood. Furthermore, some albatrosses are biennial, rather than annual, breeders and may be even more susceptible to environmental changes (Jouventin and Dobson 2002). We can better understand the conditions that shape albatross life histories and their relative abilities to tolerate change by comparing physiological, behavioral, and morphological differences among closely allied albatross species. Such comparisons further enable us to explain the occupation of specific niches and predict impacts of environmental change on the distribution and abundance of particular species (Somero 2000). For example, global wind patterns over the ocean are shifting due to climate change (Thompson and Wallace 2000; Gillet and Thompson 2003) and this has already differentially impacted the movement patterns and breeding successes within certain albatross populations (Weimerskirch et al. 2012; Thorne et al. 2016).

Conservation physiologists often monitor physiological shifts in relation to specific perturbations to identify and determine the severity of environmental stressors (Stevenson 2006; Wikelski and Cooke 2006; Cooke et al. 2014). For example, we can examine whether stress hormone levels in populations are rising and, if so, identify what factors contribute to shifts away from baseline levels (Kitaysky et al. 1999, 2010; Angelier et al. 2007b; Satterthwaite et al. 2012). We can also resolve the metabolic costs of certain foraging strategies to understand how oceanic and atmospheric conditions affect energy balance and determine what strategies or environmental stressors are most costly (Tomlinson et al. 2014). With a more robust understanding of sources of disturbances and physiological and behavioral impacts, we can better predict the population-level impacts of changing systems. Identifying factors that contribute to physiological responses has become increasingly feasible with the advancement of miniaturized tracking technologies and advanced remotely sensed environmental data (Burger and Shaffer 2008). The ability to visualize and model albatross behaviors and movements *in situ* alongside interactions with the environment puts physiological responses in a more meaningful context and can illuminate more subtle environmental changes (Louzao et al. 2014). However, in order to interpret physiological and behavioral data there must be established baselines for the species of concern along with an understanding of how the parameters of interest fluctuate across sexes, life stages, and seasons (Hays et al. 2016).

In view of the need to understand baseline physiologies and the behavioral or physiological plasticity of species in relation to environmental changes, the primary goal of my research is to compare and explain differences in the physiology and behavior of sympatrically breeding Campbell (*Thalassarche impavida*) and grey-headed (*T. chrysostoma*) albatrosses foraging over the Southern Ocean. These species have different life histories (annual vs. biennial breeders) and contrasting foraging strategies (e.g., consumption of neritic fish vs. oceanic squid), and thus presumably have different priorities for energy acquisition and allocation. These differences may result in varying physiological and behavioral responses to environmental stressors that will highlight mechanisms for coping with stressors and the aspects of their biology that allow or impede adaptability. This is particularly relevant as food resources and wind regimes continue to change in the Southern Ocean (Weimerskirch et al. 2003; Lovenduski and Gruber 2005), potentially altering foraging behaviors and physiological costs to albatrosses that heavily rely on winds to locate food.

Additional Context

Breeding Location

Campbell and grey-headed albatrosses breed in colonies along steep, muddy cliffs of the uninhabited Campbell Island (113 km^2), located in the New Zealand Subantarctic (52°S, 169°E; Fig. 1). Campbell Island was designated a UNESCO World Heritage Site in 1998 because of its high biodiversity and endemism and in 2014 the New Zealand government established the Campbell Island/Moutere Ihupuku Marine Reserve encompassing 39% of surrounding territorial waters (Department of Conservation, 2016). The island rises from a submerged continental platform, the Campbell Plateau, which spans roughly 800,000 km^2 with ocean depths averaging between 600 and 1000 m (Neil et al. 2004).

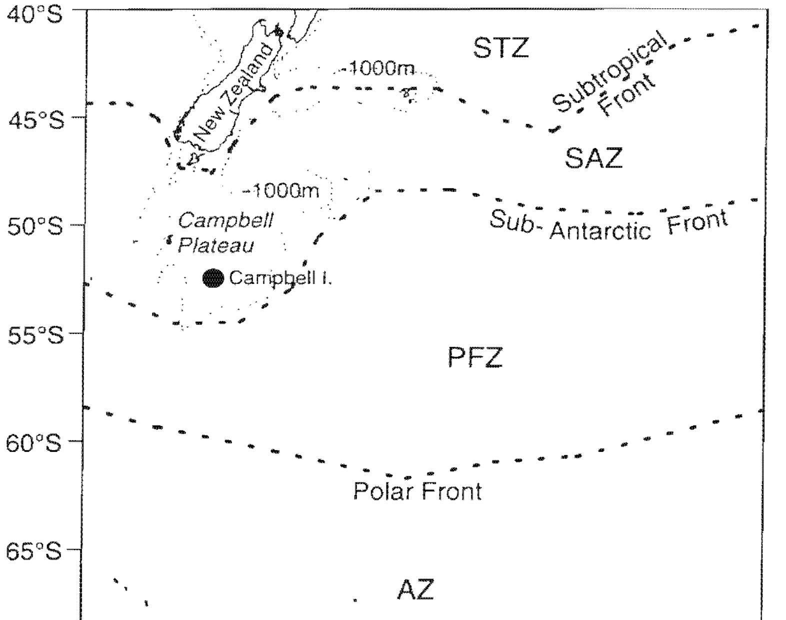


Figure 1. Study site location: Campbell Island, New Zealand sub-Antarctic territories (illustration from Waugh et al. 1999a).

Surrounding Oceanography

The Campbell Plateau is a major constriction point for the eastward flowing Antarctic Circumpolar Current (ACC), causing colder, deeper waters to intensify and deflect northward along the eastern edge, spinning off eddies that are important for foraging seabirds (Northcote and Neil 2005; Pinaud and Weimerskirch 2005). Over the plateau, shallower, gyre-like waters circulate slowly. These waters are warmer than the waters of the ACC, but cooler than the subtropical waters to the north, and generally have low primary productivity; however, there are plankton blooms during spring when waters are well mixed, resulting in an area important for commercial fisheries (Northcote and Neil 2005; Meynier et al. 2008). In addition, the region experiences strong zonal westerly winds (40°S to 60°S), with average speeds of 30 km hr^{-1} and gusts up to 96 km hr^{-1} (Neil et al. 2004). These strong winds contribute to the mixing of water layers and subsequent productivity. Intensification of winds over the Southern Ocean are already causing a poleward shift of nutrient rich upwelling fronts along the ACC (Rykaczewski and Checkley 2008; Young et al. 2011). The migration of these fronts is expected to change the distribution of forage species (krill, fish, and squid) and have negative population-level consequences for associated predators, such as seabirds (Constable et al. 2014). Toward the center of the ACC is the Antarctic Polar Front which contributes to high productivity in the region due to flow-topography interactions that bring nutrient rich waters to the surface, resulting in increased chlorophyll (Sokolov and Rintoul 2007). Typical species along the Polar Front include ommastrephid squid, myctophid fishes, copepods, and salps (Rodhouse et al. 1996; Raymond et al. 2010). To the north of Campbell Island is New Zealand and Australia, between which lies the productive Tasman Sea – an important foraging area for seabirds (Watson et al. 2013). Thus, the waters surrounding Campbell Island provide various regions in which foraging predators may locate prey.

Study Species

The Campbell albatross has been genetically split from the black-browed albatross (*T. melanophrys*) and is now considered monotypic and endemic to Campbell Island (Nunn et al. 1996). Campbell albatrosses breed annually in dense colonies from late September to early May (chicks hatch early December), with populations estimated at 21,648 breeding pairs – a 31% decrease from the 1940s (ACAP 2009, Sagar 2014). They are listed as vulnerable primarily due to fisheries interactions with moderate declines since the 1940's and uncertainty regarding the stabilization of this trend, as population increases since the mid 1980's appear to have stopped as of 2012 (Waugh et al. 1999b; IUCN 2012, Sagar 2014). Campbell albatrosses are generalist predators/scavengers with a high degree of behavioral flexibility; however, females tend to exhibit more behavioral consistency, primarily feeding over neritic waters on the Campbell Plateau, while males more often forage over deep oceanic waters along the Polar Front (Waugh et al. 2000; Sztukowski 2015). Males are 6.7% heavier than females on average (male mean body mass of 3.1 kg) but exhibit no significant difference in wing length (Sztukowski 2015). It is possible that wing loading differences lead to observed behavioral differences, though this is still unclear. Despite individual differences in foraging location, stable isotope analysis has shown that Campbell albatrosses forage at the same trophic level (Sztukowski 2015). Recent fecal DNA analysis shows that their diet consists primarily of fishes and jellyfishes, with cephalopods and crustaceans making up only a small proportion of the diet (McInnes et al. 2017). A previous study that analyzed regurgitations found a diet primarily of fishes (soft-bodied organisms such as jellyfishes would not have preserved well), but birds foraging over deeper oceanic waters consumed mainly cephalopods (Waugh et al. 1999a; Cherel et al. 2000).

Grey-headed albatrosses are a circumpolar species, with one of several breeding sites in the Subantarctic located on Campbell Island. Grey-headed albatrosses breed biennially from October to May (with chicks hatching in December) on steeper and more inland slopes of Campbell Island, often placing them along the inside edges of Campbell albatross colonies (ACAP 2010). They are listed as endangered and in decline globally, with populations on Campbell Island estimated at 8,611 breeding pairs – a steep 88% decrease from the 1940s – although it is unclear if this trend is continuing as a nonsignificant 14% increase was observed from 1995 and 2012 (Waugh et al. 1999b; IUCN 2013; Sagar 2014). Grey-headed albatrosses are more specialized foragers, primarily feeding over deep oceanic waters along the Polar Frontal Zone, though opportunistically exploiting areas over the plateau (Waugh et al. 2000). Phillips et al (2004) attributed deep ocean foraging behavior in grey-headed albatrosses from Bird Island, South Georgia, to higher wing loading allowing them to exploit windier areas compared to sympatrically breeding black-browed albatrosses. Grey-headed albatrosses weigh 3.3 kg on average, with males that are 14.7% heavier than females (Kroeger et al. 2019, Phillips et al. 2004), which is similar in mass to male Campbell albatrosses that exploit similarly windy regions near the Polar Front. The diet of grey-headed albatrosses from Campbell Island has been identified from regurgitation as primarily cephalopods taken from the Polar Frontal Zone, with some fish opportunistically consumed from over the plateau (Waugh et al. 1999a). Catry et al. (2004) suggest salps and jellyfish may contribute much more to grey-headed albatross diet than previously thought based on stomach temperature recordings that indicate prey high in water content.

Dissertation Overview

The stress hormone, corticosterone, regulates energy stores and can modulate foraging behaviors to allow animals to maintain homeostasis while coping with stress (Sapolsky et al. 2000; Angelier 2007a). This hormone is widely used to indicate environmental disturbances in wild populations (Landys et al. 2006; Satterthwaite et al. 2012; Busch and Hayward 2009), but it is not always predictable and can influence behaviors differently across ages, breeding stages, sexes, species, and environments (Angelier et al. 2007a; Crossin et al. 2012; Cottin et al. 2014). Therefore, in CHAPTER 2, I compare the functional role of corticosterone in Campbell and grey-headed albatrosses, and between Campbell albatrosses during incubation and early chick-rearing stages, to improve our understanding of how corticosterone modulates behaviors and energy stress. I predict that differences in life history traits, population dynamics, and foraging strategies will impact how corticosterone functions between species. I also predict that corticosterone modulates foraging behaviors differently to maintain energy balance across breeding stages because early chick-rearing is more energy intensive (Ricklefs 1983; Bevan et al. 1995). To address these predictions, I compare corticosterone concentrations before and after foraging trips across species and stages, then used path models to visualize and interpret interactions between variables such as food stress and foraging behaviors that may drive or be mediated by fluctuations in corticosterone.

Environmental stressors at sea can affect energy balance if adjustments to behaviors do not occur or if the adjustments are unable to compensate for the cost of the stressor. Although albatrosses have been well studied with respect to the energy efficiency of their flight (Shaffer et al. 2011), few studies compare daily energy expenditure within the same year from sympatrically breeding species with contrasting foraging strategies and life histories (but see Antolos 2017). In CHAPTER 3, I address the behavioral and environmental factors that influence energy balance in Campbell and grey-headed albatrosses during the energetically demanding early-chick rearing stage. I asses foraging trip costs during two consecutive breeding seasons using the doubly labelled water method to estimate daily energy expenditure (Speakman 1997). Using linear models, I evaluate the behavioral and environmental factors that predict energy expenditure to highlight the relative efficiency of different foraging strategies to improve our understanding of energetic responses to environmental variability. I predict that the biennially breeding grey-headed albatrosses will have greater energy costs consistent with life-history theory that long-lived animals favor self-maintenance over breeding attempts when energy deficits occur. Additionally, I predict that energy expenditure should not differ between years or sexes unless wind speeds or sea surface temperature varied, or sexes utilized different foraging habitat.

In CHAPTER 4, I use the estimates of daily energy expenditure from Chapter 2 to validate the use of a flight cost function, modified from previous studies (Felicisimo et al. 2008; Louzao et al. 2014), for Campbell and grey-headed albatrosses and estimate the mean flight costs of their incubation trips. I then use anisotropic cost analysis (Felicisimo et al. 2008) and wind-bird vector correlations (Crosby et al. 1993) to explore, respectively, flight-path cost choice and wind-use consistency in these species during incubation and early chick-rearing stages. This analysis allowed for a more nuanced understanding of flight strategy differences to reveal the interdependence of different species, stages, or sexes on particular wind patterns so that we may better predict their tolerance to forecasted changes in wind regimes. Altogether, these three chapters address the physiological and behavioral flexibility of two vulnerable seabird species that are expected to face cumulative environmental pressures over the next century. Because these species exhibit differing life histories, rely on different prey resources, exploit contrasting wind regimes, and have differing population trajectories, their relative responses to change can provide an indication of how a spectrum of other species may similarly respond during critical life stages.

References

ACAP. 2009. ACAP Species assessments: Campbell Albatross *Thalassarche impavida*. Agreem Conserv Albatrosses Petrels.

ACAP. 2010. ACAP Species assessment: Grey-headed Albatross *Thalassarche chrysostoma*. Agreem Conserv Albatrosses Petrels.

Adams A.N.J., C.R. Brown, and K.A. Nagy. 1986. Energy Expenditure of Free-Ranging Wandering Albatrosses *Diomedea exulans*. Physiol Zool 59:583–591.

Ainley D.G., G. Ballard, and K.M. Dugger. 2006. Comptetition among penguins and cetaceans reveals trhophic cascades in the western Ross Sea, Antarctica. Ecology 87:2080–2093.

Angelier F., C. Clément-Chastel, G.W. Gabrielsen, and O. Chastel. 2007a. Corticosterone and time-activity budget: An experiment with Black-legged kittiwakes. Horm Behav 52:482–491.

Angelier F., S.A. Shaffer, H. Weimerskirch, C. Trouvé, and O. Chastel. 2007b. Corticosterone and Foraging Behavior in a Pelagic Seabird. Physiol Biochem Zool 80:283–292.

Antolos M., S.A. Shaffer, H. Weimerskirch, Y. Tremblay, and D.P. Costa. 2017. Foraging behavior and energetics of albatrosses in contrasting breeding environments. Front Mar Sci 4:1–12.

Bevan R.M., P.J. Butler, A.J. Woakes, and P.A. Prince. 1995. The energy expenditure of free-ranging black-browed albatrosses. Philos Trans R Soc B Biol Sci 350:119–131.

Bost C. a., C. Cotté, F. Bailleul, Y. Cherel, J.B. Charrassin, C. Guinet, D.G. Ainley, et al. 2009. The importance of oceanographic fronts to marine birds and mammals of the southern oceans. J Mar Syst 78:363–376.

Burger A.E. and S. A. Shaffer. 2008. Application of tracking and data-logging technology in research and conservation of seabirds. Auk 125:253–264.

Busch D.S. and L.S. Hayward. 2009. Stress in a conservation context: A discussion of glucocorticoid actions and how levels change with conservation-relevant variables. Biol Conserv 142:2844–2853.

Canale C.I. and P.Y. Henry. 2010. Adaptive phenotypic plasticity and resilience of vertebrates to increasing climatic unpredictability. Clim Res 43:135–147.

Catry P., R.A. Phillips, B. Phalan, J.R.D. Silk, and J.P. Croxall. 2004. Foraging strategies of grey-headed albatrosses *Thalassarche chrysostoma*: integration of movements, activity and feeding events. Mar Ecol Prog Ser 280:261–273.

Chastel O., A. Lacroix, H. Weimerskirch, and G.W. Gabrielsen. 2005. Modulation of prolactin but not corticosterone responses to stress in relation to parental effort in a long-lived bird. Horm Behav 47:459–466.

Cherel Y., H. Weimerskirch, and C. Trouvé. 2000. Food and feeding ecology of the neritic-slope forager black-browed albatross and its relationships with commercial fisheries in Kerguelen waters. Mar Ecol Prog Ser 207:183–199.

Clarke A. 1988. Seasonality in the Antarctic marine environment. Comp Biochem Physiol 90B:461–473.

Constable A.J., J. Melbourne-Thomas, S.P. Corney, K.R. Arrigo, C. Barbraud, D.K. a Barnes, N.L. Bindoff, et al. 2014. Climate change and Southern Ocean ecosystems I: How changes in physical habitats directly affect marine biota. Glob Chang Biol 3004–3025.

Cooke S.J., D.T. Blumstein, R. Buchholz, T. Caro, E. Fernández-Juricic, C.E. Franklin, J. Metcalfe, et al. 2014. Physiology, Behavior, and Conservation. Physiol Biochem Zool 87:1–14.

Costa D.P. and P.A. Prince. 1987. Forgaing energetics of Grey-headed Albatrosses *Diomedia chrysostoma* at Bird Island, South Georgia. Ibis (Lond 1859) 129:149–158.

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.

Cottin M., A.J.J. Macintosh, A. Kato, A. Takahashi, M. Debin, T. Raclot, and Y. Ropert-Coudert. 2014. Corticosterone administration leads to a transient alteration of foraging behaviour and complexity in a diving seabird. Mar Ecol Prog Ser 496:249–262.

Crosby D.S., L.C. Breaker, and W.H. Gemmill. 1993. A proposed definition for vector correlation in geophysics: theory and application. Am Meteorol Soc 10:355–367.

Crossin G., P.N. Trathan, R. A. Phillips, K.B. Gorman, A. Dawson, K.Q. Sakamoto, and T.D. Williams. 2012. Corticosterone predicts foraging behavior and parental care in Macaroni Penguins. Am Nat 180:E31–E41.

Daunt F. and I. Mitchell. 2013. Impacts of climate change on seabirds. MCCIP Sci Rev 2013 125–133.

Dobson F.S. and P. Jouventin. 2010. The trade-off of reproduction and survival in slow-breeding seabirds. Can J Zool 88:889–899.

Doney S.C., M. Ruckelshaus, J. Emmett Duffy, J.P. Barry, F. Chan, C.A. English, H.M. Galindo, et al. 2012. Climate change impacts on marine ecosystems. Ann Rev Mar Sci 4:11–37.

Durant J.M., D. Hjermann, G. Ottersen, and N.C. Stenseth. 2007. Climate and the match or mismatch between predator requirements and resource availability. Clim Res 33:271–283.

Felicisimo A.M., J. Munoz, and J. González-Solís. 2008. Ocean surface winds drive dynamics of transoceanic aerial movements. PLoS One 3:1–7.

Froy H., R.A. Phillips, A.G. Wood, D.H. Nussey, and S. Lewis. 2013. Age-related variation in reproductive traits in the wandering albatross: Evidence for terminal improvement following senescence. Ecol Lett 16:642–649.

Ghalambor C.K., J.K. McKay, S.P. Carroll, and D.N. Reznick. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Funct Ecol 21:394–407.

Grémillet D. and A. Charmantier. 2010. Shifts in phenotypic plasticity constrain the value of seabirds. Ecol Appl 20:1498–1503.

Hays G.C., L.C. Ferreira, A.M.M. Sequeira, M.G. Meekan, C.M. Duarte, H. Bailey, F. Bailleul, et al. 2016. Key questions in marine megafauna movement ecology. Trends Ecol Evol 31:463–475.

Hoegh-Guldberg O. and J.F. Bruno. 2010. The impact of climate change on the world's marine ecosystems. Science 328:1523–1528.

Jouventin P. and F.S. Dobson. 2002. Why breed every other year? The case of albatrosses. Proc R Soc Lond B 269:1955–1961.

Louzao M., T. Wiegand, F. Bartumeus, and H. Weimerskirch. 2014. Coupling instantaneous energy-budget models and behavioural mode analysis to estimate optimal foraging strategy: an example with wandering albatrosses. Mov Ecol 2:1-15.

Kitaysky A.S., J.F. Piatt, S.A. Hatch, E. V. Kitaiskaia, Z.M. Benowitz-Fredericks, M.T. Shultz, and J.C. Wingfield. 2010. Food availability and population processes: severity of nutritional stress during reproduction predicts survival of long-lived seabirds. Funct Ecol 24:625–637.

Kitaysky A.S., J.C. Wingfield, and J.F. Piatt. 1999. Dynamics of food availability, body condition and physiological stress response in breeding Black-legged Kittiwakes. Funct Ecol 13:577–584.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuan, London.

Landys M.M., M. Ramenofsky, and J.C. Wingfield. 2006. Actions of glucocorticoids at a seasonal baseline as compared to stress-related levels in the regulation of periodic life processes. Gen Comp Endocrinol 148:132–149.

Lovenduski N.S. and N. Gruber. 2005. Impact of the Southern Annular Mode on Southern Ocean circulation and biology. Geophys Res Lett 32:1–4.

McInnes J.C., B.E. Deagle, P. Catry, S.N. Jarman, R.A.M. Lea, B. Raymond, R.A. Phillips, et al. 2017. High occurrence of jellyfish predation by black-browed and Campbell albatross identified by DNA metabarcoding. Mol Ecol 26:4831–4845.

McNamara J.M. 1998. Phenotypic plasticity in fluctuating environments: consequences of the lack of individual optimization. Behav Ecol 9:642–648.

Meynier L., P.C.H. Morel, D.D.S. Mackenzie, A. MacGibbon, B.L. Chilvers, and P.J. Duignan. 2008. Proximate composition, energy content, and fatty acid composition of marine species from Campbell Plateau, New Zealand. New Zeal J Mar Freshw Res 42:425–437.

Neil H.L., L. Carter, and M.Y. Morris. 2004. Thermal isolation of Campbell Plateau, New Zealand, by the Antarctic Circumpolar Current over the past 130 kyr. Paleoceanography 19:1-17.

Northcote L.C. and H.L. Neil. 2005. Seasonal variations in foraminiferal flux in the Southern Ocean, Campbell Plateau, New Zealand. Mar Micropaleontol 56:122–137.

Nunn G.B., J. Cooper, P. Jouventin, C.J.R. Robertson, and G.G. Robertson. 1996. Evolutionary relationships among extant albatrosses (Procellariiformes: Diomedeidae) established from complete cytochrome-B gene sequences. Auk 113:784–801.

Parmesan C. 2006. Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol Syst 37.

Phillips R.A., J.R.D. Silk, B. Phalan, P. Catry, and J.P. Croxall. 2004. Seasonal sexual segregation in two *Thalassarche* albatross species: Competitive exclusion, reproductive role specializaion or foraging niche divergence? Proc R Soc B Biol Sci 271:1283–1291.

Pinaud D. and H. Weimerskirch. 2005. Scale-dependent habitat use in a long-ranging central place predator. J Anim Ecol 74:852–863.

Raymond B., S.A. Shaffer, S. Sokolov, E.J. Woehler, D.P. Costa, L. Einoder, M. Hindell, et al. 2010. Shearwater foraging in the Southern Ocean: The roles of prey availability and winds. PLoS One 5.

Ricklefs R.E. 1983. Some considerations of the reproductive energetics of pelagic seabirds. Cooper Ornithol Scoiety 8:84–94.

Rickleffs R.E. 1990. Seabird Life Histories and the Marine Environment: Some Speculations. Colon Waterbirds 13:1–79.

Rodhouse P.G., P.A. Prince, P.N. Trathan, E.M.C. Hatfield, J.L. Watkins, D.G. Bone, E.J. Murphy, et al. 1996. Cephalopods and mesoscale oceanography at the Antarctic Polar Front: Satellite tracked predators locate pelagic trophic interactions. Mar Ecol Prog Ser 136:37–50.

Russell R.W., G.L. Hunt, K.O. Coyle, and R.T. Cooney. 1992. Foraging in a fractal environment: Spatial patterns in a marine predator-prey system. Landsc Ecol 7:195–209.

Rykaczewski R.R. and D.M. Checkley. 2008. Influence of ocean winds on the pelagic ecosystem in upwelling regions. Proc Natl Acad Sci U S A 105:1965–70.

Sagar P. 2014. Population estimates and trends of Campbell and grey-headed albatrosses at Campbell Island: Campbell and grey-headed albatross population estimates. NIWA report prepared for Department of Conservation.

Sandvik H., K.E. Erikstad, and B.E. Sæther. 2012. Climate affects seabird population dynamics both via reproduction and adult survival. Mar Ecol Prog Ser 454:273–284.

Sapolsky R.M., L.M. Romero, and A.U. Munck. 2000. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. Endocr Rev 1:55–89.

Satterthwaite W.H., A.S. Kitaysky, and M. Mangel. 2012. Linking climate variability, productivity and stress to demography in a long-lived seabird. Mar Ecol Prog Ser 454:221–235.

Shaffer S.A., D.P. Costa, and H. Weimerskirch. 2001. Behavioural factors affecting foraging effort of breeding wandering albatrosses. J Anim Ecol 70:864–874.

Shaffer S.A. 2011. A review of seabird energetics using the doubly labeled water method. Comp Biochem Physiol A Mol Integr Physiol 158:315–22.

Sims D.W., M.J. Witt, A.J. Richardson, E.J. Southall, and J.D. Metcalfe. 2006. Encounter success of free-ranging marine predator movements across a dynamic prey landscape. Proc Biol Sci 273:1195–1201.

Sokolov S. and S.R. Rintoul. 2007. On the relationship between fronts of the Antarctic Circumpolar Current and surface chlorophyll concentrations in the Southern Ocean. J Geophys Res Ocean 112:1–17.

Somero G.N. 2000. Unity in Diversity: A Perspective on the Methods, Contributions, and Future of Comparative Physiology. Annu Rev Physiol 62:927–37.

Somero G.N. 2010. The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine “winners” and “losers.” J Exp Biol 213:912–920.

Stevenson R.D. 2006. Ecophysiology and conservation: The contribution of energetics--introduction to the symposium. Integr Comp Biol 46:1088–92.

Suryan R.M., D.B. Irons, E.D. Brown, P.G.R. Jodice, and D.D. Roby. 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.

Sztukowski L.A. 2015. *Foraging ecology of the Campbell albatross: individual specialisation and fishery interactions*. PhD diss. Plymouth University and Université Pierre et Marie Curie.

Thorne L.H., M.G. Conners, E.L. Hazen, S.J. Bograd, M. Antolos, D.P. Costa, and S.A. Shaffer. 2016. Effects of El Niño-driven changes in wind patterns on North Pacific albatrosses. J R Soc Interface 13:20160196.

Thorne L.H., E.L. Hazen, S.J. Bograd, D.G. Foley, M.G. Conners, M. A. Kappes, H.M. Kim, et al. 2015. Foraging behavior links climate variability and reproduction in North Pacific albatrosses. Mov Ecol 3:27.

Tickell, W. L. N. 2000. Albatrosses. Pica, Sussex.

Tomlinson S., S.G. Arnall, A. Munn, S.D. Bradshaw, S.K. Maloney, K.W. Dixon, and R.K. Didham. 2014. Applications and implications of ecological energetics. Trends Ecol Evol 29:280–290.

Warham J ed. 1990. The petrels: their ecology and breeding systems. London, Academic Press.

Watson R.A., G.B. Nowara, S.R. Tracey, E.A. Fulton, C.M. Bulman, G.J. Edgar, N.S. Barrett, et al. 2013. Ecosystem model of Tasmanian waters explores impacts of climate-change induced changes in primary productivity. Ecol Modell 264:115–129.

Waugh S., H. Weimerskirch, and Y. Cherel. 1999a. Exploitation of the marine environment by two sympatric albatrosses in the Pacific Southern Ocean. Mar Ecol Prog Ser 177:243–254.

Waugh S.M., H. Weimerskirch, P.J. Moore, and P.M. Sagar. 1999b. 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.

Waugh S.M., H. Weimerskirch, Y. Cherel, and P.A. Prince. 2000. Contrasting strategies of provisioning and chick growth in two sympatrically breeding albatrosses at Campbell Island, New zealand. Condor 102:804–813.

Waugh S.M., H. Weimerskirch, P.J. Moore, and P.M. Sagar. 1999b. 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.

Weeks S., C. Steinberg, and B. Congdon. 2013. Oceanography and seabird foraging: within-season impacts of increasing sea-surface temperature on the Great Barrier Reef. Mar Ecol Prog Ser 490:247–254.

Weimerskirch H. 2007. Are seabirds foraging for unpredictable resources? Deep Res Part II Top Stud Oceanogr 54:211–223.

Weimerskirch H., C.P. Doncaster, and F. Cuenot-Chaillet. 1994. Pelagic seabirds and the marine environment: foraging pattern of wandering albatrosses in relation to prey availability and distribution. Proc R Soc Lond B 255:91–97.

Weimerskirch H., P. Inchausti, C. Guinet, and C. Barbraud. 2003. Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. Antarct Sci 15:249–256.

Weimerskirch H., T. Guionnet, J. Martin, S.A. Shaffer, and D.P. Costa. 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. Proc R Soc B Biol Sci 267:1869–1874.

Weimerskirch H., M. Louzao, and K. Delord. 2012. Changes in wind pattern alter albatross distribution and life-history traits. Science (80-) 335:211–214.

Weise M.J., D.P. Costa, and R.M. Kudela. 2006. Movement and diving behavior of male California sea lion (*Zalophus californianus*) during anomalous oceanographic conditions of 2005 compared to those of 2004. Geophys Res Lett 33.

Wikelski M. and S.J. Cooke. 2006. Conservation physiology. Trends Ecol Evol 21:38–46.

Wikelski M. and C. Thom. 2000. Marine iguanas shrink to survive El Niño. Nature 403:37–38.

Yoshimura J. and C.W. Clark. 1991. Individual adaptations in stochastic environments. Evol Ecol 5:173–192.

Young I.R., S. Zieger, and A.V. Babanin. 2011. Global trends in wind speed and wave height. Science 332:451–455.

Chapter 2

Variation in corticosterone levels in two species of breeding albatrosses with divergent life histories: responses to body condition and drivers of foraging behavior

Caitlin E. Kroeger, Daniel E. Crocker, David R. Thompson, Leigh G. Torres, Paul M. Sagar, and Scott A. Shaffer

Reprinted with permission.

Variation in Corticosterone Levels in Two Species of Breeding Albatrosses with Divergent Life Histories: Responses to Body Condition and Drivers of Foraging Behavior

Caitlin Kroeger[1,*]
Daniel E. Crocker[2]
David R. Thompson[3]
Leigh G. Torres[4]
Paul Sagar[3]
Scott A. Shaffer[5]
[1]Department of Ocean Sciences, Long Marine Lab, University of California, Santa Cruz, California 95060; [2]Department of Biology, Sonoma State University, Rohnert Park, California 92948; [3]National Institute of Water and Atmospheric Research, Wellington, New Zealand; [4]Department of Fisheries and Wildlife, Marine Mammal Institute, Oregon State University, Newport, Oregon 97365; [5]Department of Biological Sciences, San Jose State University, One Washington Square, San Jose, California 95192

Accepted 10/19/2018; Electronically Published 2/11/2019

ABSTRACT

Corticosterone (CORT) is a glucocorticoid hormone that maintains energy balance and can modulate foraging behaviors in seabirds. However, CORT responses are not always predictable under similar biophysical conditions and do not necessarily influence the same behaviors across breeding stages and species. To enhance our understanding of CORT's role as a proximate determinant of foraging behavior and energy maintenance, we examined the relationships between body condition, CORT, foraging behavior, and foraging success between two sympatric breeding albatross species with differing foraging strategies and life histories, the Campbell albatross (*Thalassarache impavida*) and the gray-headed albatross (*Thalassarache chrysostoma*), from Campbell Island, New Zealand. Pre- and postforaging CORT did not differ between species or stage, potentially as a result of behavioral plasticity or different functional roles of CORT across stages. Unexpectedly, body condition did not correlate with preforaging CORT during incubation, although a negative correlation was observed in Campbell albatrosses during the guard stage. Furthermore, CORT mediated foraging success in both species and stages, but CORT mediated foraging behavior only in incubation-stage Campbell albatrosses that had shorter foraging ranges with higher pretrip CORT. Additionally, CORT positively correlated with mass gain and the time elapsed since the last feeding event in guard-stage albatrosses. Our results highlight the complexity of CORT in mediating energy balance in free-ranging animals. Our results also support that if CORT is to be usefully interpreted, breeding stage must be considered because the physiological and behavioral functionality of CORT may differ across stages, with enhanced sensitivity to energy reserves during chick rearing.

Keywords: seabird, stress hormone, GPS tracking, foraging behavior, breeding stages, energy stress, path modeling.

Introduction

Glucocorticoid steroid hormones contribute to the maintenance of homeostasis through the regulation of metabolism, cardiac response, immune function, memory retention, and reproductive physiology in vertebrate animals (reviews in Sapolsky et al. 2000; Busch and Hayward 2009). The functional roles of these hormones have received wide attention in the literature, with considerable focus on how glucocorticoids influence behaviors that ultimately promote successful reproduction and survival (Wingfield et al. 1998; Sapolsky et al. 2000; Wingfield 2003). Corticosterone (CORT) is the primary glucocorticoid hormone released in birds, reptiles, and amphibians in response to perceived or unexpected stress, and functions to regulate energy stores (Moore and Jessop 2003; Wingfield and Sapolsky 2003; Busch and Hayward 2009). CORT is released when energy requirements exceed available energy, and circulating concentrations will remain high until physiological or behavioral changes restore homeostasis (McEwen and Wingfield 2003; Landys et al. 2006). For example, CORT is thought to mobilize glucose and fat stores to maintain homeostasis in fasting albatrosses (Hector and Harvey 1986), but in seabirds with more prolonged fasts, CORT concentrations may increase only with protein catabolism, as measured in king penguins (*Aptenodytes patagonicus*; Le Ninan et al. 1988). The threshold at which particular physiological and behavioral responses are induced by CORT is largely regulated by the activation and availability of specific receptors (Landys et al. 2006; Schoech et al. 2013), and thus the threshold for a stress response can differ between species or change conditionally with factors such as season

---

*Corresponding author; email: ckroeger@ucsc.edu.

Physiological and Biochemical Zoology 92(2):223–238. 2019. 1522-2152/2019/9202-8036$15.00. DOI: 10.1086/702656

and life-history stage (Romero 2002; Crespi et al. 2013). Despite conditional variation, CORT concentrations are often examined in wild populations to determine the presence and impact of environmental disturbances, especially since chronically elevated CORT can have reproductive or survival consequences (Landys et al. 2006; Busch and Hayward 2009; Satterthwaite et al. 2012).

Mechanistic responses to food stress (e.g., elicitation of CORT) have been extensively studied in seabirds because resources are generally patchy and ephemerally distributed in dynamic ocean environments, and seabirds often face a multitude of anthropogenic and environmental disturbances (Croxall et al. 2012; Sandvik et al. 2012; Satterthwaite et al. 2012). In seabirds, CORT is a well-known indicator of both population health and foraging conditions (Kitaysky et al. 2007; Benowitz-Fredericks et al. 2008; Bonier et al. 2009; Satterthwaite et al. 2012), and it modulates energy balance through foraging behaviors (Angelier et al. 2007*a*, 2008, 2009*a*). Circulating CORT, however, does not always respond predictably to biophysical conditions and does not necessarily influence the same behaviors across ages, breeding stages, sexes, species, and environments (Angelier et al. 2007*a*, 2007*c*; Crossin et al. 2012; Cottin et al. 2014). For example, body condition often influences circulating CORT in kittiwakes (Kitaysky et al. 1999; Angelier et al. 2007*a*), but this is not observed in all kittiwake breeding populations (Chastel et al. 2005) or other species, such as boobies (Lormée et al. 2003). Furthermore, elevated CORT differentially affects behaviors in related species: CORT reduces diving rate in chick-rearing Adélie penguins (*Pygoscelis adeliae*; Cottin et al. 2014) but increases diving rate in chick-rearing macaroni penguins (*Eudyptes chrysolophus*; Crossin et al. 2012). Thus, it is unclear how body condition impacts CORT or how CORT optimizes the energy balance of seabirds, given the equivocal results of published studies.

Despite the wealth of CORT studies on seabirds, few have directly compared CORT associations with behavioral and physiological traits between (1) closely related species with differing life histories and foraging behaviors or (2) breeding stages within a species, both of which limit our understanding of how CORT modulates behaviors and energy stress (but see Gorman 2015). Direct comparisons of sympatric species or of breeding stages within species can disentangle confounding factors that impact the direction and magnitude of CORT responses, thus reducing misinterpretations of CORT. Greater mechanistic resolution is essential if CORT is to be used as an indicator of environmental health or perturbations. Moreover, direct interspecific comparisons can help us understand how species with divergent life-history strategies may differentially regulate trade-offs between self-maintenance and reproduction in response to CORT (Jouventin and Dobson 2002; Lancaster et al. 2008; Crespi et al. 2013). In this study, we examined the relationship between body condition, endogenous CORT, foraging behaviors, and foraging success in two sympatric species of albatross during the same breeding season. This allowed us to minimize confounding factors that birds may experience while on land and focus on differences in the role of CORT in conferring flexibility between species and breeding stages.

We compared the functional role of CORT in Campbell albatrosses (*Thalassarache impavida*) and gray-headed albatrosses (*Thalassarache chrysostoma*). These two species breed sympatrically on Campbell Island, New Zealand, but have contrasting behavioral and life-history patterns. The annually breeding Campbell albatross population is abundant, stable, and endemic, with breeders foraging primarily on fishes in neritic regions (Waugh et al. 2000; Sagar 2014; McInnes et al. 2017). In contrast, the biennially breeding population of gray-headed albatrosses are less abundant, declining, and nonendemic, with breeders foraging primarily on squid over deep oceanic regions (Waugh et al. 1999*a*, 2000; Sagar 2014). Consequently, we predicted that these differences in life-history traits, population stability, and foraging strategies would covary with individual responses to energetic stress associated with biophysical conditions at sea, thus impacting how CORT functions between species. Furthermore, we compared responses of individuals across breeding stages within the same season to characterize changes in the role of CORT in energy maintenance through the modulation of foraging behaviors when energy demands increase during chick rearing (Ricklefs 1983; Bevan et al. 1995). Our objectives were (1) to compare CORT between species and breeding stages before and after foraging trips and (2) to create path models to visualize and interpret the interactions between variables that may be mediated by or drive fluctuations in CORT. These comparisons allowed us to visualize how differences between and within species, stages, and foraging environments relate to CORT function and mediated behaviors.

Methods

Ethics Statement

Field research was carried out under the following permits: San Jose State University Institutional Animal Care and Use Committee Protocol 976 and Wildlife Act Permit SO-26385-FAU.

Study Site and Species

This study was conducted during October–December 2013 on Campbell Island (52°S, 169°E) in the New Zealand Subantarctic. Campbell albatrosses were studied during the incubation ($N = 24$) and guard stages (early chick rearing; $N = 25$), with different individuals sampled across stages. Sympatric gray-headed albatrosses were studied only during the incubation stage ($N = 32$) because their eggs hatch later than Campbell albatrosses, which created a logistical conflict. Both species lay one egg per breeding season, and mates alternate between foraging at sea and attending the nest during both stages (Warham 1990). During the incubation stage, foraging trips are more extensive, requiring mates to fast on the nest for prolonged intervals (Campbell albatrosses: 17 ± 4 d; gray-headed albatrosses: 14 ± 4 d). Once the egg hatches, adults continue to trade attendance of the nest for about 3 wk to defend chicks from predators. During this guard stage, Campbell albatrosses shorten their foraging trips to 2–4 d.

Field Procedures

Each bird was captured on the nest for hormone sampling, body measurements, and Global Positioning System (GPS) device attachment just before switching with its returned mate and departing to sea. On capture, the head was covered with a cloth and blood was sampled within 3 min (pretrip CORT; Romero and Reed 2005). Blood was obtained from a brachial vein and transferred from the syringe into a vial (K_2 ethylenediaminetetraacetic acid BD Microtainer) and stored in a cool location until the samples could be centrifuged. Aseptic methods were used during all blood sampling procedures.

After sampling, birds were weighed in an upright sitting position using a modified pillowcase, and mass was recorded to the nearest 25 g using a spring-loaded Pesola scale. 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, Mobile Action Technology) were secured to dorsal feathers with Tesa cloth tape. All devices were waterproofed with heat-shrink tubing before deployment (total package mass: ~32 g with tape) and recorded a position at 5-min intervals. Birds were released near their nest, and the total time from release until departure to sea was recorded (1.8 ± 2.6 h) to determine whether pretrip CORT correlated with time until departure.

Researchers monitored nests daily for returning birds from approximately 0900 to 1900 hours local time. Returning birds were captured when back on the nest, and total time on the nest before capture was calculated for each bird from the GPS data. Birds were blood sampled within 3 min of recapture to obtain posttrip CORT and then weighed again to determine the success of foraging trips. GPS devices were removed, and birds that lost their device at sea were blood sampled only if the time of return was observed ($N = 4$).

Corticosterone Assays

To assess CORT concentrations, blood samples were centrifuged for 5 min at 6,000 rpm within 10 h of sampling. Plasma was removed from vials with a Hamilton syringe that was rinsed with distilled water at least three times between each use. Plasma volume (100–300 μL) was recorded to the nearest 0.5 μL, and the sample was placed in an O-ring cryovial with 70% ethanol at a 2 : 1 ratio of sample to ethanol. Each vial was wrapped in parafilm and stored in a cool, dark location. The ethanol preservation method reduces the absolute measure of corticosterone by approximately 13% but is considered effective for remote field locations (Goymann et al. 2007; Harding et al. 2009). Plasma samples were processed in September 2014 using a Corticosterone EIA Kit (Cayman Chemical 500655, Ann Arbor, MI) with a detection limit of 30 pg mL^{-1}. The assay method was validated separately for each species. We demonstrated parallelism of serial dilutions compared with the standard curve and assessed accuracy by measuring recovery of added standards (Campbell: 97.2% ± 3.1%; gray-headed: 101.2% ± 4.1%). Samples were lyophilized in a centrifuge overnight, and 0.5 mL of buffer was added to rehydrate and dilute each sample. Each reconstituted sample was agitated for 5 s before running the assays to measure total CORT in duplicate. Intra-assay and interassay coefficients of variation were 4.1% and 9.2%, respectively. Total CORT was measured because the accuracy of free CORT measurements and the actual bioavailability of bound versus unbound CORT is disputed, with some authors suggesting that measures of total CORT may be more ecologically relevant (Schoech et al. 2013).

Sex Determination

Bird sexes were predicted via discriminant function analyses using body morphometric data (Dechaume-Moncharmont et al. 2011). Details are reported in the appendix.

Body Condition

Body condition of each bird was determined separately for each species after pooling measurements from birds from previous field seasons with this study (Campbell albatross: $N = 68$; gray-headed albatross: $N = 121$). We used principal components analysis to reduce morphometric measurements (minimum bill depth, maximum bill length, and tarsus) into a body size index (Shaffer et al. 2001*b*) taken from the scores of the first principal component (PC; PC1 explained 59% variance in Campbell albatrosses and 64% variance in gray-headed albatrosses; biotools package, R 3.1; da Silva et al. 2017). To account for sexual dimorphism, we then calculated body condition as a scaled mass index (SMI; Peig and Green 2009). We used PC scores to calculate SMI because we found that they correlated better with mass than any individual measurement. To calculate pre- and posttrip SMI, we obtained a scaling exponent from the slope of the standard major axis regression of pretrip body mass and posttrip body mass separately regressed on the PC1 scores after all variables were log transformed. We standardized each raw PC1 score to the mean of the scores for each species. Because PC scores were calculated separately for each species, to compare the mass to length relationship between species, we pooled all measured birds and regressed mass on bill depth with a species effect and observed no difference in slopes, thus allowing us to compare intercepts.

Foraging Behavior, Effort, and Success

Before calculating foraging trip metrics, raw GPS data were filtered to remove points that exceeded travel speeds >150 km h^{-1} as gray-headed albatrosses are recorded sustaining mean ground speeds up to 127 km h^{-1} during a storm (Catry et al. 2004*a*). Points over land were also excluded. Remaining points were linearly interpolated to 1-min intervals (IKNOS toolkit, Matlab 2015a; MathWorks, Natick, MA). Kernel density utilization maps were created to map foraging areas using a smoothing factor of 1.5% and cell size of 0.4% of the mean X and Y spatial extents of the data, allowing us to optimize visualization at any scale (adehabitatHR package, R 3.1; Calenge 2006; fig. 1). Foraging trip metrics (i.e., total trip duration, maximum range, outbound azimuth, azimuth from colony to location at maximum range, total distance, average speed, daily number of landings on the water) were then calculated for each individual, with landings on the water determined by the occurrences where speed transitioned to <5 km h^{-1}.

To classify behavioral states at sea, data points that corresponded to area-restricted search (ARS; active foraging), rest, and

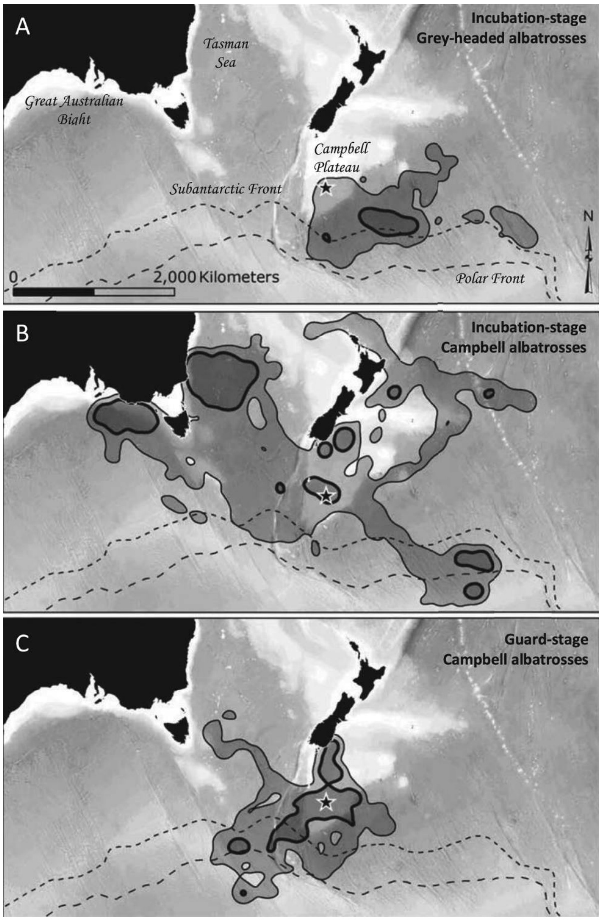


Figure 1. Kernel density utilization distribution map shown with 50% and 95% contours overlaid on bathymetry map from incubation-stage gray-headed albatrosses (*A*), incubation-stage Campbell albatrosses (*B*), and guard-stage Campbell albatrosses (*C*). Black shading denotes the land mask, and the star indicates Campbell Island; gray shading denotes bathymetry, with lighter to darker shading indicating increasing depth.

transit were determined using the residence in space and time method with dynamically scaled radii using R statistical software (Torres et al. 2017). To correct potentially misidentified resting points, we assigned all points with speeds <5 km h^{-1} as rest. During the breeding season, albatrosses typically rest on the water only after landing for a feeding event because take-offs are energetically expensive (Weimerskirch et al. 2000; Shaffer et al. 2001*a*). Therefore, we assume here that each transition from foraging to rest corresponds to a feeding event. Using these behavioral state classifications, we calculated the time elapsed between last feeding and returning to the nest to test whether anticipation of returning to the nest correlated with posttrip CORT values.

Foraging effort was calculated as the number of landings per day, and concentrated foraging effort was calculated as the total number of landings per minute of active foraging. Foraging success was then determined by the proportion of mass gained relative to the birds' initial body mass. To determine the concentrated foraging success (foraging efficiency), we calculated the proportion of mass gained per minute of active foraging.

Statistical Analysis

To identify differences between species and stages, we compared pretrip CORT, posttrip CORT, proportional mass gain, and foraging trip metrics between species and stages with two-sample *t*-tests. The change in CORT from pre- to postforaging trips was also tested within each species and stage using paired *t*-tests. Correlations between circular variables (azimuths and time of day or year) and linear variables (CORT concentrations and proportional mass gain) were tested with circular-linear regressions (circular package, R 3.3; Agostinelli and Lund 2017). For circular independent variables, we used the significant zero crossing of the derivative (SiZer) method (Chaudhuri and Marron 1999) to assess statistically significant gradients (NPCirc package, R 3.1; Oliveira et al. 2014). Difference in variance for circular data was assessed with one-criterion ANOVA (circular package, R 3.3; Agostinelli and Lund 2017). Linear relationships between variables were tested and visualized using path analysis (i.e., structural equation modeling; lavaan and semPlot packages, R 3.1; Rosseel 2012; Epskamp and Stuber 2017). Path analyses for endocrine studies are recommended by Dantzer et al. (2016) to identify direct and indirect effects of independent variables.

We constructed a structural equation model (SEM) to test our hypotheses regarding how the following variables interact for each species and stage: body condition, pretrip CORT, proportional mass gain, foraging activity metric (individually substituted maximum range, mean landing distance, total distance traveled, trip duration, foraging effort, concentrated foraging effort, and proportion of active foraging per trip), change in CORT, and time since last feeding event. Because some birds were not immediately captured on return, we removed values from change in CORT and time since last feeding event from all birds captured >1.5 h from return to the colony. Also, because mass changed faster with birds feeding chicks, we applied the same rule to proportional mass gain for guard-stage birds. Pretrip CORT and posttrip CORT were log transformed to meet the assumptions of normality for the model. The SEM function standardized variables for direct comparison within the model and handled missing values present in the different variables (lavaan package, R 3.1; Rosseel 2012). We used maximum likelihood estimation and did not use fit scores to choose a model because our goal was to test a specific hypothesis. The effect of sex on each variable assessed in the model was independently tested with two-sample *t*-tests to determine placement of the sex covariate in the path model. Significance for statistical analyses was assessed as $P < 0.05$.

Results

Foraging Behaviors

Analysis of foraging behaviors highlighted distinct differences in habitat preferences, foraging effort, and foraging success between species and stage that are essential for interpreting the interactions between variables in our path analysis. During foraging trips, incubation-stage gray-headed albatrosses consistently traveled to the southeast of Campbell Island to forage over deep oceanic water along the Subantarctic Front (fig. 1*A*). Conversely, incubation-stage Campbell albatrosses traveled to regions over the Campbell Plateau and exhibited much more variation ($F_{1,42} = 89.7$, $P < 0.001$) by also traveling nearly twice the maximum distance of any group from the breeding colony to the Polar Front, Tasman Sea, and Great Australian Bight (table 1; fig. 1*B*). Campbell albatrosses significantly reduced their foraging range during the guard stage (table 1) and exhibited less variation among individuals ($F_{1,38} = 13.9$, $P < 0.001$). Birds largely remained over the Campbell Plateau and traveled to nearer southwest regions of the Subantarctic and Polar Fronts (fig. 1*C*). While at sea, gray-headed albatrosses exhibited greater foraging effort (daily landings) than incubation-stage Campbell albatrosses but had marginally less foraging success (proportional mass gain; table 1). Foraging effort was similar between Campbell albatross stages, but foraging success was marginally lower during the guard stage (table 1). Concentrated foraging effort was equivalent between each group comparison, and concentrated foraging success was equivalent between species but higher in guard-stage albatrosses (table 1). In both species, sex affected proportional mass gain (fig. 2*A*, 2*B*), as females gained marginally more proportional mass during the incubation stage ($P < 0.1$). The time since the last feeding event was equivalent between all groups (table 1).

Pretrip and Posttrip Corticosterone Concentrations

The time elapsed before centrifugation of blood samples had no effect on pretrip CORT ($r^2 = 0.04$, $F_{1,34} = 2.3$, $P = 0.14$) or posttrip CORT ($r^2 = -0.02$, $F_{1,33} = 0.17$, $P = 0.7$). There was also no effect of sample storage duration on pretrip CORT concentrations (mean duration: 303 ± 18 d; $r^2 = -0.014$, $F_{1,62} = 0.15$, $P = 0.7$) or posttrip CORT concentrations (mean duration: 290 ± 13 d; $r^2 = -0.03$, $F_{1,33} = 0.004$, $P = 0.9$). Furthermore, there was no correlation between pretrip CORT and elapsed time between blood sampling and

Table 1: Species and stage comparisons

	Species comparison during incubation						Campbell albatross stage comparison					
Parameters	Gray-headed	*N*	Campbell	*N*	*t*	*P*	Incubation	*N*	Guard	*N*	*t*	*P*
Pretrip CORT (ug mL^{-1})	1.8 ± .9	32	2.0 ± .8	23	1.2	.25	2.0 ± .8	23	2.0 ± 1.4	25	.00	1.0
Posttrip CORT (ug mL^{-1})	.8 ± .5	17	.8 ± .3	16	−.08	.93	.8 ± .3	16	.9 ± .2	11	1.14	.27
Change in CORT	−1.1 ± 1.3	17	−1.4 ± .7	16	−.93	.36	−1.4 ± .7	16	−1.2 ± 1.7	11	.40	.70
Pretrip body condition	3.0 ± .26	36	...	...	...	...	3.0 ± .34	22	3.0 ± .20	22	.57	.58
Posttrip body condition	3.5 ± .33	26	...	...	...	...	3.7 ± .57	17	3.5 ± .21	11	−1.2	.23
Mass gain (%)	18 ± 10	26	23 ± 6	17	1.9	.06^{+}	23 ± 6	17	18 ± 7	11	−1.9	.07^{+}
Mass gain per ARS (%)	2.8e^{-3} ± 1.4e^{-3}	18	4.5e^{-3} ± 3.8e^{-3}	15	1.7	.11	4.5e^{-3} ± 3.8e^{-3}	15	1.5e^{-2} ± 1.05e^{-2}	10	3.0	.01*
Mass gain per day (%)	1.4 ± 1.0	21	1.5 ± 1.0	16	.19	.85	1.5 ± 1.0	16	7 ± 5	10	3.0	.01*
No. daily landings	26 ± 6	23	21 ± 4	20	−3.5	<.001***	21 ± 4	20	22 ± 9	20	.59	.56
No. landings per ARS	.05 ± .01	23	.06 ± .02	20	1.2	.26	.06 ± .02	20	.06 ± .03	20	.12	.90
Forage per trip (%)	36 ± 4	23	27 ± 8	20	−4.1	<.001***	27 ± 8	20	29 ± 8	20	.59	.56
Rest per trip (%)	40 ± 5	23	45 ± 9	20	2.2	.04*	45 ± 9	20	28 ± 13	20	−4.4	<.001***
Trip duration (d)	15 ± 3	27	17 ± 4	21	2.1	<.05*	17 ± 4	21	3 ± 1	20	−14.8	<.001***
Total distance (km)	7,398 ± 2,402	23	9,268 ± 2,630	20	2.4	.02*	9,268 ± 2,630	20	2,519 ± 1,466	20	−10.0	<.001***
Maximum range (km)	1,239 ± 571	23	2,268 ± 636	20	5.5	<.001***	2,268 ± 636	20	823 ± 511	20	−7.9	<.001***
Time since ARS bout (h)	4.5 ± 3.5	13	16.4 ± 17.2	14	2.6	.02*	16.4 ± 17.2	14	6.8 ± 6.7	10	−1.9	.07^{+}
Time since feeding (h)	10.3 ± 6.4	13	8.14 ± 5.4	14	−.90	.38	8.14 ± 5.4	14	8.7 ± 5.7	10	.23	.82

Note. *t*-tests were used to test for differences between species and stages. Data are presented as means ± SD. *N* = sample size. Ellipses indicate values that were removed from the analysis because they were noncomparable. CORT = corticosterone; ARS = area-restricted search.

$^{+}P < 0.10$.

$^{*}P < 0.05$.

$^{***}P < 0.001$.

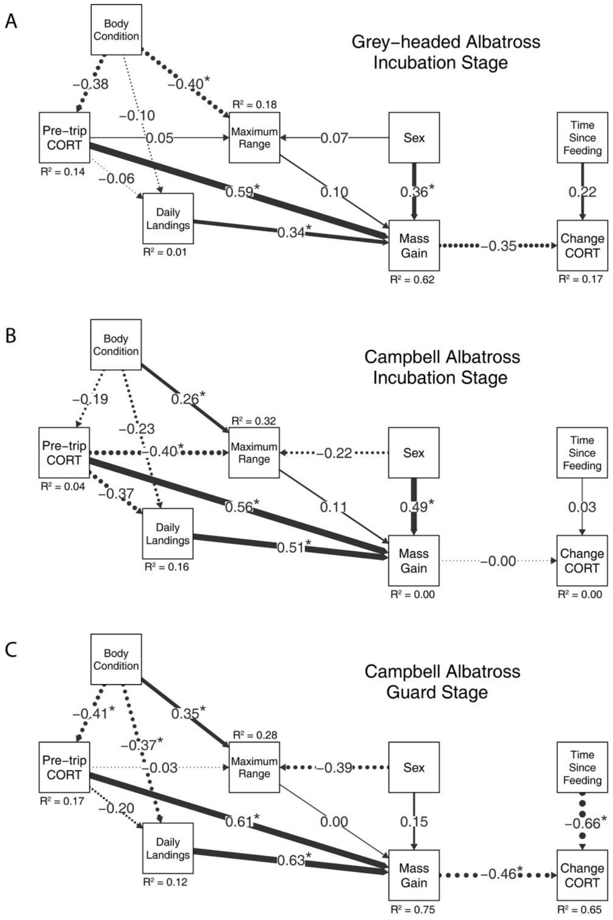


Figure 2. Path diagrams of structural equation models (SEMs) showing relationships between ecological drivers of corticosterone (CORT) and responses to CORT within each group (incubation-stage gray-headed albatrosses, incubation-stage Campbell albatrosses, and guard-stage Campbell albatrosses). Diagrams illustrate the difference between species in pre-CORT as a driver of foraging range during incubation and the differences in drivers of postforaging CORT across stages in Campbell albatrosses. Additionally, the diagram depicts a strong relationship between pre-CORT as a driver of mass gain in each group, as the widths of the arrow lines in each diagram are proportional to the standardized partial regression coefficients from the SEM. Dotted lines depict negative correlations, and solid lines depict positive correlations. Significant ($P < 0.05$) relationships are indicated with an asterisk.

recorded departures for any group (mean time until departure was 1.4 ± 2.5 h; $r^2 = 0.007$, $F_{3,56} = 1.13$, $P = 0.3$).

The effect of elapsed time between a birds' return to the colony and final sampling (hereafter, elapsed time) on posttrip CORT was also not significant for either species during the incubation stage (gray-headed albatrosses: $r^2 = 0.012$, $F_{1,23} = 1.13$, $P = 0.3$; Campbell albatrosses: $r^2 = 0.003$, $F_{1,18} = 1.06$, $P = 0.3$). However, posttrip CORT was positively correlated with elapsed time at a decreasing rate in guard-stage Campbell albatrosses ($r^2 = 0.51$, $F_{1,16} = 18.4$, $P < 0.001$; fig. 3*A*). Additionally, proportional mass gain was negatively correlated with elapsed time at a decreasing rate in Campbell albatrosses feeding chicks ($r^2 = 0.32$, $F_{1,16} = 9.0$, $P < 0.01$; fig. 3*B*). Last, posttrip CORT was significantly higher during the guard stage compared with concentrations measured during the incubation stage for Campbell albatrosses by a mean of 0.36 μg mL^{-1} ($t = 3.0$, df $= 34.3$, $P < 0.01$). To account for possibility of energy loss from feeding chicks, we excluded posttrip CORT values from birds sampled beyond 1.5 h after return. This threshold matched the limit used for our path model variables and eliminated the difference in posttrip CORT between stages and the curvilinear relationships in figure 3.

Pretrip CORT was similar between species and stages (table 1). CORT decreased significantly across foraging trips in all groups ($P < 0.05$), and posttrip CORT was not significantly different between species and stages (table 1). However, as a proportional change from pretrip concentration, CORT decreased marginally less in guard-stage Campbell albatrosses compared with incubation-stage albatrosses (table 1). The proportional reduction in CORT was not significantly different between species (table 1). In all groups, there were no observed effects of sex, time of day, or time of year on pretrip or posttrip CORT ($P > 0.1$); the only observed differences between groups were in proportional changes in CORT and those previously influenced by elapsed time on the nest before recapture in guard-stage Campbell albatrosses.

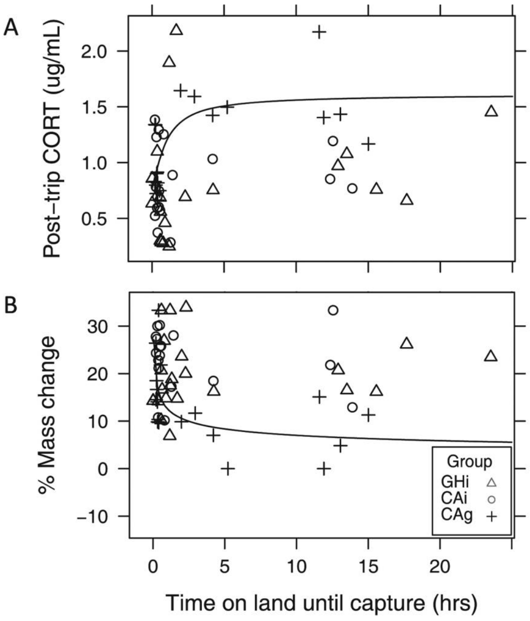


Figure 3. Plots of posttrip corticosterone (CORT) concentrations (*A*) and proportional change in body mass (*B*) regressed on elapsed time from returning to the nest until sampling of posttrip CORT. Guard-stage Campbell albatrosses (CAg) exhibited significant effects of sampling time on posttrip CORT and on change in body mass (depicted by lines). GHi = incubation-stage gray-headed albatrosses; CAi = incubation-stage Campbell albatrosses.

Corticosterone as Response

Path analysis was used to test the response of CORT to initial body condition and the replenishment of energy stores at sea and to observe path differences between species and stage. Pretrip CORT responded negatively to pretrip body condition only in guard-stage Campbell albatrosses (fig. 2*C*), despite having equivalent body condition to incubation-stage Campbell albatrosses (table 1). Campbell albatrosses had less mass per measure of bill depth than gray-headed albatrosses (fig. 4), suggesting that Campbell albatrosses had either lower body condition or structural size differences. No relationship was observed between pretrip CORT and body condition in incubation-stage Campbell or gray-headed albatrosses (fig. 2*A*, 2*B*). In guard-stage Campbell albatrosses, foraging effort responded negatively to pretrip body condition, but this relationship was not mediated by pretrip CORT (fig. 2*C*). The restoration of CORT after foraging (percent change in CORT) responded to proportional mass gain only in guard-stage Campbell albatrosses, where birds that gained more mass had a greater reduction in CORT (fig. 2*C*). Proportional change in CORT also responded negatively to the time since last feeding within only this group (fig. 2*C*). The restoration of CORT showed no response to foraging effort in any group ($P > 0.05$), so we removed the path between these variables to simplify and improve the model. Although CORT did not respond to at-sea behavior, concentrations responded to body condition and the quantity and timing of replenishment of energy reserves in guard-stage Campbell albatrosses.

Corticosterone as a Driver

The path model was also used to examine whether pretrip CORT influenced behaviors at sea and foraging success and how these relationships compared between species and stage. Albatrosses in all groups that had higher pretrip CORT concentrations experienced greater foraging success (proportional mass gain; fig. 2). Foraging effort (daily water landings) was also positively correlated with foraging success in all groups (fig. 2). Pretrip CORT was not a driver of foraging effort in any group, and the relationship between pretrip CORT and foraging success was not mediated by foraging effort (fig. 2). When foraging effort was substituted with other foraging behavior metrics in the path model, we found that maximum range was negatively predicted by pretrip CORT among incubation-stage Campbell albatrosses, as was mean landing distance; however, these foraging metrics were highly correlated ($r^2 = 0.92$, $F_{1,19} = 8.2$, $P < 0.001$), so only the former was retained in the path model (fig. 2*B*). None of the remaining foraging metrics were predicted by pretrip CORT for any group in our model.

Although pretrip CORT predicted proportional mass gain, this relationship was not mediated by maximum range. Among incubation-stage Campbell albatrosses, separately performed circular-linear regressions revealed that maximum range correlated with maximum range azimuth ($b \pm \mathrm{SE} = -3.2e^{-4} \pm 8.4e^{-5}$, $t = 3.8$, $P < 0.001$) and that pretrip CORT predicted maximum range azimuth ($b \pm \mathrm{SE} = 0.19 \pm 0.07$, $t = 2.6$, $P < 0.01$) while maximum range azimuth was also correlated with proportional mass gain ($b \pm \mathrm{SE} = 4.5 \pm 1.4$, $t = 3.2$, $P < 0.001$; fig. 5). Thus,

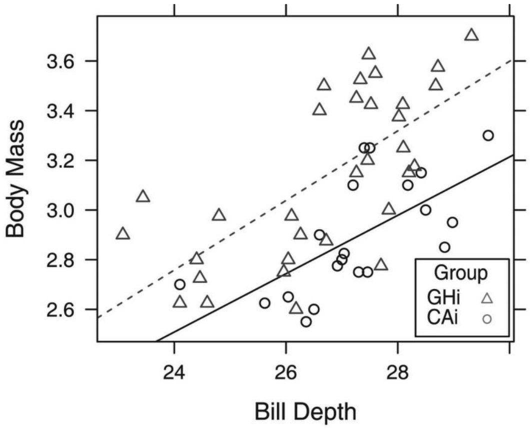


Figure 4. Regression lines depicting 23 differences in body mass per measure of bill depth in incubating Campbell and gray-headed albatrosses. A significant difference in intercept ($F_{2,49} = 27.03$, $P < 0.001$) but not slope was found. GHi = incubation-stage gray-headed albatrosses; CAi = incubation-stage Campbell albatrosses.

CORT appeared to drive mass gain within all groups, and foraging location may mediate this relationship in incubation-stage Campbell albatrosses, as indicated by circular statistics, but these circular variables could not be included as mediators in our path model.

Discussion

Previous studies on various seabird species have demonstrated significant relationships between CORT and foraging locations (Angelier et al. 2007*b*; Benowitz-Fredericks et al. 2008; Harding et al. 2013; Schultner et al. 2014), foraging effort (Angelier et al. 2008; Doody et al. 2008; Cottin et al. 2014), and foraging success (Angelier et al. 2007*a*, 2007*b*). We found that relationships varied depending on species and stage. Additionally, we did not identify any influence of CORT on foraging effort, but higher pretrip CORT predicted an increase in foraging success in all groups. The only relationship between CORT and foraging behavior was detected in incubation-stage Campbell albatrosses, which demonstrated greater diversity in foraging strategy (fig. 1*B*), with higher CORT predicting trips with shorter maximum range. Although CORT did not appear to drive behaviors in the other groups, CORT did relate to body condition and the quantity and timing of food consumption in guard-stage Campbell albatrosses, potentially as a result of the higher energy demands associated with this stage. Regardless of shifting energy requirements and differing foraging strategies, CORT concentrations were remarkably similar between groups.

Comparisons of Pretrip and Posttrip Corticosterone Concentrations

Given that albatrosses of each species and stage exploit different regions at sea and employ different foraging strategies while doing so—combined with differences in fasting durations and energy demands—we expected that pretrip CORT would differ between both species and stages. Specifically, we predicted that Campbell albatrosses would have higher pretrip CORT than gray-headed albatrosses because of energy reserve depletion from longer fasts at the nest (Hector and Harvey 1986; Cherel et al. 1994; Angelier et al. 2007*c*). Prolonged fasts while incubating the egg should create the need to mobilize energy in preparation for greater travel distances to replenish reserves while foraging (Angelier et al. 2007*b*). Furthermore, we expected pretrip CORT to be even higher in guard-stage Campbell albatrosses because of the greater energy demands of chick rearing and associated changes in foraging activity (Kitaysky et al. 1999*b*; Lormée et al. 2003). However, genetic differences between species and phenotypic variability may confound our expectations and subsequent interpretations (Garland and Adolph 1994). Although groups had different fasting durations, there were no significant differences in pretrip CORT, consistent with no observed differences in pretrip body condition between stages. Despite greater fasting durations and potentially lower body condition than gray-headed albatrosses, incubation-stage Campbell albatrosses are likely above a minimum threshold to elicit an increase in CORT (Angelier et al.

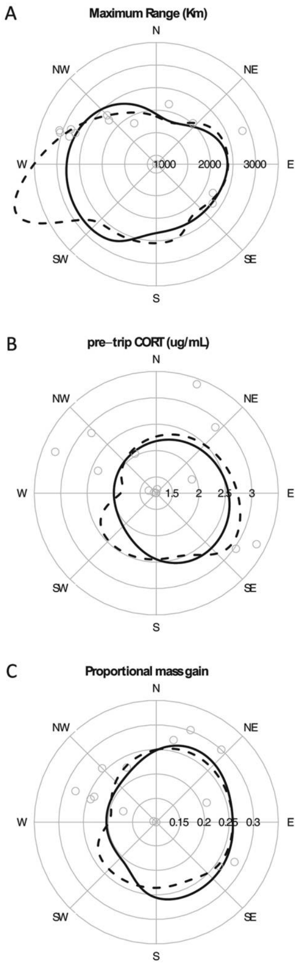


Figure 5. Nonparametric regression plots for incubation-stage Campbell albatrosses using the Nadaraya-Watson estimator (solid lines) and the local-linear estimator (dashed lines) for circular linear data, taking the von Mises distribution as kernel. *A*, Maximum range relates to foraging location (bearing to the maximum range); thus, the relationship between pretrip corticosterone (CORT) and maximum range may be driven by location. *B*, *C*, Pretrip CORT and foraging success also relate to foraging location.

2009*b*; Romero et al. 2009). Mean pretrip CORT concentrations also did not reflect observed differences in foraging strategy between groups. If specific foraging behaviors incur different energetic costs (e.g., Weimerskirch et al. 2000; Shaffer et al. 2001*a*), then pretrip CORT should adjust accordingly in preparation (Romero 2002); thus, our results suggest that the strategies employed did not require different levels of energy mobilization between groups, at least not enough to initiate the release of CORT immediately before trips.

Given differences regarding life-history strategy, population stability, and population abundance on Campbell Island, it is possible that Campbell albatrosses are more energy-efficient central place foragers in this region than gray-headed albatrosses, lowering CORT concentrations in general, and thus offsetting our expected increase in pretrip CORT. This is further supported by the observation that pretrip CORT was lower than expected in guard-stage Campbell albatrosses because the energy demands of this stage are generally high in comparison to incubation (Ricklefs 1983). Body condition of guard-stage albatrosses did not decline as might be expected (Weimerskirch et al. 1997; Weimerskirch 1998; Clarke 2001; Shaffer et al. 2001*b*), especially since near-shore resources can be less productive (Baudini and Hyrenbach 2003; Thorne et al. 2015). Furthermore, concentrated foraging success was higher in guard-stage albatrosses. These results indicate that food may have been regionally abundant for guard-stage albatrosses during our study year, which may have caused reduced energetic stress and offset the need to elevate CORT. CORT secretion may have been additionally attenuated because of this period of high parental investment (Angelier and Chastel 2009; Krause et al. 2016). Alternatively, our use of ethanol to preserve CORT could have affected concentrations, but CORT stored in ethanol does not degrade over long time periods (Goymann et al. 2007), and we found no effects of storage duration on CORT. Overall, pretrip CORT was remarkably similar between both species and stages despite the differences in behavior and energy needs, demonstrating an ability to exploit resources over large oceanic expanses to obtain sufficient energy and maintain homeostasis.

Because CORT functions to mobilize energy stores and promote locomotor activity in birds (Breuner et al. 1998; Angelier et al. 2007*a*), circulating concentrations typically increase before foraging and decrease when nutritional needs have been restored and rest is initiated (Angelier et al. 2007*b*, 2008). Unsurprisingly, posttrip CORT was lower than pretrip CORT. There were also no significant differences between groups in posttrip CORT (table 1), suggesting that albatrosses experienced similar conditions of food availability (Kitaysky et al. 2007; Benowitz-Fredericks et al. 2008; Barrett et al. 2015). Our results also suggest that CORT rose rapidly from lower posttrip concentrations in guard-stage birds, given the relationship between time on the nest and posttrip CORT (fig. 2*A*), although additional sampling would be required to confirm this trend. The loss of food fed to the chick (Kitaysky et al. 1999) and the need to remobilize sooner than during incubation may lead to a rapid increase in CORT on return to the nest. Given the increased energy demands, posttrip CORT during the guard stage may prove to be a good indicator of food abundance in years when ocean productivity is low, as CORT is likely to remain elevated if energy needs are not met.

Response of Corticosterone to Body Condition, Foraging Behavior, and Foraging Success

We observed an elevation of pretrip CORT resulting from the depletion of nesting energy reserves only in guard-stage Campbell albatrosses (fig. 2*C*). It is counterintuitive that the other groups did not exhibit a response of pretrip CORT to energy reserves, as guard-stage pretrip body condition was similar to that of incubation-stage birds. This result suggests that, in guard-stage birds, the CORT response is more sensitive to deficits in energy reserves, with a lower threshold below which CORT responds to stressors because of the anticipation of greater energy demands. Body condition also predicted foraging behaviors in this group, as it was negatively correlated with foraging effort and positively correlated with maximum range; however, we found no indirect effect of body condition on either metric through pretrip CORT. These results are consistent with the idea that pretrip CORT influences foraging behaviors in synergy with body condition rather than as a result of body condition (Landys et al. 2006; Angelier et al. 2007*a*). Nonetheless, our results reveal that pretrip CORT responds to pretrip body condition differently between stages, with guard-stage albatross CORT responses more sensitive to energy demands.

Similar to pretrip CORT, the response of posttrip CORT also depends on stage: the timing and proportion of food intake contributes to the restoration of posttrip CORT in guard-stage Campbell albatrosses but not in incubation-stage albatrosses. In guard-stage Campbell albatrosses, CORT decreased more with respect to pretrip concentrations when proportional mass gain and the time since last feeding were greater (fig. 2*C*). The latter relationship suggests that the anticipation of sitting on the nest contributes to CORT reduction (Angelier et al. 2008). Harvey and Klandorf (1983) show that CORT declines within 30–45 min of visually locating food and then begins to increase as time passes, with concentrations rising more slowly in chickens that have consumed more food. Therefore, a longer time since last feeding should allow CORT to continue to rise, unless the cessation of foraging and anticipation of rest supersedes the rise of CORT with time.

Although the above relationship was not seen in incubation-stage birds, the time since the last feeding event was equivalent between stages despite greater distances traveled and similar travel speeds, suggesting that incubation-stage birds augment their energy reserves as they return to the colony. Because time since last foraging, proportional mass gain, and posttrip CORT were similar between stages (table 1), we expected similar relationships among stages. Our results contradicted this prediction, which may indicate various possibilities. First, CORT could be modulated differently between stages, perhaps through sensitivity changes at some level of the hypothalamic–pituitary–adrenal axis, as seen in aging seabirds (Heidinger et al. 2008), or with changes to CORT receptors or clearance rates (Schoech et al. 2013). Second, the timing of bulk food consumption may play a larger role in modulating CORT than the timing of last feeding. Third, because incubation-stage birds had more time to rest, they may land without feeding more often than guard-stage birds. Consequently, we may be unable to accurately measure time since last feeding events without using devices such as stomach temperature loggers that precisely measure food ingestion rates (Wilson et al. 1995; Catry et al. 2004*b*). Regardless, our results support that the restoration of CORT is at least partially dependent on the quantity of food consumed in albatrosses (Angelier et al. 2007*b*), with mass gain and the anticipation of rest contributing to CORT restoration in guard-stage birds that may be more responsive to energy requirements because of higher parental investment at this stage.

Foraging Strategy and Corticosterone as Drivers of Mass Gain

Foraging success was driven by foraging effort in all groups, with no indirect effect of pretrip CORT on foraging success through foraging effort (fig. 2). Incubation-stage gray-headed albatrosses had both greater effort and marginally less success per trip than incubation-stage Campbell albatrosses; however, the two species exhibited equal foraging effort and success per active search period (table 1). Therefore, differences in foraging effort per trip were likely driven by the greater proportion of transit time in incubation-stage Campbell albatrosses, which should not cause substantial energy deficits (Pennycuick 1982; Costa and Prince 1987; Weimerskirch et al. 2000). Additionally, because Campbell albatrosses target more energy-dense prey (i.e., more fish than squid; Waugh et al. 1999*b*), they may gain more mass per unit of effort (Clarke and Prince 1980). Overall, foraging success appeared to be largely driven by foraging strategies that differed between species and not indirectly mediated by CORT.

Pretrip CORT predicted only maximum range in incubation-stage albatrosses, and this relationship did not appear to mediate foraging success. We expected a positive correlation between pretrip CORT and maximum range on the basis of observations of wandering albatrosses, *Diomedea exulans* (Angelier et al. 2007*b*), and because longer trips should elevate CORT if pretrip CORT prepares birds for locomotor activity at sea (Kitaysky et al. 2001). Conversely, we found that albatrosses with higher pretrip CORT had shorter maximum ranges (fig. 2*B*). On the basis of the three-way correlation between maximum range, pretrip CORT, and maximum range azimuth (fig. 5), it is possible that pretrip CORT actually predicts foraging location. Because Campbell albatrosses exhibit individual specialization (Sztukowski 2016), experience may influence pretrip CORT levels, although the relationship between CORT and breeding experience varies in other albatross species (Angelier et al. 2006, 2007*c*). Breeding experience may be more directionally evident in the Campbell albatrosses that had high foraging location variability and were less reliant on the polar front than gray-headed albatrosses. Additionally, incubation-stage Campbell albatrosses may have more diversity in prey type on the basis of foraging habitat preference, and the different strategies required may relate to pretrip CORT. Last, because foraging location also correlated with proportional mass gain in this group (fig. 5), it is possible that the mechanism by which pretrip CORT affects foraging success is through location.

Conclusion

Despite differences in life history and foraging strategy between species, the mobilization of CORT was similar, and each species and stage appeared to maintain homeostasis. Guard-stage albatrosses that had higher energy demands were most sensitive to changes in energy balance; therefore, measuring CORT after guard-stage foraging trips may be most informative for monitoring the status of foraging conditions for threatened albatrosses. The role of CORT in guard-stage gray-headed albatrosses needs further study to evaluate whether they exhibit a similar pattern as in Campbell albatross. Among incubation-stage Campbell albatrosses with diverse foraging locations, pretrip CORT appears to be related to foraging destination; however, further investigation needs to be done to determine whether pretrip CORT is more indicative of breeding experience. The consistent relationship between CORT and foraging success in every group and our inability to determine a mechanism for this relationship indicate that we were unable to fully capture behavioral patterns with our methods. We suggest that along with examining the potential effects of age-related experience, future studies should use additional biologging devices (e.g., accelerometers, wet-dry loggers) to capture more fine-scale behaviors.

Acknowledgments

We thank Allyson Larned and Ray Bucheit for their tireless assistance in the field, Dr. Lisa Sztukowski for providing supplemental data, Dr. Luis Huckstadt and Dr. Marm Kilpatrick for help with data processing and analyses, Jonathan Felis for his expertise in mapping, and Henk Haazen and crew for safe transportation to and from Campbell Island. We also thank the New Zealand Department of Conservation for permitting this project and providing logistical support. The National Institute of Water and Atmospheric Research made the expedition to Campbell Island possible with funding from the New Zealand Ministry of Business, Innovation, and Employment. The Friends of Long Marine Lab Graduate Student Research Award funded laboratory analyses.

APPENDIX

Sex Determination

Bird sexes were predicted via discriminant function analyses using body morphometric data (Dechaume-Moncharmont et al. 2011). Linear functions for each species were created from postforaging mass, minimum bill depth, and wing chord of molecularly sexed birds from previous field seasons. Molecular sexes were identified by amplification of the sex chromosomes with polymerase chain reaction using the methods of Quintana et al. (2008), with minor modifications. The Campbell albatross data were supplemented with additional molecularly sexed birds from a previous study (Sztukowski et al. 2017) to increase predictive power of the linear function ($N = 68$; MASS package, R 3.1; Venables and Ripley 2002); however, these data were not available for our gray-headed albatross linear function ($N = 31$).

Our 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. Box's *M*-tests confirmed homogeneity of the variance-covariance matrices of the morphometric measurements for each species (biotools package, R 3.1; da Silva et al. 2017). Discriminant function analysis correctly assigned the sex of Campbell albatrosses 79% of the time with a cutoff of 0.10 using the regression $Y = -2.033 \times$ postforaging mass $-0.197 \times$ minimum bill depth $-0.045 \times$ wing chord, and it correctly assigned the sex of gray-headed albatrosses 87% of the time with a cutoff of 0.30 using the regression $Y = -1.344 \times$ postforaging mass $- 0.706 \times$ minimum bill depth $- 0.061 \times$ wing chord.

We used mass as a predictor in our discriminant function analysis because it provided the greatest separation of sexes for both species and improved the accuracy of our predictions by 7% in Campbell albatrosses and 3% in gray-headed albatrosses. The discriminant functions were applied to predict sex using the mean mass (from the pre- and postforaging masses) of the unknown birds. We used postforaging body mass to build our functions for each species because molecularly sexed birds were from the guard stage, and the postforaging body masses from the molecularly sexed birds were equivalent to the mean body masses for unknown birds of the same species in our study, regardless of breeding stage (table A1). This method provided a sample size of 30 male and 17 female Campbell albatrosses for subsequent analyses, which together matched 83% of 24 observation-based sex estimations, and a sample size of 21 male and 15 female gray-headed albatrosses, which together matched 100% of 22 observation-based sex estimations.

Table A1: Body mass comparisons

Species	Postforage mass of known sexes	*N*	Mean mass of unknown sexes	*N*	*t*	*P*
	Guard stage		Incubation stage			
Gray-headed	3.4 ± .3	29	3.4 ± .3	37	.3	.7
Campbell	3.2 ± .4	64	3.2 ± .3	23	.02	1.0
	Guard stage		Guard stage			
Campbell	3.2 ± .4	64	3.3 ± .3	22	−.7	.5

Note. *t*-tests were used to test for mass (kg) differences before and after foraging. All data are presented as means ± SD. N = sample size.

Literature Cited

Agostinelli C. and U. Lund. 2017. R package 'circular': circular statistics. Version 0.4-93. https://r-forge.r-project.org/projects/circular/.

Angelier F., C.-A. Bost, M. Giraudeau, G. Bouteloup, S. Dano, and O. Chastel. 2008. Corticosterone and foraging behavior in a diving seabird: the Adélie penguin, *Pygoscelis adeliae*. Gen Comp Endocrinol 156:134–44.

Angelier F. and O. Chastel. 2009. Stress, prolactin and parental investment in birds: a review. Gen Comp Endocrinol 163: 142–148.

Angelier F., C. Clément-Chastel, G.W. Gabrielsen, and O. Chastel. 2007*a*. Corticosterone and time-activity budget: an experiment with black-legged kittiwakes. Horm Behav 52: 482–491.

Angelier F., C. Clément-Chastel, J. Welcker, G.W. Gabrielsen, and O. Chastel. 2009*a*. How does corticosterone affect parental behaviour and reproductive success? a study of prolactin in black-legged kittiwakes. Funct Ecol 23:784–793.

Angelier F., B. Moe, S. Blanc, and O. Chastel. 2009*b*. What factors drive prolactin and corticosterone responses to stress in a long-lived bird species (snow petrel *Pagodroma nivea*)? Physiol Biochem Zool 82:590–602.

Angelier F., S.A. Shaffer, H. Weimerskirch, and O. Chastel. 2006. Effect of age, breeding experience and senescence on corticosterone and prolactin levels in a long-lived seabird: the wandering albatross. Gen Comp Endocrinol 149:1–9.

Angelier F., S.A. Shaffer, H. Weimerskirch, C. Trouvé, and O. Chastel. 2007*b*. Corticosterone and foraging behavior in a pelagic seabird. Physiol Biochem Zool 80:283–292.

Angelier F., H. Weimerskirch, S. Dano, and O. Chastel. 2007*c*. Age, experience and reproductive performance in a long-lived bird: a hormonal perspective. Behav Ecol Sociobiol 61:611–621.

Barrett R.T., K.E. Erikstad, H. Sandvik, M. Myksvoll, S. Jenni-Eiermann, L. Kristensen, T. Moum, T.K. Reiertsen, and F. Vikebø. 2015. The stress hormone corticosterone in a marine top predator reflects short-term changes in food availability. Ecol Evol 5:1306–1317.

Baudini C.L. and D. Hyrenbach. 2003. Biogeography of proccellariiform foraging strategies: does ocean productivity influence provisioning? Mar Ornithol 31:101–112.

Benowitz-Fredericks Z.M., M.T. Shultz, and A.S. Kitaysky. 2008. Stress hormones suggest opposite trends of food availability for planktivorous and piscivorous seabirds in 2 years. Deep-Sea Res II 55:1868–1876.

Bevan R.M., P.J. Butler, A.J. Woakes, and P.A. Prince. 1995. The energy expenditure of free-ranging black-browed albatrosses. Philos Trans R Soc B 350:119–131.

Bonier F., P.R. Martin, I.T. Moore, and J.C. Wingfield. 2009. Do baseline glucocorticoids predict fitness? Trends Ecol Evol 24:634–642.

Breuner C.W., A.L. Greenberg, and J.C. Wingfield. 1998. Noninvasive corticosterone treatment rapidly increases activity in Gambel's white-crowned sparrows (*Zonotrichia leucophrys gambelii*). Gen Comp Endocrinol 111:386–394.

Busch D.S. and L.S. Hayward. 2009. Stress in a conservation context: a discussion of glucocorticoid actions and how levels change with conservation-relevant variables. Biol Conserv 142:2844–2853.

Calenge C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol Modell 197:516–519.

Catry P., R.A. Phillips, and J.P. Croxall. 2004*a*. Sustained fast travel by a gray-headed albatross (*Thalassarche chrysostoma*) riding an antarctic storm. Auk 121:1208–1213.

Catry P., R.A. Phillips, B. Phalan, J.R.D. Silk, and J.P. Croxall. 2004*b*. Foraging strategies of grey-headed albatrosses *Thalassarche chrysostoma*: integration of movements, activity and feeding events. Mar Ecol Prog Ser 280:261–273.

Chastel O., A. Lacroix, H. Weimerskirch, and G. Gabrielsen. 2005. Modulation of prolactin but not corticosterone responses to stress in relation to parental effort in a long-lived bird. Horm Behav 47:459–466.

Chaudhuri P. and J.S. Marron. 1999. SiZer for exploration of structures in curves. J Am Stat Assoc 94:807–823.

Cherel Y., R. Mauget, A. Lacroix, J. Gilles, and Y. Cherel. 1994. Seasonal and fasting-related changes in circulating gonadal steroids and prolactin in king penguins, *Aptenodytes patagonicus*. Physiol Zool 67:1154–1173.

Clarke A. and P.A. Prince. 1980. Chemical composition and calorific value of food fed to mollymauk chicks *Diomedea melanophris* and *D. chrysostoma* at Bird Island, South Georgia. Ibis 122:488–494.

Clarke J.R. 2001. Partitioning of foraging effort in Adélie penguins provisioning chicks at Bechervaise Island, Antarctica. Polar Biol 24:16–20.

Costa D.P. and P.A. Prince. 1987. Foraging energetics of grey-headed albatrosses *Diomedia chrysostoma* at Bird Island, South Georgia. Ibis 129:149–158.

Cottin M., A.J.J. Macintosh, A. Kato, A. Takahashi, M. Debin, T. Raclot, and Y. Ropert-Coudert. 2014. Corticosterone administration leads to a transient alteration of foraging behaviour and complexity in a diving seabird. Mar Ecol Prog Ser 496:249–262.

Crespi E.J., T.D. Williams, T.S. Jessop, and B. Delehanty. 2013. Life history and the ecology of stress: how do glucocorticoid hormones influence life-history variation in animals? Funct Ecol 93–106.

Crossin G., P.N. Trathan, R.A. Phillips, K.B. Gorman, A. Dawson, K.Q. Sakamoto, and T.D. Williams. 2012. Corticosterone predicts foraging behavior and parental care in macaroni penguins. Am Nat 180:E31–E41.

Croxall J.P., S.H.M. Butchart, B. Lascelles, A.J. Stattersfield, B. Sullivan, A. Symes, and P. Taylor. 2012. Seabird conservation status, threats and priority actions: a global assessment. Bird Conserv Int 22:1–34.

Dantzer B., S.E. Westrick, and F. van Kesteren. 2016. Relationships between endocrine traits and life histories in wild animals: insights, problems, and potential pitfalls. Integr Comp Biol 56:185–197.

da Silva A.R., G. Malafaia, and I.P.P. Menezes. 2017. biotools: an R function to predict spatial gene diversity via an individual-based approach. Genet Mol Res 16:gmr16029655.

Dechaume-Moncharmont F., K. Monceau, and F. Cezilly. 2011. Sexing birds using discriminant function analysis: a critical appraisal. Auk 128:78–86.

Doody L.M., S.I. Wilhelm, D.W. McKay, C.J. Walsh, and A.E. Storey. 2008. The effects of variable foraging conditions on common murre (*Uria aalge*) corticosterone concentrations and parental provisioning. Horm Behav 53:140–148.

Epskamp S. and S. Stuber. 2017. semPlot: path diagrams and visual analysis of various SEM packages' output. R package version 1.1. https://CRAN.R-project.org/package=semPlot.

Garland T., Jr., and S.C. Adolph. 1994. Why not to do two-species comparative studies: limitations on inferring adaptation. Physiol Zool 67:797–828.

Gorman K.B. 2015. Integrative studies of Southern Ocean food-webs and *Pygoscelis* penguin demography: mechanisms of population response to environmental change. PhD diss. Simon Fraser University, Burnaby, British Columbia.

Goymann W., I. Schwabl, M. Trappschuh, and M. Hau. 2007. Use of ethanol for preserving steroid and indoleamine hormones in bird plasma. Gen Comp Endocrinol 150:191–195.

Harding A.M., A.S. Kitaysky, M.E. Hall, J. Welcker, N.J. Karnovsky, S.L. Talbot, K.C. Hamer, and D. Grémillet. 2009. Flexibility in the parental effort of an Arctic-breeding seabird. Funct Ecol 23:348–358.

Harding A., R. Paredes, R. Suryan, D. Roby, D. Irons, R. Orben, H. Renner, et al. 2013. Does location really matter? an inter-colony comparison of seabirds breeding at varying distances from productive oceanographic features in the Bering Sea. Deep-Sea Res II 94:178–191.

Harvey S. and H. Klandorf. 1983. Reduced adrenocortical function and increased thyroid function in fasted and refed chickens. J Endocrinol 98:129–135.

Hector J.A.L. and S. Harvey. 1986. Corticosterone secretion through long incubation shifts in *Diomedea* albatrosses. Gen Comp Endocrinol 62:349–352.

Heidinger B.J., I.C.T. Nisbet, and E.D. Ketterson. 2008. Changes in adrenal capacity contribute to a decline in the stress response with age in a long-lived seabird. Gen Comp Endocrinol 156:564–568.

Jouventin P. and F.S. Dobson. 2002. Why breed every other year? the case of albatrosses. Proc R Soc B 269:1955–1961.

Kitaysky A.S., J.F. Piatt, and J.C. Wingfield. 2007. Stress hormones link food availability and population processes in seabirds. Mar Ecol Prog Ser 352:245–258.

Kitaysky A.S., J.C. Wingfield, and J.F. Piatt. 1999. Dynamics of food availability, body condition and physiological stress response in breeding black-legged kittiwakes. Funct Ecol 13:577–584.

———. 2001. Corticosterone facilitates begging and affects resource allocation in the black-legged kittiwake. Behav Ecol 12:619–625.

Krause J.S., J.H. Pérez, H.E. Chmura, S.L. Meddle, K.E. Hunt, L. Gough, N. Boelman, and J.C. Wingfield. 2016. The stress response is attenuated during inclement weather in parental, but not in pre-parental, Lapland longspurs (*Calcarius lapponicus*) breeding in the Low Arctic. Horm Behav 83:68–74.

Lancaster L.T., L.C. Hazard, J. Clobert, and B.R. Sinervo. 2008. Corticosterone manipulation reveals differences in hierarchical organization of multidimensional reproductive tradeoffs in r-strategist and K-strategist females. J Evol Biol 21:556–565.

Landys M.M., M. Ramenofsky, and J.C. Wingfield. 2006. Actions of glucocorticoids at a seasonal baseline as compared to stress-related levels in the regulation of periodic life processes. Gen Comp Endocrinol 148:132–149.

Le Ninan F., Y. Cherel, C. Sardet, and Y. LeMaho. 1988. Plasma hormone levels in relation to lipid and protein metabolism during prolonged fasting in king penguin chicks. Gen Comp Endocrinol 71:331–337.

Lormée H., P. Jouventin, C. Trouve, and O. Chastel. 2003. Sex-specific patterns in baseline corticosterone and body condition changes in breeding red-footed boobies *Sula sula*. Ibis 145:212–219.

McEwen B.S. and J.C. Wingfield. 2003. The concept of allostasis in biology and biomedicine. Horm Behav 43:2–15.

McInnes J.C., B.E. Deagle, P. Catry, S.N. Jarman, R.A.M. Lea, B. Raymond, R.A. Phillips, et al. 2017. High occurrence of jellyfish predation by black-browed and Campbell albatross identified by DNA metabarcoding. Mol Ecol 26:4831–4845.

Moore I.T. and T.S. Jessop. 2003. Stress, reproduction, and adrenocortical modulation in amphibians and reptiles. Horm Behav 43:39–47.

Oliveira M., R.M. Crujeiras, and A. Rodriguez-Casal. 2014. NPCirc: an R package for nonparametric circular methods. J Stat Softw 61:1–26. http://www.jstatsoft.org/v61/i09/.

Peig J. and A.J. Green. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos 118:1883–1891.

Pennycuick C.J. 1982. The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity. Philos Trans R Soc B 300:75–106.

Quintana F., G.C. Lopez, and G. Somoza. 2008. A cheap and quick method for DNA-based sexing of birds. Waterbirds Int J Waterbird Biol 31:485–488.

Ricklefs R.E. 1983. Some considerations of the reproductive energetics of pelagic seabirds. Cooper Ornithol Soc 8:84–94.

Romero L.M. 2002. Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. Gen Comp Endocrinol 128:1–24.

Romero L.M., M.J. Dickens, and N.E. Cyr. 2009. The reactive scope model: a new model integrating homeostasis, allostasis, and stress. Horm Behav 55:375–389.

Romero L.M. and J.M. Reed. 2005. Collecting baseline corticosterone samples in the field: is under 3 min good enough? Comp Biochem Physiol A 140:73–79.

Rosseel Y. 2012. lavaan: an R package for structural equation modeling. J Stat Softw 48:1–36. http://www.jstatsoft.org/v48/i02/.

Sagar P. 2014. Population estimates and trends of Campbell and grey-headed albatrosses at Campbell Island. National Institute of Water and Atmospheric Research, Christchurch, New Zealand.

Sandvik H., K.E. Erikstad, and B.E. Sæther. 2012. Climate affects seabird population dynamics both via reproduction and adult survival. Mar Ecol Prog Ser 454:273–284.

Sapolsky R.M., L.M. Romero, and A.U. Munck. 2000. How do glucocorticoids influence stress responses? integrating permissive, suppressive, stimulatory, and preparative actions. Endocr Rev 1:55–89.

Satterthwaite W.H., A.S. Kitaysky, and M. Mangel. 2012. Linking climate variability, productivity and stress to demography in a long-lived seabird. Mar Ecol Prog Ser 454: 221–235.

Schoech S.J., L.M. Romero, I.T. Moore, and F. Bonier. 2013. Constraints, concerns and considerations about the necessity of estimating free glucocorticoid concentrations for field endocrine studies. Funct Ecol 27:1100–1106.

Schultner J., B. Moe, O. Chastel, S. Tartu, C. Bech, and A. Kitaysky. 2014. Corticosterone mediates carry-over effects between breeding and migration in the kittiwake *Rissa tridactyla*. Mar Ecol Prog Ser 496:125–133.

Shaffer S.A., D.P. Costa, and H. Weimerskirch. 2001*a*. Behavioural factors affecting foraging effort of breeding wandering albatrosses. J Anim Ecol 70:864–874.

Shaffer S.A., H. Weimerskirch, and D.P. Costa. 2001*b*. Functional significance of sexual dimorphism in wandering albatrosses, *Diomedea exulans*. Funct Ecol 15:203–210.

Sztukowski L.A. 2016. Foraging ecology of the Campbell albatross: individual specialisation and fishery interactions. PhD diss. University of Plymouth.

Sztukowski L.A., M.L. van Toor, H. Weimerskirch, D.R. Thompson, L.G. Torres, P.M. Sagar, P.A. Cotton, and S.C. Votier. 2017. Tracking reveals limited interactions between Campbell albatross and fisheries during the breeding season. J Ornithol 158:725–735.

Thorne L.H., E.L. Hazen, S.J. Bograd, D.G. Foley, M.G. Conners, M.A. Kappes, H.M. Kim, D.P. Costa, Y. Tremblay, and S.A. Shaffer. 2015. Foraging behavior links climate variability and reproduction in North Pacific albatrosses. Mov Ecol 3:27.

Torres L.G., R.A. Orben, I. Tolkova, and D.R. Thompson. 2017. Classification of animal movement behavior through residence in space and time. PLoS One 12:e0168513.

Venables W.N. and B.D. Ripley. 2002. Modern applied statistics with S. 4th ed. Springer, New York.

Warham J. 1990. The petrels: their ecology and breeding systems. Academic Press, San Diego, CA.

Waugh S., H. Weimerskirch, and Y. Cherel. 1999*a*. Exploitation of the marine environment by two sympatric albatrosses in the Pacific Southern Ocean. Mar Ecol Prog Ser 177:243–254.

Waugh S.M., H. Weimerskirch, Y. Cherel, and P.A. Prince. 2000. Contrasting strategies of provisioning and chick growth in two sympatrically breeding albatrosses at Campbell Island, New Zealand. Condor 102:804–813.

Waugh S.M., H. Weimerskirch, Y. Cherel, U. Shankar, P.A. Prince, and P.M. Sagar. 1999*b*. Exploitation of the marine environment by two sympatric albatrosses in the Pacific Southern Ocean. Mar Ecol Prog Ser 177:243–254.

Weimerskirch H. 1998. How can a pelagic seabird provision its chick when relying on a distant food resource? cyclic attendance at the colony, foraging decision and body condition in sooty shearwaters. J Anim Ecol 67:99–109.

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

Weimerskirch H., T. Guionnet, J. Martin, S.A. Shaffer, and D.P. Costa. 2000. Fast and fuel efficient? optimal use of wind by flying albatrosses. Proc R Soc B 267:1869–1874.

Wilson R.P., K. Pütz, D. Grémillet, B.M. Culik, M. Kierspel, J. Regel, C.A. Bost, J. Lage, and J. Cooper. 1995. Reliability of stomach temperature changes in determining feeding characteristics of seabirds. J Exp Biol 1135:1115–1135.

Wingfield J.C. 2003. Control of behavioural strategies for capricious environments. Anim Behav 66:807–815.

Wingfield J.C., D.L. Maney, C.W. Breuner, J.D. Jacobs, S. Lynn, M. Ramenofsky, and R.D. Richardson. 1998. Ecological bases of hormone-behavior interactions: the "emergency life history stage." Am Zool 38:191–206.

Wingfield J.C. and R.M. Sapolsky. 2003. Reproduction and resistance to stress: when and how. J Neuroendocrinol 15: 711–724.

Chapter 3

Similarity in foraging energetics of two sympatric albatrosses of the Southern Ocean despite contrasting life histories and foraging strategies

Caitlin E. Kroeger

Abstract

Understanding 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, I used doubly-labelled water to measure the at-sea daily energy expenditure (DEE) of two sympatrically breeding seabirds, Campbell (*Thalassarche impavida*) and grey-headed (*T. chrysostoma*) albatrosses. I 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, strong tailwinds (> 12 ms^{-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 stronger 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 utilize this region during early-chick rearing. Female Campbell albatrosses that do not use poleward regions may be negatively impacted by forecasted slackening winds at lower latitudes that may lead to a greater reliance on less energy efficient sit-and-wait foraging strategies. Finally, behavioral plasticity associated with environmental variation may influence future population responses to climate change.

Introduction

Animals make adjustments to their behavior in order 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 (Ropert-Coudert et al. 2009; 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). Over evolutionary time scales, species either genetically adapt to prolonged changes in their environment or become extinct (Somero 2010; Hoffmann and Sgró 2011). However, adaptation does not occur within an individual lifetime and species with long-lived individuals depend on phenotypic plasticity to adjust to the rapid pace of climate change (Reed et al. 2011). Thus, studying behavioral strategies and the 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 stressors impact the energy balance of organisms in addition to normal variability from intrinsic factors such as breeding status or sex (Schneider 2004; Wingfield et al. 2011). This sensitivity is acutely relevant to seabirds that face a multitude of challenges from climate-driven and other human-induced environmental changes (Croxall 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 (Suryan et al. 2006; Weimerskirch 2007; Kitaysky et al. 2010; Thorne et al. 2015). When individuals are near their energetic limits, extrinsic perturbations have a greater impact on energy balance and can impact reproductive success and survival (Weiner 1992, Elliott et al. 2014). In some cases, however, external changes can be energetically beneficial. For example, wandering albatrosses (*Diomedea exulans*) have experienced 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; Weimerskirch et al. 2000, 2005, Shaffer et al. 2001b, 2004; Sachs et al. 2012). 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 Antolos et al. 2017). Comparing the energy costs of alternative chick provisioning strategies from sister groups and sexes within those species may highlight the relative efficiency of certain strategies. This comparison, in combination with energetic responses to environmental variability across years, can improve our understanding of life-history patterns and population trajectories.

In this study, I measured the at-sea DEE of two closely related seabird species with contrasting foraging strategies, life histories, and population trends – the Campbell (*Thalassarche impavida*) and grey-headed (*T. chrysostoma*) albatrosses – during early chick-rearing across two years. Campbell albatrosses are annually breeding neritic foragers with a currently stable population. Grey-headed albatrosses are biennially breeding oceanic foragers and the population on Campbell Island, New Zealand, has been in steep decline since the 1940’s, although this decline may have stopped in the last decade (Sagar 2014).

My 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. I hypothesized that 1) the biennially breeding grey-headed albatrosses should have higher DEE, consistent with life history theory that organisms will balance future reproduction with current reproductive costs, and 2) there should be no difference in energy expenditure between years or sexes unless there are environmental differences across years or if sexes utilize different foraging strategies that would lead to different environmental interactions. This study illuminates the phenotypic plasticity of seabirds and identifies energetically expensive environmental conditions, enabling us to better forecast 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 #976 and New Zealand Wildlife Act Permit #SO-26385-FAU. Blood samples were imported into the United States for analysis using permits issued by USDA-APHIS (119370).

Study Species and Site

Campbell and grey-headed albatrosses 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 three 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 field metabolic rates, foraging behavior, and mass gain (Table 1).

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 ga. needle and 1 mL syringe then transferred into dry spray-coated lithium heparin blood collection tubes (BD Vacutainer^{TM} plastic, 2011; BD Vacutainer^{TM} glass, 2012). Doubly labeled water (DLW; 1.8 mL) containing 0.9% NaCl with 42.15 APE ^{18}O and 5.39 MBq g^{-1} ^{3}H (2011) or 43.70 APE ^{18}O and 5.91 MBq g^{-1} ^{3}H (2012) or 43.87 APE ^{18}O and 5.91 MBq g^{-1} ^{3}H (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 birds (6-8) from each species were contained for an equilibration period of 90 minutes (Shaffer et al. 2001a), after which a second blood sample was obtained for the calculation of total body water (Nagy and Costa 1980). This allowed us to use the single-sample method of determining total body water on the remaining birds to minimize disturbance and potential changes in natural behaviors (Speakman 1997; Schultner et al. 2010).

After DLW injection, birds were weighed using a spring-loaded Pesola scale (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 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 hours, an additional mass measurement and a second final blood sample (final 2) were collected.

In 2011, samples were packaged and stored in a cool location 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 United States 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, 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).

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 (Appendix 1) from Nagy (1983) to account for changes in percentage of total body water across the foraging trip (Shaffer et al. 2006). This was compared against the dilution space from the ^{3}H isotope to assess the percentage of error (^{3}H typically overestimates the body water pool by about 4%; Nagy and Costa 1980; Speakman 1997; Shaffer et al. 2006). The plateau approach was also used to estimate the ^{18}O and ^{3}H dilutions spaces of the isotopes with an equation (17.11) from Speakman (1997). The percent mass approach was used to estimate final 1 and final 2 total body water (Speakman, 1997). The dilution space ratio of each bird and the ratio of mean isotopic turnover rates (k_t/k_o) were calculated to ensure reliable estimates of CO_2 production and any birds that had dilution spaces outside 0.97–1.1 or turnover rates outside 0.5–0.9 were excluded from further energetics calculations (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 (mL kg^{-1} d^{-1}) were calculated using equations (4) and (6), respectively, from Nagy and Costa (1980). 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).

Calculation of CO2 production

CO_2 production (mL g^{-1} h^{-1}) was then calculated using a one-pool method equation (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 (Shaffer et al. 2001b, 2003, Antolos et al. 2017), which facilitated comparison to 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. 2001b), 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: (total CO_2 production * total time - nest-only CO_2 * total nest time)/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 kg^{-1} d^{-1}; Gesseman and Nagy 1988). This was calculated using a conversion factors 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 albatross consisting of approximately 40% fishes, 37% jellyfish, 22% crustacea, and 1% cephalopod (McInnes et al. 2014) and a combination of stomach content and temperature-logger derived diets from grey-headed albatross consisting of approximately 72% squid, 25% jellyfish, and 3% fish (Waugh et al. 1999b; Catry et al. 2004). The energy densities of the components were approximated as a proportion of the dry mass for fish as 53.3 kJ g^{-1} P, 37.1 kJ g^{-1} L, 5.2 kJ g^{-1} C (Lenky et al. 2012); for squid as 57.9 kJ g^{-1} P, 32.9 kJ g^{-1} L , 0.7 kJ g^{-1} C (Eder and Lewis 2005); for jellyfish as 16.5 kJ g^{-1} P, 0.5 kJ g^{-1} L, and 0.9 kJ g^{-1} C (Doyle et al. 2007); and for crustacea as 8.2 kJ g^{-1} P, 14.0 kJ g^{-1} L, and 3.5 kJ g^{-1} C (Holland and Walker 1975). Cost of flight was then calculated for each species following Costa and Prince (1987) as: (DEE $_{\text{at-sea}}$ – (% trip on water * mean DEE $_{\text{on-nest}}$))/ (1 – % 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); however, supplemental data were not available for grey-headed albatrosses. Box's M-tests confirmed homogeneity of the variance-covariance matrices of the morphometric measurements for each species (biotools package, R 3.1). Discriminant function analysis correctly assigned the sex of Campbell albatrosses (N = 68) 79% of the time with a cutoff of 0.10 using the following regression: Y = -2.033*post-foraging mass - 0.197*minimum bill depth - 0.045*wing chord, and correctly assigned the sex of grey-headed albatrosses (N = 31) 87% of the time with a cutoff of 0.30 using the following regression: Y = -1.344*post-foraging mass - 0.706*minimum bill depth - 0.061*wing chord. These regressions were applied to predict sex using the mean mass (from the pre- and post-foraging masses).

Morphometrics

Wing loading

Wing traces were used from 10 random individuals of each species to calculate wing loading and wing aspect ratios (Pennycuick 2008). Surface area of the wing was determined following methods of Shaffer et al. (2001b), with the exception that the mean shoulder width (19.5 cm, N=20) of black-browed albatrosses, *T. melanophrys*, breeding on Kerguelen Island (49°S, 70°E) was used to estimate the root-box (Shaffer unpublished data) as these data were not available 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 package, R 3.1). To account for sexual dimorphism, body condition was calculated as a Scaled Mass Index (SMI; Peig and Green, 2009) as described in Kroeger et al. (2019). Because PC scores were calculated separately for each species, to compare the mass to length relationship between species, measured birds from each field season were pooled and mass was regressed on bill depth or bill length with a species effect.

Foraging Behavior

Before calculating foraging trip metrics, raw GPS data were filtered to remove points that produced speeds > 150 km h^{-1} and rediscretized at 10-min intervals (adehabitatLT package, R 3.3). 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-labelled 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% and cell size of 0.4% of the mean X and Y spatial extents of the data, allowing us to optimize visualization at any scale (adehabitatHR package, R 3.1; Fig. 1).

To classify behavioral states at sea, data points corresponding to Area Restricted Search (ARS), rest, and transit were located 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 km h^{-1} as were assigned as rest. During the guard stage, albatrosses typically only rest on the water after landing for a feeding event because takeoffs are energetically expensive (Weimerskirch et al. 2000; Shaffer et al. 2001b). 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 I 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 landing can occur within 10-minute 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 (SST) were extracted at 0.28° and 3-hourly resolution from the ERA5 climate reanalysis dataset along the albatross tracks (raster package, R 3.3). At the recorded mean maximum bird ground speed (~25 m s^{-1}) from this study, an albatross should have at least one point within gridded datasets.

Wind and SST interactions

The bearing of each bird between consecutive locations was calculated using the bearing function of the ‘geosphere’ package (a=6378137, f=1/298.26; R 3.1). 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 toward each bird location was calculated in degrees as 180*(1 + atan2(u,v)/pi), where u and v are wind components in the east and north direction (R 3.3). The bearing of the wind toward the bird relative the 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°) for assessment of wind effects from head to tail irrespective of the side of the bird. The mean angle was calculated using the ‘circular.mean’ function (circular package, R 3.3). The magnitude of flight compensation for the wind compared to 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 m s^{-1} and from 330° to 360° and 0° to 30° during flight (ARS and transit states). The percentage of strong tailwinds was similarly calculated, but for angles between 150° and 210°. 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° to 120° and 140° to 300°. Finally, the mean SST 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. Interactions terms were removed when not significant and three-way ANOVAs were rerun 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 ANOVA (‘circular’ package, R3.3). 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 % TBW, mean air flight speed, mean SST at rest; boxcox function, ‘MASS’ package, R 3.3), or analyzed using a gamma distribution from the gamlss function (pre-trip fasting, post-trip nest time; ‘gamlss’ package, R 3.3). In the case of proportion variables with high zero frequency (% light winds, % strong head/tailwinds), a compound poisson-gamma distribution was used (‘tweedie’ package, R 3.3). Welch 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.

DEE (kJ d^{-1}) was regressed on: foraging metrics (foraging duration, daily distance, maximum range, daily take-offs, % rest on water, mean flight air speed), environmental metrics (mean wind speed at take-off, % light winds, % strong headwinds, % strong tailwinds, % crosswinds, mean wind bearing on bird, wind-drift compensation magnitude, mean SST), and morphometrics (body condition before and after foraging, % body mass gain) with species, year, and sex as factors (lm function, base R 3.3). Highly correlated variables and variables with variance inflation factors (VIF) > 4 were removed backward step-wise from a base linear model (vif function, ‘car’ package, R 3.3). The number of daily landings and % 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 function, ‘MuMIn’ package, R 3.3). A model was selected from the list using the model.avg function 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.

Results

During the 2011 and 2012 field seasons, 14 and 20 grey-headed albatrosses and 17 and 20 Campbell albatrosses were sampled, respectively. Molecular sex determination and discriminant function analyses revealed a final sample size of 14 male and 12 female Campbell albatrosses and 18 male and 8 female grey-headed albatrosses after exclusions (Table 1). Grey-headed albatross mean chick age during initial sampling was 2.6 days older in grey-headed albatross compared to Campbell albatross (Table A1). Time fasting on the nest before trips was equivalent across species, sex, and years (Table A1). Time on the nest after foraging before capture was also equivalent across species, sex, and years (Table A1).

Total Body Water, Water Flux, and Energy Expenditure

The effect of species on total body water (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 A2). Moreover, male grey-headed albatrosses had 8% lower TBW in 2011 compared to 2012 (Table A2). Water influx rate was higher in grey-headed albatrosses by 32% (63 mL d^{-1}) in 2012 compared to 2011 and by 26% (54 mL d^{-1}) compared to Campbell albatrosses in 2012 (Table A2). There were no significant differences in water influx rate between years in Campbell albatrosses, between species in 2011, or between sexes (Table A2).

The mean DEE of both species were above the regression line for the allometric equation for smaller albatrosses (Fig. 3; adjusted from Antolos et al. 2018): mean DEE was 2,039 ± 571 kJ d^{-1} (655 ± 172 kJ kg^{-1} d^{-1}) for Campbell albatrosses and 2,163 ± 672 kJ d^{-1} (684 ± 223 kJ kg^{-1} d^{-1}) for grey-headed albatrosses. Mean DEE was 29% higher for Campbell albatrosses in 2011 compared to 2012 and 23% higher for grey-headed albatrosses in 2011 compared to 2012 but was similar between species and sex (Table A1). 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. 2) and, respectively, 2.1 and 2.2 times greater than FMR on the nest. Flight costs were 2.9 and 2.8 times greater than estimated BMR and 2.8 and 2.7 times greater than FMR on the nest.

Morphometrics

Using wing loading estimates, it was determined that grey-headed albatrosses had greater wing loading than Campbell albatrosses (118 N m^{-2} vs. 109 N m^{-2}; $t = -2.7$, df = 12.4, $P = 0.019$). Likewise, estimated mean aspect ratio of grey-headed albatrosses was higher than Campbell albatrosses (14.3 vs. 13.5; $t = -3.6$, df = 11.9, $P = 0.004$).

To compare body condition between species, morphometric measurements were regressed on body mass with a species effect. Among all sampled birds, when bill depth (BD) or bill length (BL) was regressed on pre-foraging body mass—which was equivalent between species, sex, and years (Table A1)—there were no differences between species in the in slope ($P > 0.05$ for species:bill interaction term) or intercept ($P > 0.05$ for species term), including when the model was separated by year. There were also no differences between species in the slope when BL or BD was regressed against post-foraging body mass, including when the model was separated by year. The grey-headed albatross intercept was significantly higher for both measurements regressed against post-foraging body mass (BD: $F_{1,49} = 12.4$, $P < 0.001$; BL: $F_{1,49} = 5.5$, $P = 0.02$). When the model was separated by year, the grey-headed albatross intercept was only marginally higher in 2011 with the BD model ($F_{1,19} = 3.1$, $P = 0.09$) and only marginally higher in 2012 with the BL model ($F_{1,27} = 3.6$, $P = 0.07$).

Within both Campbell albatrosses and grey-headed albatrosses, the scaled mass indices for pre-foraging and post-foraging body condition did not differ across years ($P > 0.05$), but post-foraging body condition was marginally higher for grey-headed albatrosses in 2012 compared to 2011 ($t = -1.9$, df = 17.8, $P = 0.08$). Body condition increased after foraging in grey-headed albatrosses in both years (2011: $t = -3.6$, df = 9, $P = 0.006$; 2012: $t = -9.4$, df = 15, $P < 0.001$) and increased after foraging in Campbell albatrosses in 2012 ($t = -5.0$, df = 14, $P < 0.001$). There was no difference in body condition after foraging in Campbell albatrosses in 2011 ($t = -0.84$, df = 10, $P = 0.41$)

Foraging Behaviors

Campbell albatross foraging was primarily concentrated over the Campbell plateau northeast of the island in both years, with some foraging extending over deeper waters southward toward 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 than in 2012 (Table A2). 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% vs. 25% in 2012) and gained less mass as a proportion of their pre-trip body mass (1.8% vs. 10% in 2012; Table A2). 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 A2 and A1).

In contrast, 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 A2). 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% vs. 19%; Appendix 1). Proportional mass gain was also lower for grey-headed albatross in 2011 (11% vs. 18% of pre-trip body mass; Appendix 1). Opposite to Campbell albatrosses, female grey-headed albatrosses spent less time on the water and had the fastest air speeds compared to males, despite similar take-offs and proportional mass gain (Tables A2 and A1).

For both species and years, males had farther maximum ranges and had longer foraging trips than females (Table A2). In both years, grey-headed albatrosses exhibited greater trip duration, daily distance, maximum range, air speed, and proportional mass gain compared to Campbell albatrosses (Tables A1 and A2). 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 A2).

Environmental Metrics

Mean wind speeds encountered by Campbell and grey-headed albatrosses were, respectively, 2.2 m s^{-1} and 1.3 m s^{-1} higher in 2012 compared to 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 A3). 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 A3). 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, though the amount was minimal at 2% (Table A3). 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 experience almost no light winds during flight (0.4%; Table A3). The mean proportion of crosswinds in flight was lowest for female Campbell albatrosses at only 18% in 2011 compared to roughly 48% for female grey-headed albatrosses (Table A3).

The mean bearing of the wind on birds during flight was consistent between species, sexes, and years, with birds primarily experiencing crosswinds (Table A3). No significant differences or interactions between species, sex, and year were found in the magnitude of compensation for the wind during transit (Table A2).

Mean SST encountered by birds on the water was lower for grey-headed albatrosses by about 2 °C (Table A3). Mean SST 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 DEE

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 contain chick age, which when included reduced the sample size in Model 2 (N=47). In Model 2, younger chicks were associated with greater DEE expended by adults (Table 2). Year had the largest effect in both models, with higher DEE in 2011 (Table 2), though 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, 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 albatrosses (Est = 27.3, SE = 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 (Jouventin and Dobson 2002). Biennially breeding grey-headed albatross also had greater wing loading due to both morphological differences and greater proportional mass gains at sea which I expected to contribute to higher foraging costs in lower wind fields. However, these birds are likely aided by the use of favorable wind fields associated with their preferred foraging location along the ACC (Fig. 1; Weimerskirch et al. 2000; Wakefield et al. 2009) including high windspeeds at take-off that influenced lower DEE. Male albatrosses expended more energy to achieve high proportional mass gain compared to females with similar proportional mass gains. Again, this result is consistent with greater wing loading in male albatrosses (Shaffer et al. 2001, Phillips et al. 2004). However, I found that males had higher DEE in 2011 when their mass gain was lower than 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.

Species Differences in Daily Energy Expenditure

Campbell albatross and grey-headed albatross had similar energy expenses at sea compared to other *Thalassarche* species relative to both body size and BMR (with the exception of the much smaller Indian yellow-nosed albatross, *T. carteri*, that appear even more economical; Figs. 2 & 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. 1999). 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; Waugh et al. 1999b; Xavier et al. 2003; Mcinnes et al. 2017), 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) if they 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.

The similar guard-stage costs between Campbell albatrosses and grey-headed albatrosses on Campbell Island were inconsistent with my predictions based on their differing life histories and foraging strategies. Biennial breeding is thought to result from higher breeding costs associated with traveling farther distances to forage, which extends the breeding season and leaves little time to recover body reserves before breeding again (Jouventin and Dobson 2002; Dobson and Jouventin 2010). Indeed, grey-headed albatrosses travel farther distances during the guard stage but breeding durations for this species overlap with the annually breeding Campbell albatrosses (chick rearing lasts approximately 116-152 vs. 130 days, respectively; Moore and Moffat 1990, ACAP 2010) and are 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 primarily forage on squid that contain 4-6 times less calcium and fewer calories than the krill and fish (Clarke and Prince 1980) typically consumed by annual breeders (Waugh et al. 1999b; Hedd and Gales 2001). 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 likely offset wing loading and reduce the cost of larger food loads that may compensate for lower quality (Table A1; Weimerskirch et al. 2000, 2012). Grey-headed albatrosses exhibited higher total body water as a percentage of initial mass (although this was year and sex dependent) compared to Campbell albatrosses, suggesting lower lipid reserves despite similar costs (Speakman 1997). A greater allocation of energy to chicks rather than self-maintenance 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 farther north during the incubation stage (Furness and Bryant 1996; Wakefield et al. 2009; Louzao et al. 2014; Sztukowski 2015). The proportion of light winds experienced varied by species, sex and year, but female Campbell albatrosses generally experienced the greatest proportion of lighter winds and were less impacted by light winds at take-off. Their lower wing loading could reduce the cost of these conditions relative to grey-headed albatrosses. Moreover, Campbell albatrosses have lower aspect ratios which increases maneuverability in lighter winds and may aid in foraging efficiency (Rayner 1988;

Phillips et al. 2004; Pennycuick 2008). I was unable to directly test the effect of wing loading because I did not have wing measurements from individuals that were sampled for energy expenditure. However, differences in wing loading between species likely 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 to other albatross species (Fig. 3), as expected from Southern Ocean species that forage in more productive waters than North Pacific albatrosses (Antolos et al. 2018). 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 (Pennycuick 1975; 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 farther 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, were likely more important drivers of 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

(Weimerskirch et al. 2000, Shaffer et al. 2001b; Sakamoto et al. 2013). 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 A1 and A2). Gaining less mass with more water landings and performing more landings in energetically expensive wind speeds are somewhat counter-intuitive because birds should limit landings to when food is located to conserve time and energy during chick rearing (Weimerskirch et al. 2000; Shaffer et al. 2001b). 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 (Louzao et al. 2014; Conners et al. 2015). 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; Weimerskirch et al. 2000; Wakefield et al. 2009). 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 on DEE, I found an effect of the proportion of strong headwinds during flight (> 12 m s^{-1}) on DEE. Strong headwinds can offset flight direction and potentially force more energetically expensive corrective maneuvering (Wakefield et al. 2009; Louzao et al. 2014; Tarroux et al.

2016), 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 A3), so the proportion of strong headwinds encountered should be costlier. Accordingly, DEE was higher when the proportion of strong headwinds was higher for grey-headed albatrosses compared to Campbell albatrosses under the same model conditions. Furthermore, although the consequences of strong tailwinds on soaring seabirds has received less attention (but see Spear and Ainley 1997; Alerstam et al. 2019) and most cost models do not include this effect (Felicisimo et al. 2008; Raymond et al. 2010; Louzao et al. 2014), I 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 occurred when strong tailwinds could be most destabilizing to flight (Alerstam et al. 2019).

The Influence of Chick Age

Although the sample size reduced 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 likely 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 the 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, individuals in 2012 that were more successful foragers and likely 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, I was able to link a suite of behavioral, morphometric, and environmental measures to variations in DEE among 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 they 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 impact productivity in the Southern Ocean (Constable et al. 2014). In addition, wind fields are projected to weaken toward lower latitudes while becoming stronger toward higher latitudes (Thompson and Wallace 2000; Lovenduski and Gruber 2005), 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 albatross range (Lovenduski and Gruber 2005) could entail more individuals using a less energetically efficient sit-and-wait strategy. Indeed, population trends in the last decade have shown that the stable Campbell albatross population may be entering another decline. The grey-headed albatross population at Campbell Island has been in steep decline due to unknown environmental factors (Waugh et al. 1999c) with only recent indications of stabilization (Sagar 2014), so additional research is necessary to understand the implications of changing wind fields. Understanding factors that influence the DEE of animals is essential for predicting how future environmental changes will impact vulnerable species. 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).

References

ACAP. 2009. ACAP Species assessment: Black-browed Albatross *Thalassarche melanophris*. Agreem Conserv Albatrosses Petrels.

ACAP. 2010. ACAP Species assessment: Grey-headed Albatross *Thalassarche chrysostoma*. Agreem Conserv Albatrosses Petrels.

Adams A.N.J., C.R. Brown, and K.A. Nagy. 1986. Energy Expenditure of Free-Ranging Wandering Albatrosses *Diomedea exulans*. Physiol Zool 59:583–591.

Alerstam T., J. Bäckman, and T.J. Evans. 2019. Optimal central place foraging flights in relation to wind. J Ornithol: 1-12.

Antolos M., S.A. Shaffer, H. Weimerskirch, Y. Tremblay, and D.P. Costa. 2017. Foraging Behavior and Energetics of Albatrosses in Contrasting Breeding Environments. Front Mar Sci 4:1–12.

Berlincourt M. and J.P.Y. Arnould. 2015. Influence of environmental conditions on foraging behaviour and its consequences on reproductive performance in little penguins. Mar Biol 162:1485–1501.

Cai W., G. Shi, T. Cowan, D. Bi, and J. Ribbe. 2005. The response of the Southern Annular Mode, the East Australian Current, and the southern mid-latitude ocean circulation to global warming. Geophys Res Lett 32:1–4.

Catry P., R.A. Phillips, B. Phalan, J.R.D. Silk, and J.P. Croxall. 2004. Foraging strategies of grey-headed albatrosses *Thalassarche chrysostoma*: integration of movements, activity and feeding events. Mar Ecol Prog Ser 280:261–273.

Clarke A. and P.A. Prince. 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.

Conners M.G., E.L. Hazen, D.P. Costa, and S.A. Shaffer. 2015. Shadowed by scale: subtle behavioral niche partitioning in two sympatric, tropical breeding albatross species. Mov Ecol 3:1–20.

Constable A.J., J. Melbourne-Thomas, S.P. Corney, K.R. Arrigo, C. Barbraud, D.K. a Barnes, N.L. Bindoff, et al. 2014. Climate change and Southern Ocean ecosystems I: How changes in physical habitats directly affect marine biota. Glob Chang Biol 3004–3025.

Cooke S.J., L. Sack, C.E. Franklin, A.P. Farrell, J. Beardall, M. Wikelski, and S.L. Chown. 2013. What is conservation physiology? Perspectives on an increasingly integrated and essential science. Conserv Physiol 1:1–23.

Costa D.P. and P.A. Prince. 1987. Forgaing energetics of Grey-headed Albatrosses *Diomedia chrysostoma* at Bird Island, South Georgia. Ibis (Lond 1859) 129:149–158.

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.

Croxall J.P., S.H.M. Butchart, B. Lascelles, A.J. Stattersfield, B. Sullivan, A. Symes, and P. Taylor. 2012. Seabird conservation status, threats and priority actions: a global assessment. Bird Conserv Int 22:1–34.

Crossin G.T., R.A. Phillips, K.E. Wynne-edwards, and T.D. Williams. 2013. Postmigratory Body Condition and Ovarian Steroid Production Predict Breeding Decisions by Female Gray-Headed Albatrosses. Physiol Biochem Zool 86:761–768.

Daunt F. and I. Mitchell. 2013. Impacts of climate change on seabirds. MCCIP Sci Rev 2013 125–133.

Dechaume-Moncharmont F., K. Monceau, and F. Cezilly. 2011. Sexing birds using discriminant function analysis: a critical appraisal. Auk 128:78–86.

Dobson F.S. and P. Jouventin. 2010. The trade-off of reproduction and survival in slow-breeding seabirds. Can J Zool 88:889–899.

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.

Elliott K.H., M. Le Vaillant, A. Kato, A.J. Gaston, Y. Ropert-Coudert, J.F. Hare, J.R. Speakman, et al. 2014. Age-related variation in energy expenditure in a long-lived bird within the envelope of an energy ceiling. J Anim Ecol 83:136–46.

Felicisimo A.M., J. Munoz, and J. González-Solís. 2008. Ocean Surface Winds Drive Dynamics of Transoceanic Aerial Movements. PLoS One 3:1–7.

Furness R.W. and D.M. Bryant. 1996. Effect of wind on field metabolic rates of breeding Northern Fulmars. Ecology 77:1181–1188.

Hedd A. and R. Gales. 2001. The diet of shy albatrosses (*Thalassarche cauta*) at Albatross Island, Tasmania. J Zool 253:69–90.

Hetem R.S., W.M. Strauss, L.G. Fick, S.K. Maloney, L.C.R. Meyer, M. Shobrak, A. Fuller, et al. 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.

Hoffmann A.A. and C.M. Sgró. 2011. Climate change and evolutionary adaptation. Nature 470:479–485.

Huin N., P. Prince, and D.R. Briggs. 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.

Jodice P.G.R., D.D. Roby, R.M. Suryan, D.B. Irons, K.R. Turco, E.D. Brown, J.F. Thedinga, et al. 2006. Increased energy expenditure by a seabird in response to higher food abundance. Mar Ecol Prog Ser 306:283–293.

Jouventin P. and F.S. Dobson. 2002. Why breed every other year? The case of albatrosses. Proc R Soc Lond B 269:1955–1961.

Kitaysky A.S., J.F. Piatt, S.A. Hatch, E. V. Kitaiskaia, Z.M. Benowitz-Fredericks, M.T. Shultz, and J.C. Wingfield. 2010. Food availability and population processes: severity of nutritional stress during reproduction predicts survival of long-lived seabirds. Funct Ecol 24:625–637.

Louzao M., T. Wiegand, F. Bartumeus, and H. Weimerskirch. 2014. Coupling instantaneous energy-budget models and behavioural mode analysis to estimate optimal foraging strategy: an example with wandering albatrosses. Mov Ecol 2:8.

Lovenduski N.S. and N. Gruber. 2005. Impact of the Southern Annular Mode on Southern Ocean circulation and biology. Geophys Res Lett 32:1–4.

McNamara J.M. and A.I. Houston. 2008. Optimal annual routines: Behaviour in the context of physiology and ecology. Philos Trans R Soc B Biol Sci 363:301–319.

Mcinnes J.C., B.E. Deagle, P. Catry, S.N. Jarman, R.A.M. Lea, B. Raymond, R.A. Phillips, et al. 2017. High occurrence of jellyfish predation by black-browed and Campbell albatross identified by DNA metabarcoding. Mol Ecol 26:4831–4845.

Moore P.J. and R.D. Moffat. 1990. Mollymawks on Campbell Island. Sci Res Intern Rep 59:1–44.

Nagy A. and P. Costa. 1980. Water flux in animals: analysis of potential errors in the tritiated water method. Am J Physiol 238:R454-465.

Ortiz C.L., D. Costa, and B.J. Le Boeuf. 1978. Water and energy flux in elephant seal pups fasting under natural conditions. Physiol Zool 51:166–178.

Pelletier L., A. Kato, A. Chiaradia, and Y. Ropert-Coudert. 2012. Can thermoclines be a cue to prey distribution for marine top predators? A case study with Little Penguins. PLoS One 7:e31768.

Pennycuick, C.J. 1975. Mechanics of flight. Avian biol 5:1-73.

Pennycuick C.J. 1982. The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity. Philos Trans R Soc B Biol Sci B:75–106.

Pennycuick, C.J. 2008. Modelling the flying bird (Vol. 5). Elsevier.

Phillips R.A., J.R.D. Silk, B. Phalan, P. Catry, and J.P. Croxall. 2004. Seasonal sexual segregation in two Thalassarche albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence ? 1283–1291.

Quintana F., G.C. Lopez, and G. Somoza. 2008. A cheap and quick method for DNA-based sexing of birds. Waterbirds Int J Waterbird Biol 31:485–488.

Raymond B., S.A. Shaffer, S. Sokolov, E.J. Woehler, D.P. Costa, L. Einoder, M. Hindell, et al. 2010. Shearwater foraging in the Southern Ocean: The roles of prey availability and winds. PLoS One 5.

Reed T.E., D.E. Schindler, and R.S. Waples. 2011. Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. Conserv Biol 25:56–63.

Ricklefs R.E., D.D. Roby, and J.B. Williams. 1986. Daily expenditure by adult Leach's storm-petrels during the nesting cycle. Physiol Zool 59:649–660.

Ropert-Coudert Y., A. Kato, and A. Chiaradia. 2009. Impact of small-scale environmental perturbations on local marine food resources: A case study of a predator, the little penguin. Proc R Soc B Biol Sci 276:4105–4109.

Sachs G. 2005. Minimum shear wind strength required for dynamic soaring of albatrosses. Ibis (Lond 1859) 147:1–10.

Sachs G., J. Traugott, A.P. Nesterova, G.D. Omo, F. Ku, W. Heidrich, A.L. Vyssotski, et al. 2012. Flying at no mechanical energy cost: disclosing the secret of wandering albatrosses. PLoS One 7:e41449.

Sagar P. 2014. Population estimates and trends of Campbell and grey-headed albatrosses at Campbell Island: Campbell and grey-headed albatross population estimates. NIWA report prepared for Department of Conservation.

Sakamoto K.Q., A. Takahashi, T. Iwata, T. Yamamoto, M. Yamamoto, and P.N. Trathan. 2013. Heart rate and estimated energy expenditure of flapping and gliding in black-browed albatrosses. J Exp Biol 216:3175–3182.

Schneider J.E. 2004. Energy balance and reproduction. Physiol Behav 81:289–317.

Schultner J., J. Welcker, J.R. Speakman, E.S. Nordøy, and G.W. Gabrielsen. 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 213:2958–66.

Shaffer S.A. 2011. A review of seabird energetics using the doubly labeled water method. Comp Biochem Physiol A Mol Integr Physiol 158:315–22.

Shaffer S.A., D.P. Costa, and H. Weimerskirch. 2001a. Comparison of methods for evaluating energy expenditure of incubating wandering albatrosses. Physiol Biochem Zool 74:823–31.

Shaffer S.A., D. Costa, and H. Weimerskirch. 2003. Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. Funct Ecol 66–74.

Shaffer S.A., D.P. Costa, and H. Weimerskirch. 2001b. Behavioural factors affecting foraging effort of breeding wandering albatrosses. J Anim Ecol 70:864–874.

Shaffer S.A., D.P. Costa, and H. Weimerskirch. 2004. Field metabolic rates of black-browed albatrosses *Thalassarche melanophrys* during the incubation stage. J Avian Biol 35:551–558.

Shaffer S.A., G.W. Gabrielsen, J. Verreault, and D.P. Costa. 2006. Validation of water flux and body composition in glaucous gulls (*Larus hyperboreus*) 79:836–845.

Shaffer S.A., H. Weimerskirch, and D.P. Costa. 2001c. Functional significance of sexual dimorphism in wandering albatrosses, *Diomedea exulans*. Funct Ecol 15:203–210.

Somero G.N. 2010. The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine "winners" and "losers." J Exp Biol 213:912–920.

Speakman J.R. 1997. Doubly Labelled Water: Theory and Practice. Chapman & Hall.

Speakman J.R. and C. Hambly. 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 Part A.

Spear L.B. and D.G. Ainley. 1997. Flight behaviour of seabirds in relation to wind direction and wing morphology. Ibis (Lond 1859) 139:221–233.

Suryan R.M., D.J. Anderson, S. a. Shaffer, D.D. Roby, Y. Tremblay, D.P. Costa, P.R. Sievert, et al. 2008. Wind, waves, and wing loading: Morphological specialization may limit range expansion of endangered albatrosses. PLoS One 3.

Suryan R.M., D.B. Irons, E.D. Brown, P.G.R. Jodice, and D.D. Roby. 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.

Sztukowski, L.A. 2015. Foraging ecology of the Campbell albatross: individual specialisation and fishery interactions. *Unpublished dissertation.* Plymouth University.

Sztukowski L.A., M.L. van Toor, H. Weimerskirch, D.R. Thompson, L.G. Torres, P.M. Sagar, P.A. Cotton, et al. 2017. Tracking reveals limited interactions between Campbell albatross and fisheries during the breeding season. J Ornithol 158:725–735.

Tarroux A., H. Weimerskirch, S.H. Wang, D.H. Bromwich, Y. Cherel, A. Kato, Y. Ropert-Coudert, et al. 2016. Flexible flight response to challenging wind conditions in a commuting Antarctic seabird: Do you catch the drift? Anim Behav 113:99–112.

Thorne L.H., E.L. Hazen, S.J. Bograd, D.G. Foley, M.G. Conners, M. A. Kappes, H.M. Kim, et al. 2015. Foraging behavior links climate variability and reproduction in North Pacific albatrosses. Mov Ecol 3:27.

Tuomainen U. and U. Candolin. 2011. Behavioural responses to human-induced environmental change. Biol Rev 86:640–657.

Wakefield E.D., R.A. Phillips, J. Matthiopoulos, A. Fukuda, H. Higuchi, G.J. Marshall, P.N. Trathan, et al. 2009. Wind field and sex constrain the flight speeds of central-place foraging albatrosses. Ecol Monogr 79:663–679.

Warham J. 1977. Wing loadings, wing shapes, and flight capabilities of procellariiformes. New Zeal J Zool 4:73–83.

Warham J ed. 1990. The petrels: their ecology and breeding systems. London, Academic Press.

Waugh S.M., P.A. Prince, and H. Weimerskirch. 1999. Geographical variation in morphometry of black-browed and grey-headed albatrosses from four sites. Polar Biol 22:189–194.

Waugh S.M., H. Weimerskirch, Y. Cherel, U. Shankar, P.A. Prince, and P.M. Sagar. 1999b. Exploitation of the marine environment by two sympatric albatrosses in the Pacific Southern Ocean. Mar Ecol Prog Ser 177:243–254.

Waugh S.M., H. Weimerskirch, P.J. Moore, and P.M. Sagar. 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.

Weimerskirch H. 2007. Are seabirds foraging for unpredictable resources? Deep Res Part II Top Stud Oceanogr 54:211–223.

Weimerskirch H., A. Ancel, M. Caloin, A. Zahariev, J. Spagiari, M. Kersten, and O. Chastel. 2003. Foraging efficiency and adjustment of energy expenditure in a pelagic seabird provisioning its chick. J Anim Ecol 72:500–508.

Weimerskirch H., A. Gault, and Y. Cherel. 2005. Prey distribution and patchiness: factors in foraging success and efficiency of wandering albatrosses. Ecology 86:2611–2622.

Weimerskirch H., T. Guionnet, J. Martin, S.A. Shaffer, and D.P. Costa. 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. Proc R Soc B Biol Sci 267:1869–1874.

Weimerskirch H., M. Louzao, and K. Delord. 2012. Changes in wind pattern alter albatross distribution and life-history traits . Science 335:211–214.

Weimerskirch H. and P. Lys. 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. and D. Pinaud. 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.

Weimerskirch H., L. Zimmermann, and P. A. Prince. 2001. Influence of environmental variability on breeding effort in a long-lived seabird, the yellow-nosed albatross. Behav Ecol 12:22–30.

Wingfield J.C. 2013. Ecological processes and the ecology of stress: The impacts of abiotic environmental factors. Funct Ecol 27:37–44.

Wingfield J.C., J.P. Kelley, and F. Angelier. 2011. What are extreme environmental conditions and how do organisms cope with them? Curr Zool 57:363–374.

Ydenberg R.C., C.V.J. Welham, R. Schmid-Hempel, P. Schmid-Hempel, and G. Beauchamp. 1994. Time and energy constraints and the relationships between cuurencies in foraging theory. Behav Ecol 5:28–34.

Xavier J.C., J.P. Croxall, and K. Reid. 2003. Interannual variation in the diets of two albatross species breeding at South Georgia: Implications for breeding performance. Ibis (Lond 1859) 145:593–610.

Figures and Tables

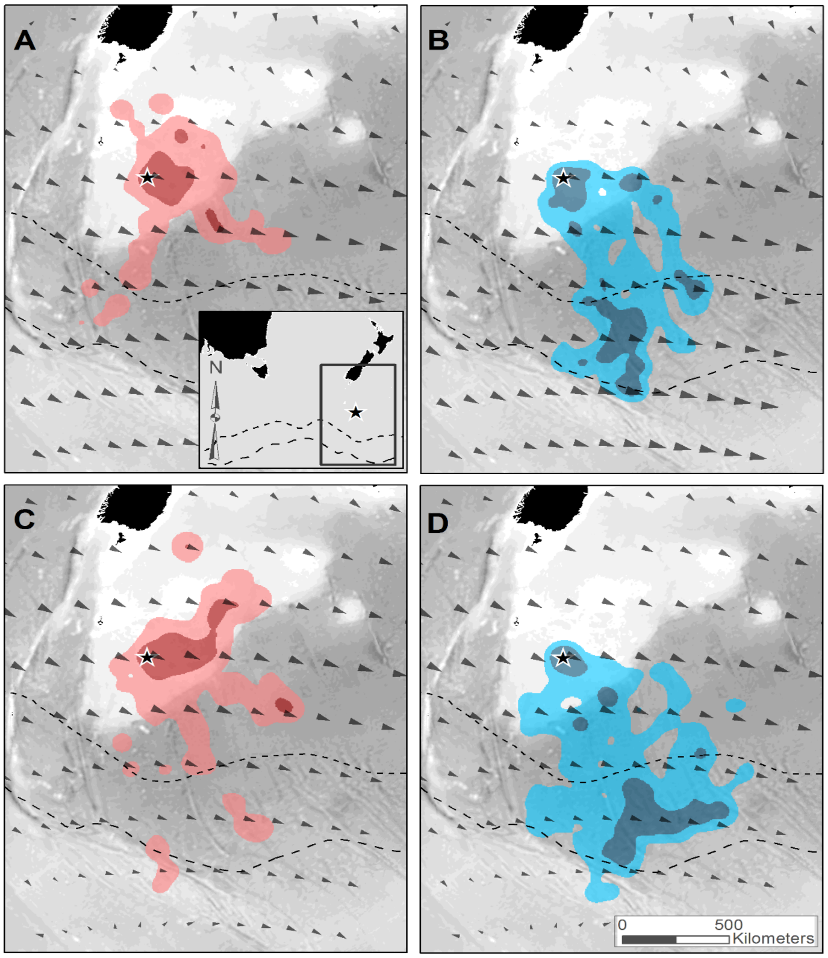


Figure 1. Kernel density estimates depicting foraging patterns during the guard stage for Campbell (red) and grey-headed (blue) albatrosses in 2011 (top) and 2012 (bottom). Arrows depict monthly (December) wind direction and speed at 1000 mb from a base period of 1971-2000, with the size of the arrow scaled to the magnitude of the wind speed. The dashed lines depict the Subantarctic (upper) and Polar (lower) fronts. Star represents breeding colony on Campbell Island. Inset provided for orientation on globe. Map boundaries: -45°S to -65°S and 157.5°E to 172.5°W.

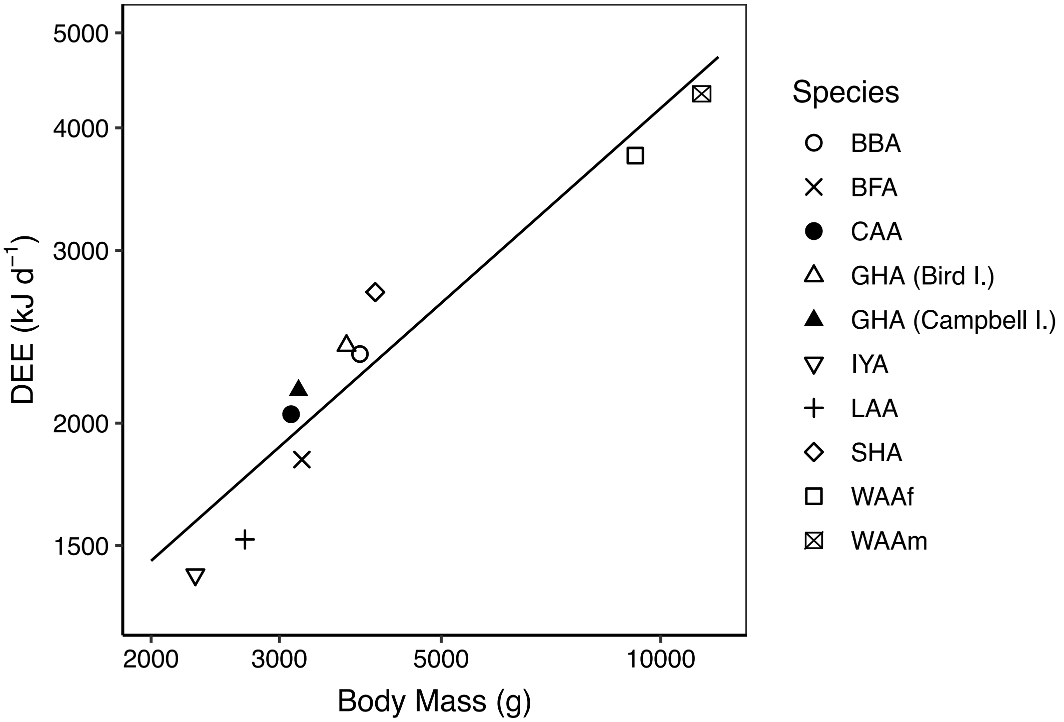


Figure 2. Updated allometric relationship between body mass and daily energy expenditure for albatross species on logarithmic scale. Regression line includes: black-browed (*T. melanophrys*, BBA), black-footed (*Phoebastria nigripes,* BFA), Campbell (*T. impavida*, CAA), grey-headed (*T. chrysostoma*, GHA Bird I. and GHA Campbell I.), Indian yellow-nosed (*Thalassarche carteri*, IYA), Laysan (*P. immutabilis,* LAA), and shy albatrosses (*T. cauta,* SHA), and female and male wandering albatrosses (*Diomedea exulans*, WAAf and WAAm; see Appendix A. Shaffer 2011 and Antolos et al. 2018). The allometric equation is DEE = 0.98 + 0.66 * body mass.

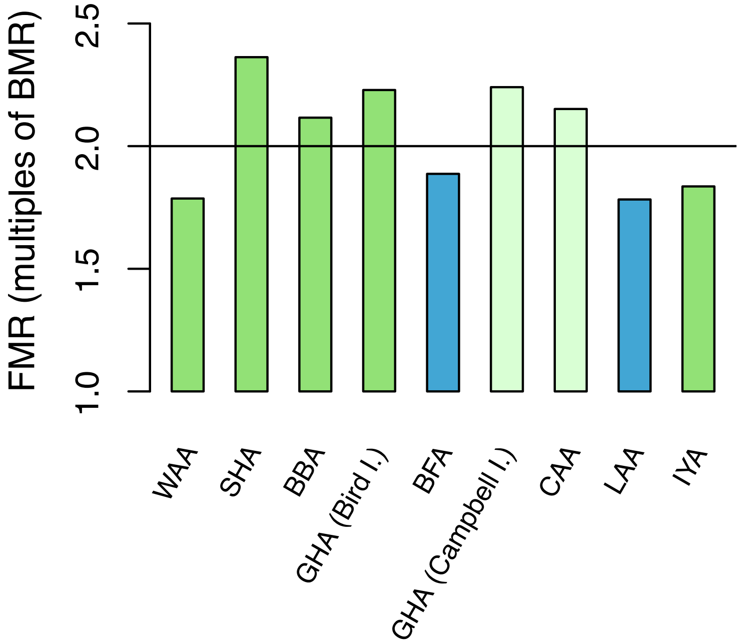
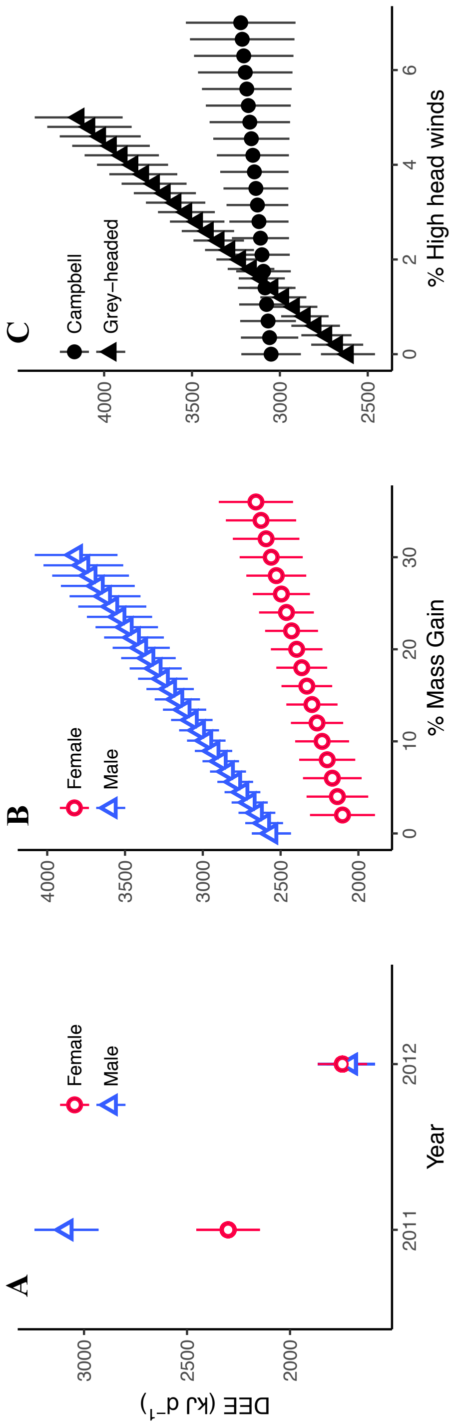


Figure 3. Relative differences in energy expenditure across albatross species based on expressing field metabolic rate as a multiple of basal metabolic rate. The horizontal line at 2x BMR represents the mean ratio across species. Bars are ordered by body mass from largest to smallest. Blue bars represent 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 (*Thalassarche cauta,* SHA), black-browed (*T. melanophrys*, BBA), grey-headed (*T. chrysostoma*, GHA from Bird Island and Campbell Island), black-footed (*Phoebastria 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. 2018).

Figure 4. Interaction plot depicting predicted daily energy expenditure regressed against (a) year by sex, (b) mass gain as a percentage of pre-foraging body mass by sex, and (c) the proportion of high headwinds during foraging by species. DEE was fit 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 for 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.


A
B
C
DEE (kJ d^{-1})
3000
2500
2000
Female
Male
2011
2012
Year
4000
3500
3000
2500
2000
0
10
20
30
% Mass Gain
4000
3500
3000
2500
Campbell
Grey-headed
0
2
4
6
% High head winds

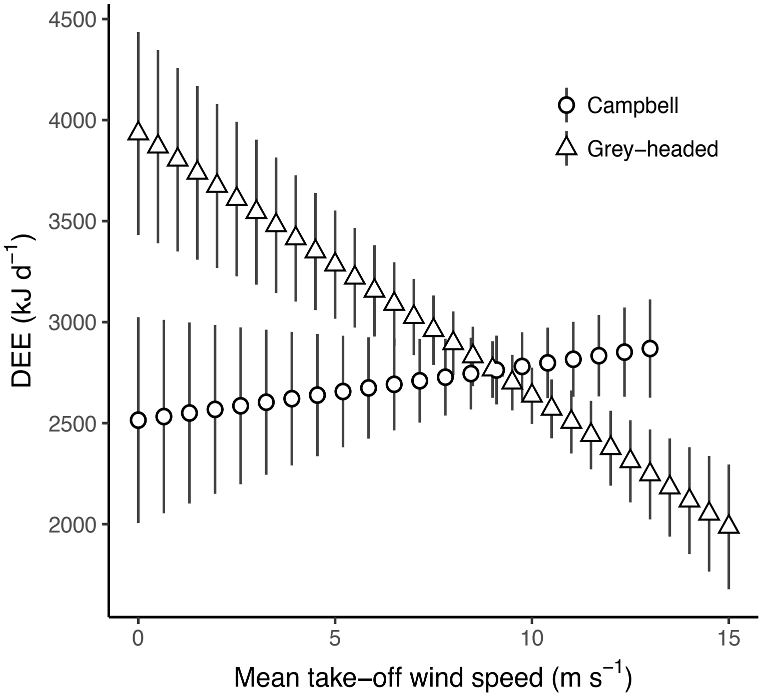


Figure 5. Interaction plot depicting predicted daily energy expenditure regressed against mean take-off wind speed by species. DEE was fit from the Model 1 (Table 2) function using male albatrosses in 2011 and the means of the remaining independent variables in the model (predict function, R 3.3). The 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.

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	11	15	10	16

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

Table 2. Linear model assessing factors influencing daily energy expenditure during early chick rearing.

	Dependent variable: Daily Energy Expenditure (kJ d^{-1})			
	Model 1 (N=52)		Model 2 (N=47)	
	Std β	Centered β coefficient	Std 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 Std. Error	429		338	
F Statistic	5.96 (df = 10; 41) ***		11.5 (df = 11; 35) ***	

Note: Model 85% confidence intervals in parentheses. ♦p<0.1; *p<0.05; **p<0.01; ***p<0.001

Appendix

Table A1. Effects of species, sex, and year and their interaction on sampling and energetic variables during guard stage. Means ± SD are presented for each species with N (year 2011/2012) in parentheses.

	Campbell		Grey-headed		F Ratio				
	Female (5/7)	Male (6/8)	Female (3/5)	Male (7/11)	Sp	Sex	Yr	Sp*Yr	Sp*Sex *Yr
Chick age (days)	8.5 ± 8.6	6.0 ± 5.0 (4)	14 ± 8.0	11 ± 6.6	5.52*	0.06	0.62	--	--
	4.3 ± 2.3 (6)	7.2 ± 2.5 (6)	7.7 ± 3.0	6.9 ± 2.3					
Pre-trip fasting duration (days)	6.8 ± 8.8 (3)	1.6 ± 1.0 (4)	3.7 ± 1.6	3.1 ± 1.1 (6)	-0.55^t	-1.00^t	-0.83^t	--	--
	4.2 ± 3.15	3.6 ± 3.3 (6)	4.6 ± 2.3	4.9 ± 2.2					
Post-trip nest time (hours)	1.2 ± 0.7	1.7 ± 1.3	1.3 ± 0.5	3.7 ± 5.0	-1.61^t	1.82^t	0.84^t	--	--
	1.1 ± 0.8	1.7 ± 2.1	1.5 ± 0.7	2.3 ± 2.0					
Pre-trip body mass (kg)	2.88 ± 0.39	3.28 ± 0.27	2.64 ± 0.12	3.15 ± 0.26	3.26	32.5*	1.33	--	--
	2.80 ± 0.13	3.13 ± 0.21	2.73 ± 0.17	3.04 ± 0.26					
TBW (% initial mass)	52 ± 1.8	53 ± 3.2	56 ± 3.3	52 ± 1.6	0.06	0.06	1.71	21.8*	4.13*
	50 ± 1.8	51 ± 1.4	56 ± 1.1	60 ± 4.4					
Mass gain (% initial mass)	3.4 ± 7.9	0.5 ± 8.2	21 ± 12	6.6 ± 4.8	11.7*	2.34	16.0*	--	--
	9.1 ± 8.9	11 ± 7.2	21 ± 10	17 ± 7.4					
Water influx (mL d^{-1})	166 ± 27.6	205 ± 94.3	244 ± 41.0	182 ± 30.6	5.58*	0.21	7.12*	--	--
	202 ± 37.4	216 ± 53.1	286 ± 103	252 ± 63.5					
DEE (kJ d^{-1})	2070 ± 596	2540 ± 782	2370 ± 1480	2480 ± 275	0.61	0.07	8.33*	--	--
	1880 ± 309	1750 ± 279	2080 ± 310	1940 ± 682					
DEE (kJ kg^{-1} d^{-1})	714 ± 214	770 ± 206	813 ± 500	765 ± 105	0.51	1.38	9.30*	--	--
	639 ± 85.5	534 ± 90.2	690 ± 101	594 ± 212					

Note: Variables that contributed to linear models are in bold. Values for 2011 are in white and 2012 are in grey. F values from three-way ANOVAs are presented for main effects and interaction effects. Only significant interactions are shown in table to conserve space. Where there are no significant interaction effects, F and P values are reported from the additive model. Transformations and distributions are described in methods. A t superscript indicates t values from gamlss functions. DEE calculated with the Speakman 1-pool model (Campbell albatross: 1775 ± 529 kJ d^{-1}; grey-headed albatross: 1846 ± 645 kJ d^{-1}) followed the same trends as the Nagy model. $*P<0.05$

Table A2. Effects of species and year and their interaction on foraging behaviors during guard stage. Means ± SD are presented for each species with N (year 2011/2012) in parentheses.

	Campbell		Grey-headed		F Ratio			
	Female (5/7)	Male (6/8)	Female (3/5)	Male (7/11)	Sp	Sex	Yr	Sp*Sex
Trip duration (days)	2.4 ± 0.7	3.7 ± 0.8	4.3 ± 0.8	4.8 ± 1.7	15.8*	4.87*	1.05	--
	2.9 ± 0.6	3.0 ± 1.3	3.4 ± 0.7	4.5 ± 1.2				
Daily distance (km)	323 ± 179	481 ± 164	687 ± 196	550 ± 151	8.80*	4.99*	25.4*	7.24*
	520 ± 85	605 ± 124	855 ± 87	794 ± 118				
Maximum Range (km)	197 ± 75	594 ± 214	961 ± 92	969 ± 186	60.5*	8.95*	2.97	--
	490 ± 132	628 ± 413	900 ± 174	1074 ± 84				
Daily water take-offs	8.5 ± 2.0	8.3 ± 2.4	5.8 ± 1.8	6.7 ± 1.4	5.69*	1.33	14.9*	--
	5.5 ± 1.0	6.0 ± 2.1	4.5 ± 1.13	5.6 ± 1.8				
Percent trip on water	52 ± 18	40 ± 12	27 ± 9.2	35 ± 6.1	1.54	3.03	36.6*	5.39*
	27 ± 9.4	25 ± 8.5	16 ± 5.8	21 ± 8.0				
Mean bird air speed (m s^{-1})	8.7 ± 1.4	11.6 ± 1.7	12.1 ± 1.1	13.0 ± 2.4	1.60	10.8*	21.0*	5.63*
	12.2 ± 1.5	13.5 ± 1.3	14.5 ± 1.2	13.8 ± 0.9				
Compensation magnitude	0.56 ± 0.03	0.54 ± 0.05	0.52 ± 0.02	0.53 ± 0.04	0.02	0.81	0.18	--
	0.52 ± 0.04	0.52 ± 0.06	0.50 ± 0.08	0.56 ± 0.1				

Note: Values for 2011 are in white and 2012 are in grey. F values from three-way ANOVAs are presented for main effects and interaction effects. Only significant interactions are shown in table to conserve space. Where there are no significant interaction effects, F and P values are reported from the additive model. Transformations and distributions are described in methods. *P<0.05

Table A3. Effects of species and year and their interaction on environmental variables during guard stage. Means ± SD are presented for each species with N (year 2011/2012) in parentheses.

	Campbell		Grey-headed		F Ratio						
	Female (5/7)	Male (6/8)	Female (3/5)	Male (7/11)	Sp	Sex	Yr	Sp* Sex	Sp* Yr	Sex* Yr	Sp*Sex *Yr
Mean wind speed (m s^{-1})	6.9 ± 1.2	9.13 ± 1.5	9.3 ± 1.3	9.4 ± 1.7	0.37*	9.06*	16.0*	8.20*	--	--	--
	9.5 ± 2.6	11.0 ± 1.7	11.5 ± 0.5	10.3 ± 0.8							
Mean wind speed at takeoff (m s^{-1})	6.8 ± 1.7	9.0 ± 1.3	8.6± 1.9	9.3 ± 2.3	0.44	6.40*	8.63*	4.33*	--	--	--
	9.17 ± 2.9	10.8 ± 1.8	10.9 ± 1.5	9.9 ± 1.3							
Mean wind angle on bird (180°)	85 ± 9.3	90 ± 12	94 ± 6.0	83 ± 6.0	1.75	0.00	0.96	--	--	--	--
	82 ± 5.6	85 ± 5.4	93 ± 9.0	90 ± 5.8							
% Light wind ^{t}	5.2 ± 8.4	5.2 ± 4.3	4.6 ± 7.6	2.9 ± 5.1	-0.8*	0.00	-2.6*	0.36	2.49 *	2.58*	-2.26*
	9.11 ± 16	0.4 ± 0.7	3.3 ± 2.0	4.4 ± 3.7							
% Strong headwind ^{t}	1.1 ± 2.4	0.7 ± 1.5	1.4 ± 1.9	1.0 ± 0.9	10.07	0.31	1.89	--	--	--	--
	1.7 ± 2.11	2.4 ± 2.5	2.3 ± 0.9	1.6 ± 1.3							
% Strong tailwind ^{t}	0.0 ± 0.0	0.8 ± 1.4	2.0 ± 2.0	1.0 ± 1.0	-0.18	-2.5*	1.03	2.64*	--	--	--
	0.3 ± 0.7	1.5 ± 2.7	2.0 ± 2.7	1.2 ± 1.0							
% Crosswind	18 ± 13	33 ± 8.4	48 ± 9.3	41 ± 9.4	4.04	7.95*	13.6*	9.09 *	5.82*	--	--
	37 ± 15	44 ± 9.4	48 ± 5.0	41 ± 7.8							
Mean SST at rest (°C)	8.6 ± 0.3	7.7 ± 1.2	5.1 ± 0.7	6.5 ± 1.6	40.1*	3.18	0.15	--	--	--	--
	8.6 ± 0.3	7.5 ± 1.6	6.7 ± 1.2	5.7 ± 1.0							

Note: Variables that contributed to linear models are in bold. Values for 2011 are in white and 2012 are in grey. F values from three-way ANOVAs are presented for main effects and interaction effects. Only significant interactions are shown in table to conserve space. Where there are no significant interaction effects, F and P values are reported from the additive model. Transformations and distributions are described in methods. A t superscript indicates t values from gamlss or Tweedie functions. *P<0.05

Chapter 4

Flight path cost choice and wind-use consistency in two species of albatross from incubation to early chick-rearing stages

Caitlin E. Kroeger

Abstract

Climate-driven changes in wind patterns are expected to alter the distribution and life-histories of seabirds that are energetically reliant on wind to varying extents depending on their morphology or breeding colony location. In the Southern Ocean, winds are expected to intensify toward higher latitudes and lighten toward lower latitudes, but it is unclear how this will affect central place foragers that must navigate wind fields to find prey for their young. I examined the dynamics of wind-use patterns in two sympatrically breeding albatrosses that differ in wing loading and utilize different wind fields to target prey: the grey-headed (*Thalassarche chrysotoma*) and Campbell albatrosses (*T. impavida*). Wind dynamics were compared by species, breeding stage (incubation and guard), and sex using anisotropic cost analysis based on a pre-existing flight cost model and an indicator of wind-use consistency from vector correlation coefficients. Incubation-stage grey-headed albatrosses had the greatest flight costs, overall. Campbell albatrosses had greater wind-use consistency than grey-headed albatrosses, which also correlated with lower mean wind speeds. Greater wind-use consistency also correlated with lower mean flight costs and greater foraging success in all individuals. Grey-headed albatrosses made the costliest flight path choices, likely driven by a higher frequency of area restricted prey searches and upwind tacking upon return to their colony. During incubation, both species exhibited a negative relationship between cost choices and wind-use consistency during inbound transit, but wind-use strategies differed. Finally, guard stage individuals that made costlier path choices had greater wind-use consistency during outbound transit, with individuals trading the energy inefficiency of direct routes for greater food rewards. Greater flight costs of grey-headed albatrosses during the incubation stage may contribute to biennial breeding in this species relative to annually breeding Campbell albatrosses that had lower flight costs. The projected increase in wind speeds will likely impact the flight efficiency of male Campbell albatrosses and both grey-headed albatross sexes. Overall, this study reveals more nuanced patterns of wind use by

foraging albatrosses, which improves our understanding of how different species may be impacted by future climate-drive changes.

Introduction

Animal movement patterns are influenced by the structure and medium of their environment but can also be influenced by factors like memory and choice in non-passive animals (Chapman et al. 2011; Fagan et al. 2013; Shepard et al. 2016). For example, actively flying animals are influenced by winds, but sensory cues and resource distribution knowledge allows them to optimally navigate their environment to reach resources (Liechti 2006; Chapman et al. 2011; Goto et al. 2017; Sage et al. 2019). In pelagic seabirds, movement patterns in relation to atmospheric conditions (Weimerskirch et al. 2016), oceanographic features (Nel et al. 2001; Tew Kai et al. 2009), and prey patches have been extensively investigated (Weimerskirch et al. 1997b, 2005; Fritz et al. 2003; Weimerskirch 2007; Raymond et al. 2010). The effect of wind on seabird movement and ultimately, individual life histories and population dynamics, has become an increasingly popular field of study as rapid climate change is forecasted to alter wind patterns and lead to more extreme weather events (Weimerskirch et al. 2012; Elliott et al. 2014; Thorne et al. 2016; Masson-Delmotte et al. 2018).

Within the Southern Ocean region were many seabirds breed and forage, wind fields are intensifying toward higher latitudes (~60°S) and weakening toward lower latitudes as a result of ozone depletion (~40°S; Gillett and Thompson 2003; Cai et al. 2005; Lovenduski and Gruber 2005). These changes are projected to continue over the next century and may alter the locations and/or dynamics of prey-aggregating nutrient-rich oceanic fronts in proximity to breeding colonies (Oke and England 2004; Rykaczewski and Checkley 2008; Bost et al. 2009). This change may also impact the flight costs of many seabirds that depend on prolific winds for travel (Weimerskirch et al. 2000; Wakefield et al. 2009; Weimerskirch et al. 2012; Louzao et al. 2013; Cornioley et al. 2016). The impact of these changes on the maintenance of energy balance for breeding creates a questionable future for some seabird populations and may lead to at least temporary advantages for others. Male wandering albatrosses (*Diomedea exulans*) on Crozet Island (46°S, 51°E) have experienced an adjustment in foraging range with poleward shifting winds, but this change has resulted in faster travel speeds, greater foraging success, and an overall increase in reproductive success (Weimerskirch et al. 2012). Albatrosses are well known for their ability to harness wind energy to power dynamic soaring flight, a maneuver that results in remarkably low flight costs despite long distance journeys and extreme weather conditions (Costa and Prince 1987; Weimerskirch et al. 2000; Shaffer et al. 2001b, 2004; Sachs et al. 2012; Antolos et al. 2017). However, flight costs are non-linear with wind speeds and direction (Alerstam et al. 1993; Weimerskirch et al. 2000) and continued changes to wind patterns may eventually negatively impact soaring flight.

Despite advantages observed in wandering albatrosses, soaring seabirds have intra- and interspecific morphological differences that confer distinct abilities (Warham 1977; Wakefield et al. 2009), allowing them to exploit different foraging habitats. Species or sexes with higher wing loading favor high-wind areas while birds with lower wing loading – and thus lower stalling speeds – can better utilize low-wind regions (Spear and Ainley 1997; Shaffer et al. 2001a; Phillips et al. 2004; Suryan et al. 2008). A better understanding of the mechanisms by which wind shapes movement patterns and foraging distributions in soaring birds has been gained through the use of least-cost pathway analysis (Felicisimo et al. 2008; Raymond et al. 2010). This method can also reveal the willingness of species to make higher cost choices relative to alternative routes, but cost choices are less informative without an understanding of wind-use dependency; individuals that fly irrespective of the wind may show an equal amount of high and low-cost choices (Felicisimo et al. 2008). Moreover, few studies have attempted to validate flight cost models with actual measures of energy expenditure. Louzao et al. (2014) altered the flight cost function developed by Felicisimo et al. (2008) using heart rate measurements and then validated this approach with measures of CO_2 production as a proxy for metabolic rates (Shaffer et al. 2003). However, their study was done with large-bodied wandering albatrosses, and it is unknown if this function applies to smaller albatross species with 27-38% less wing loading (Warham 1977; Chapter 3). However, if validated, the function can be applied to quantify flight costs relative to alternative routes which can reveal the flexibility and efficiency of foraging strategies.

Vector correlation coefficients, which were originally developed by physical oceanographers to indicate the interdependence of current vectors with overlying wind (Crosby et al. 1993; Breaker et al. 1994), can be used as a method to quantify wind-use dependency. Adams and Flora (2010) demonstrated the association between seabird movement and wind, suggesting that it could be used to quantify the variability between species or even populations of the same species. The application of this method – which to my knowledge has only been used in two other seabird studies (Yonehara et al. 2016; Goto et al. 2017) - can help us understand species differences in behavioral strategies when applied in conjunction with cost choice indices. Unlike flight cost functions, vector correlation coefficients cannot be used to compare directionality or magnitudes of the vector correlations, as similar values can result from differing directions or magnitudes (Crosby et al. 1993). However, the values are useful in verifying the consistency of flight patterns relative to wind velocities. If birds travel irrespective of the wind, vectors should be less correlated and cost choices should be equally low and high, but these relationships remain untested. Thus, combining least-cost pathway and vector correlation coefficient methods may reveal the interdependency of pelagic seabirds on certain wind patterns and their resiliency to expected future changes.

The goal of the present analysis was to determine the relationships between wind and seabird movement patterns across species, sexes, and stages to understand the flexibility of foraging strategies of albatrosses in relation to the wind fields they travel through. I also examined how individuals maintain energy balance with different wind-use strategies, particularly given the constraints of breeding periods or physical limitations conferred by their species or sex. Here, I compared the foraging behavior of two sympatrically breeding albatross species – grey-headed (*Thalassarche chrysostoma*) and Campbell (*T. impavida*) albatrosses – that utilize different foraging strategies (Waugh et al. 1999b, 2000) and have different body morphometrics (Chapter 3). Campbell albatrosses, which have lower wing loading, forage in lighter winds and have more variable trajectories whereas grey-headed albatrosses primarily forage near the Subantarctic and Polar Fronts in stronger winds (Waugh et al. 2000; Sztukowski 2015; Kroeger et al. 2019). Moreover, Campbell albatrosses breed annually whereas grey-headed albatrosses are biennial breeders, which may be related to differences in flight performance and diets (Waugh et al. 1999b; Jouventin and Dobson 2002; Chapter 3). In the present study, I first determined whether the flight cost function developed by Louzao et al. (2014) can be applied to these smaller bodied albatrosses. I examined whether optimal flight paths or consistency in wind interaction influenced flight costs and how flight path choices and wind-use consistency varied with behavioral states. Finally, I explored the relationship between flight cost choice and wind-use consistency by species, stage, and sex. Overall, this study focused on the behavioral flexibility associated with albatross species, stages, and sexes to help us understand their exploitation of different oceanic regions. Behavioral flexibility is important for central place foragers that must return to the nest to feed their offspring because forecasted changes in wind regimes may impact their energy balance and life history during an already costly reproductive period (Ydenberg et al. 1994).

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 #976 and New Zealand Wildlife Act Permit #SO-26385-FAU.

Study species and site

Campbell and grey-headed albatrosses were studied during the breeding season in 2011 (guard stage), 2012 (guard stage), and 2013 (incubation and guard stage, but no guard-stage grey-headed albatross; see Table 1). Both species breed on the north cape of Campbell Island (52°S, 169°E), New Zealand Subantarctic territory. Pairs incubate a single egg for 72-74 days and guard the chick for three weeks post-hatch (ACAP 2009, 2010). During each stage, mates exchange tasks of attending the nest and foraging at sea (Warham 1990). Grey-headed and Campbell albatross incubation-stage foraging trips are, respectively, 15 ± 3.4 and 17 ± 4.2 days and guard-stage trips are 3.9 ± 1.5 and 3.1 ± 1.5 days.

Field and laboratory procedures

Adults were captured just before departure to sea and weighed using a spring-loaded Pesola scale (nearest 25 g). To obtain flight paths and differentiate 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 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, 2013) intervals. Once birds returned from foraging trips, they were captured and weighed to measure mass change as a proportion of initial body mass and GPS devices were collected. Guard stage individuals in 2011 and 2012 were also sampled for estimates of daily energy expenditure (DEE) using the doubly labelled water method, as described in Chapter 3 (same individuals). Sex was determined by molecular methods following modifications of Quintana et al. (2008) for birds in 2011 and 2012 and by discriminant function analysis for remaining birds as described in Kroeger et al. (2019).

Bird movement data

All GPS tracks were trimmed to remove a 5 km radius buffer around the breeding colony to ensure behaviors not associated with transiting or foraging (e.g., rafting and circling the breeding colony) were excluded. Tracks were then rediscretized to 10 min intervals (‘adehabitatLT’ package, R 3.3; Calenge 2006). Individual tracks were further processed as described in Kroeger et al. (2019) using the Residence Space and Time method to assign behavioral states to each point (Torres et al. 2016). Behavioral states included transiting, area restricted search (i.e., “foraging”), or sitting on the water. Hereafter, I refer to transit and foraging states collectively as “in flight”. The proportion of time spent in each behavioral state was calculated for each species by stage. Foraging trip metrics such as trip duration, bird trajectories, and location farthest from the colony were calculated (R 3.3). The location farthest from the colony was used to classify preceding locations as “outbound” and subsequent locations as “inbound” for each individual. Finally, tracks were plotted by species and stage and sex to visualize basic differences between the groups and aid in the interpretation of results where sex differences may be present (Fig. 1).

Wind parameters

Along each track, ocean surface wind vectors were extracted from 10 m altitude at 0.28° and 3-hourly resolution from the ERA5 climate reanalysis dataset. Wind speeds and the wind angle on the bird relative to the bird's trajectory were calculated as described in Chapter 3. Rose plots were created for each species by stage for foraging and transit states to visualize frequencies of wind speeds and wind angles relative to horizontal bird movement. Wind angle on the bird was then transformed to 0-180° for use in the flight cost function and statistical models.

Cost of choice index for flight paths

Wind speeds (w) and relative wind angles (θ) were used to calculate the instantaneous flight costs for each track location using the following flight cost function estimated for wandering albatrosses (*Diomedea exulans*) by Louzou et al. (2014): *Flight Cost* = a + b * θ - c * w + d * θ * w; where a = 30, b = 2.38e^{-09} deg^{-1}, c = 9.67e^{-01} s m^{-1}, and d = .09e^{-02} deg^{-1} m^{-1} s (Fig. 2). Flight cost is expressed here non-dimensionally and can be considered to have arbitrary units. Flight cost values were adjusted using correction factors formulated by Louzao et al. (2014) to account for decreasing heart rate after take-off. An additional correction factor was used to account for inbound food loads, based on flight modeling suggestions from Alerstam et al. (2019). All inbound cost values were multiplied by ($1 + m^{1.5}$) following the flight power scaling relationship (Pennycuick 1975): $P \propto m^{1.5} * f^{0.25}$, where m is the mass gained by the individual during foraging as a proportion of their initial body mass and f is the maximum frontal area. Maximum frontal area measurements were not collected from individuals for the scaling relationship, but albatrosses carry food in the forestomach (Cherel and Klages 1997), which contributes less drag than seabirds that bill-carry prey. Total flight costs and mean flight costs were calculated for each individual from the instantaneous flight costs.

A flight cost "choice" score was given to each instantaneous flight cost estimate. The cost of alternative trajectories in 15° increments that the individual could have traveled was calculated based on anisotropic cost model methods from Felicisimo et al. (2008). The number of alternative trajectories less costly than the true path cost was divided by the total number of trajectories. A cost choice score of 1 indicates the costliest trajectory was taken, whereas a score of 0 indicates the optimal trajectory was taken. A mean cost choice score was calculated for each individual. Mean cost choice scores were calculated for entire trips for three states: in flight, foraging only, and transit only. The transit only state was further subset to calculate means for the outbound and inbound portions of each track.

Finally, the daily flight cost (kJ d^{-1}) was calculated from doubly labelled water estimates of at-sea daily energy expenditure ($DEE_{at\text{-}sea}$). $DEE_{at\text{-}sea}$ estimates were adjusted from mean measures of on-nest daily energy expenditure (mean $DEE_{on\text{-}nest}$; Campbell = 990 kJ d^{-1}, grey-headed = 979 kJ d^{-1}) using the following equation from Costa and Prince (1987): $(DEE_{at\text{-}sea} - (\%\ trip\ on\ water * mean\ DEE_{on\text{-}nest}))/ (1 - \%\ trip\ on\ water)$. This daily flight cost was multiplied by the trip duration so that it could be compared with the total flight cost from the cost function.

Vector correlation coefficients as wind-use consistency measure

Vector correlation coefficients were calculated to determine the interdependence of bird flight trajectories and wind trajectories (Crosby et al. 1993; Adams and Flora 2010). Because albatrosses change flight direction at any moment, except in cases of overpowering winds, I refer to this as a measure of wind-use consistency. A vector correlation coefficient was calculated for flight, foraging, transit, outbound transit, and inbound transit portions of each bird track following recommendations of Adams and Flora (2010). Values near 0 indicate no wind-use consistency (no correlation) whereas values near 2 indicate complete wind-use consistency (perfect correlation). For each vector correlation coefficient calculated, the same vector pairings were resampled with replacement (N=1000) to calculate 95% confidence intervals which were on average within ± 0.1 from the values estimates. A single vector correlation coefficient value was calculated from full trips and separated behavioral states; however, variability in the number of data points within trips or behavioral states could contribute to variability in vector correlations (Crosby et al. 1993; Adams and Flora 2010). These values are still ecologically meaningful, and comparisons are instructive if time scales are considered in the interpretation. Finally, wind variability on spatial scales smaller than a 28 km grid and temporal scales less than 3 hours, was not accounted for in the estimates of wind-use consistency due to the resolution of the wind data (ERA 5 climate reanalysis).

Statistical analysis

To determine the applicability of the flight cost function for each species, log-transformed total flight cost from doubly labelled water estimates were linearly regressed on total flight costs from the cost function with species, year, and sex as factors. Vector correlation coefficients were linearly regressed on mean cost choice scores to determine correlation between these variables with species, stage, year, and sex as factors. To avoid multicollinearity, mean total costs were separately linearly regressed on both cost choice scores and vector correlation coefficients with species, stage, year, and sex as factors. Proportional mass gain was similarly linearly regressed on cost choice scores and vector correlation coefficients. Within linear models, main effects are presented with the estimate slope (β), standard error (SE), and t-value.

Differences in mean flight costs, vector correlation coefficients, proportional mass gain, and mean wind speed across species, stage, year and sex were tested with multifactorial ANOVAs by Type III sums of squares. Differences in cost choice scores across species, stage, year and sex were tested with beta regressions using a logit link (‘betareg’ package, R 3.3; Cribari-Neto and Zeileis 2010). Vector correlation coefficients and cost choice scores were tested for differences between transit and foraging behavioral states and between outbound and inbound transit states with two sample t tests and two proportion z tests (‘BSDA’ package, R 3.3; Arnholt and Evans 2017), respectively. Differences in the circular means of wind angles on birds were compared between species, separately for each stage and within foraging-only then transit-only states, using one criterion analysis of variance for circular data (‘circular’ package, R 3.3; Agostinelli and Lund 2007). Differences in variance were tested with F tests.

For all models, interactions were tested, and simple slopes analysis was performed when linear model interactions were found with the continuous variable ($p < 0.1$; ‘interactions’ package, R 3.3; Long 2019). If a year effect for 2013 was identified, the model was separated by stage to differentiate whether the effect was due to the year or stage as this was the only year with incubating birds. Likewise, if stage differences were found, differences were tested within year and within species because Campbell albatrosses in 2013 where the only species and year to contain both stages. When factor interactions were present, relationships were examined with interaction plots and post hoc Tukey’s Honest Significant Difference tests designed for unequal sample sizes (TukeyHSD, R 3.3). When factors were not significant, they were removed from the model step-wise by highest p-value. Model residuals were visually inspected for homoskedasticity and normality. When model assumptions were not met a BoxCox transformation was applied except in the cases of aforementioned log transformations (‘caret’ package, R 3.3; Kuhn 2008).

Results

Comparing flight cost estimation methods

Total flight costs estimated from the flight cost function were positively associated with total flight costs estimated from the doubly labeled water method ($r^2 = 0.49$, $F_{2,49} = 23.8$, p

< 0.001; Fig. 3). The daily flight costs estimated by the doubly labelled water method (guard stage only, 2011 and 2012) were 2,750 ± 1,080 kJ d^{-1} and 2,670 ± 1,160 kJ d^{-1} for Campbell and grey-headed albatrosses, respectively. Daily flight costs were not significantly different between species within the linear model ($p = 0.81$) but were 37% higher in 2011 compared to 2012 ($p < 0.001$). ANOVA showed that mean function-derived flight costs from the same pool of individuals measured with doubly labeled water (Table 1) were not different between species ($F_{1,48} = 1.83$, $p = 0.18$) and, unlike daily flight costs, mean flight costs were similar between years ($F_{1,48} = 0.02$, $p = 0.89$).

Differences in mean flight costs and foraging success

When differences in mean flight costs were tested among all individuals, differences in species depended on the stage ($F_{1,123} = 7.9$, $p < 0.01$). Tukey's post hoc tests revealed that mean flight costs were 6% higher in incubation stage grey-headed albatrosses compared to incubation stage Campbell albatrosses ($p < 0.001$). Additionally, incubation-stage grey-headed albatrosses had 6% higher mean flight costs than guard-stage grey-headed albatrosses ($p < 0.001$). However, grey-headed albatross stages were not compared within the same year. There were no differences between years, sex, or species in the guard stage, or stage in Campbell albatross ($p > 0.05$).

When differences in proportional mass gains were tested, there was also significant interaction between species and stage ($F_{1,123} = 7.6$, $p < 0.001$). Incubation-stage relative mass gain was 137% higher than guard-stage relative mass gain but only for Campbell albatrosses ($p < 0.001$). Grey-headed albatross relative mass gain was 42% higher than Campbell albatross relative mass gain but only within the guard stage ($p = 0.001$). Among guard-stage individuals, proportional mass gain in 2012 was 114% higher than in 2011 ($p < 0.001$) but there was no difference between 2012 and 2013 ($p = 0.33$). There were no sex differences in relative mass gain, so they were removed from the model.

The relationship between mean flight cost and relative mass gain depended on year, where higher mean flight costs resulted in lower relative mass gain in 2011 (β = -0.03, SE = 0.01, t = -2.9, p = 0.01) but higher relative mass gain in 2013 (β = 0.01, SE = 0.00, t = 3.3, p = 0.00), regardless of stage. The overall model fit was r^2 = 0.38 ($F_{6,122}$, p < 0.001).

Cost choice and wind-use on flight cost and foraging success

Mean flight cost choice scores positively correlated with mean flight costs (β = 0.51, SE = 0.09, t = 5.5, p < 0.001). The overall model fit for the mean flight costs regressed on mean flight cost choice scores, including factors, was r^2 = 0.69 ($F_{7,121}$ = 39, p < 0.001). Incubation-stage male grey-headed albatrosses with higher flight cost choice scores had marginally lower relative mass gain (β=-1.1, SE = 0.47, t = -2.3, p = 0.03; r^2 = 0.29, $F_{2,37}$ = 2.1, p = 0.06). Incubation stage males from both species that had high outbound transit cost choice scores also had lower relative mass gain (β = -0.44, SE = 0.14, t = -3.2, p = 0.00), but females had marginally higher relative mass gain (β = 0.41, SE = 0.22, t = 1.9, p = 0.07; r^2 = 0.31, $F_{4,40}$ = 4.5, p < 0.01). Guard-stage individuals in 2011 with higher flight cost choice scores gained less relative mass (β = -0.73, SE = 0.20, t = -3.7, p = 0.0; r^2 = 0.41, $F_{6,77}$ = 8.9, p < 0.001). However, guard stage Campbell albatrosses with higher outbound transiting cost choice scores gained more relative mass (β = 0.23, SE = 0.10, t = 2.2, p = 0.03; r^2 = 0.34, $F_{6,77}$ = 6.7, p < 0.001).

Flight vector correlation positively affected mean flight cost within all species, stages, years, and sexes (r^2 = 0.32, $F_{6,122}$ = 9.5, p < 0.001). Within the incubation stage, male grey-headed albatrosses with higher flight vector correlations had higher relative mass gain (β = 0.55, SE = 0.20, t = 2.7, p = 0.01). Guard stage individuals with higher flight vector correlation coefficients had greater relative mass gain in 2011 (β = 0.12, SE = 0.06, t = 2.1, p = 0.04), although relative mass gain was lowest in 2011 and lower in the guard stage (see above).

The overall model fit was $r^2 = 0.43$ ($F_{13,115} = 6.7$, $p < 0.001$). Furthermore, grey-headed albatrosses with higher outbound transiting vector correlations had greater relative mass gain ($\beta = 0.10$, SE = 0.04, $t = 2.3$, $p = 0.02$), but there was no effect of outbound transit on relative mass gain in Campbell albatrosses ($\beta = -0.01$, SE = 0.05, $t = -0.13$, $p = 0.89$; $r^2 = 0.34$, $F_{6, 121} = 10.5$, $p < 0.001$).

Cost choice: species, stage, and behavioral differences

Mean flight cost choice scores ranged between 0.25-0.62 and were similar between species overall (Campbell: 0.45 ± 0.09; grey-headed: 0.49 ± 0.04); however, during the incubation stage, mean flight cost choice scores were 17% lower in Campbell albatrosses (0.42 ± 0.06) compared to grey-headed albatrosses (0.49 ± 0.04; $\beta = 0.28$, SE = 0.06, $z = 5.0$, $p < 0.001$). In Campbell albatrosses, mean flight cost choice scores where 10% higher during the guard stage compared to the incubation stage (interaction: $\beta = 0.2$, SE = 0.11, $z = 2.7$, $p < 0.01$), but not within the same year (i.e., not within 2013; $z = 0.09$, $p = 0.9$). Mean flight cost choice scores did not differ between grey-headed albatross stages, but both stages were not measured within the same year. During both stages, Campbell albatrosses showed greater variation in cost choice than grey-headed albatrosses (incubation: $F_{1,20} = 2.5$, $p = 0.03$; guard: $F_{1,31} = 3.0$, $p = 0.001$). In both species, the guard stage showed more variation in cost choices scores than the incubation stage (grey-headed: $F_{1,23} = 2.3$, $p = 0.05$; Campbell: $F_{1,20} = 2.3$, $p = 0.02$).

During the incubation stage only, individuals with lower mean flight cost choice scores had longer trip durations ($r^2 = 0.13$, $F_{1,43} = 6.5$, $p = 0.01$). Mean foraging cost choice scores (0.52 ± 0.08) were 30% higher than mean transit cost choice scores (0.40 ± 0.08) for all stages and species ($z = -12$, $p < 0.001$). Mean outbound transiting cost choice scores (range: 0.32-0.35) were lower than mean inbound transiting cost choice scores (range: 0.45-

0.49) for all species and stages (z = -6.9, p <0.001) except for Campbell albatrosses during incubation (inbound = 0.34 ± 0.1; z = -0.14, p = 0.88).

Wind-use consistency: species, stage, and behavioral differences

Differences in mean flight vector correlation coefficients varied by stage and species ($F_{1,124}$ = 4.6, p = 0.03). Vector correlation coefficients were 58% higher in Campbell albatrosses (0.49 ± 0.25) compared to grey-headed albatrosses (0.31 ± 0.24, p < 0.001) in the incubation stage; however, species differences did not apply to the guard stage (p = 0.18). In addition, guard-stage vector correlation coefficients (0.50 ± 0.26) were two times greater than in the incubation-stage (0.25 ± 0.18, p < 0.001) with the exception that guard-stage grey-headed albatrosses did not differ from incubation-stage Campbell albatrosses. Overall, incubation-stage grey-headed albatrosses had the lowest mean vector correlations. Within both stages, vector correlation coefficients did not vary with trip duration (β = -0.41, SE = 1.0, t = -0.41, p = 0.68). No sex differences in vector correlation coefficients were found (p > 0.1). During flight, the proportion of foraging was greatest in incubation-stage grey-headed albatrosses (z = 2.6, p < 0.01). During transit only, incubation-stage grey-headed albatrosses still had the lowest mean vector correlation coefficients (p < 0.001 for all post-hoc species-stage comparisons were incubation-stage grey-headed albatross were lowest).

For all species and stages, mean transit vector correlation coefficients (0.61 ± 0.30) were higher than mean foraging vector correlation coefficients (0.25 ± 0.22; $F_{1,124}$ = 6.492, p = 0.01). Mean outbound transiting vector correlation coefficients (0.38 ± 0.21) were 40% lower than mean inbound transiting vector correlation coefficients (0.63 ± 0.34) for both species in the incubation stage (t_{73} = -4.0, p < 0.001), but there was no difference within guard stage Campbell albatrosses (t_{97} = -1.2, p = 0.23) and only marginally higher mean inbound coefficients within guard stage grey-headed albatrosses (t_{59} = -1.9, p = 0.06).

Relationship between cost choice and wind-use consistency

In both stages, there was a parabolic relationship between correlation coefficients and cost choice scores during foraging states ($r^2 = 0.52$, $F_{6,122} = 22.1$, $p < 0.001$; Fig. 4). All individuals with high transiting vector correlations had low transiting cost choice scores ($F_{5,123} = 13.0$, $r^2 = 0.35$, $p < 0.001$). For both species in the incubation stage, high inbound transiting vector correlations correlated with low inbound cost choice scores ($r^2 = 25$, $F_{2,42} = 7.0$, $p < 0.01$; Fig. 5). However, there was no relationship between inbound transiting vector correlation coefficients and inbound cost choice scores in guard-stage individuals ($p = 0.70$). Furthermore, guard-stage individuals exhibited a positive relationship between outbound transiting vector correlation coefficients and outbound transiting cost choices ($\beta = 0.68$, SE = 0.28, $t = 2.5$, $p = 0.02$; $r^2 = 0.07$, $F_{1,81} = 6.0$, $p = 0.02$; Fig. 6).

Wind speed and angles: species, stage, and behavioral differences

Within each species, stage, year, and sex, individuals that experienced lower mean wind speeds in flight (transit and foraging) had higher mean flight vector correlation coefficients ($\beta = 0.68$, SE = 0.28, $t = 2.5$, $p = 0.02$; $r^2 = 0.37$, $F_{3,125} = 24.3$, $p < 0.001$). However, inbound transiting individuals that experienced lower wind speeds had lower inbound transiting vector correlation coefficients ($r^2 = 0.06$, $F_{3,125} = 2.7$, $p = 0.05$). Outbound transiting individuals that experienced lower wind speeds also had lower vector correlation coefficients, but only during the guard stage ($\beta = 0.02$, SE = 0.01, $t = 2.3$, $p = 0.02$; $r^2 = 0.26$, $F_{4,123} = 10.9$, $p < 0.001$).

Within Campbell albatrosses only, males experienced mean wind speeds 1.7 m s^{-1} greater than females ($F_{5,124} = 12.8$, $p < 0.001$). Grey-headed albatrosses experienced mean wind speeds 1.7 m s^{-1} greater than Campbell albatrosses ($p < 0.001$). Multiple comparisons showed that wind speeds were greatest in 2012 and lowest in 2011 (all $p < 0.05$). There were no significant mean wind speed differences between stages for either species ($p = 0.30$). Moreover, mean wind speed during outbound transiting was 1.1 m s^{-1} lower than inbound transiting, but only in guard stage Campbell albatrosses ($t_{98} = -2.0$, $p = 0.05$).

The lowest mean vector correlation coefficients occurred when birds experienced crosswinds (Fig. 7). Mean wind angles on birds were significantly different between species for both stages for each behavioral state in flight. Incubation stage grey-headed albatrosses foraged with winds slightly more toward the head than incubation stage Campbell albatrosses (77° vs. 88°, respectively; $\chi^2 = 474$, $p < 0.001$; Fig. 8). Campbell albatrosses transited with winds more toward the tail than grey-headed albatrosses in both stages (incubation: 102° vs. 115°; guard: 98° vs. 107°), but less so during the guard stage ($p < 0.001$; Fig. 9).

Discussion

Validating the flight cost function

The flight cost function validated for wandering albatrosses (Louzao et al. 2014) works for at least two smaller albatrosses (this study) that utilize contrasting foraging strategies with respect to their prey preferences and foraging habitat (Waugh et al. 1999a, 2000). Thus, the flight cost function can be used to examine how flight specific behaviors affect energy balance at sea for incubation-stage periods that were too long to measure with doubly labeled water (Speakman 1997). Flight costs estimated with the cost function suggest that grey-headed albatrosses have higher mean flight costs during incubation than both Campbell albatrosses and guard stage albatrosses**.** However, incubation stage grey-headed albatrosses did not have significantly greater relative mass gain than incubation stage Campbell albatrosses. Thus, higher estimated flight costs in the incubation stage grey-headed albatross can be attributed to the higher wind speeds encountered combined with a higher frequency of head winds experienced, but not larger food loads per se (Figs. 8 and 9).

Headwinds were more heavily used during foraging for this species and stage (Fig. 8), which may be advantageous for locating prey (Spear and Ainley 1997; Weimerskirch et al. 1997c, 2012), although their relative mass gain does not support this. A comparison across years in incubation-stage grey-headed albatrosses is likely to be more revealing, but higher flight costs during the incubation stage in grey-headed albatrosses may contribute to biennial breeding in grey-headed albatrosses relative to Campbell albatrosses (Waugh et al. 1999b; Jouventin and Dobson 2002). Chapter 3 demonstrated that daily energy expenditure at sea did not differ between species during the guard stage despite differing foraging strategies and life histories, but there was a significant difference in daily energy expenditure across years which was not found when estimating mean flight costs with the cost function. This result suggests the importance of potential non-flight factors (e.g., prey-type, mass gain, etc.) on daily energy demands at sea that are not captured by the flight cost function (Weimerskirch et al. 2000). Moreover, Chapter 3 showed that low take-off wind speed and a higher proportion of strong tailwinds led to greater daily energy expenditure and these factors were not represented in the flight cost function. Therefore, further investigation is needed to fully understand life history differences.

Cost choice, wind-use uniformity, and mean flight cost

Mean flight cost choice scores positively correlated with mean flight costs calculated from the cost function as expected given that the former was derived from the latter. While individuals who chose optimal pathways had the greatest flight efficiency, foraging efficiency was variable, as low-cost choices did not always equate to high relative mass gains (see below). However, it is possible for cost choice scores to be relatively high even if total instantaneous costs are low and vice versa. For example, the majority of options can be low cost in lower wind speeds, but the individual could be flying in a high cost direction (Fig. 2). Another caveat is that the flight cost function does not account for the possibility of strong tailwinds increasing energy expenditure as found in Chapter 3. These caveats are not a major consideration in this study due to the high correlation between cost choice scores and mean flight costs.

For all individuals, higher vector correlation coefficients in flight were associated with lower mean flight costs. Thus, individuals that use the wind more uniformly minimized their flight costs. Alerstam et al. (2019) predict that uniform wind fields will result in more crosswind flight and subsequent lower flight costs; however, grey-headed albatrosses using the most uniform westerly wind fields had the lowest wind-use consistency and wind-use consistency was lowest during crosswind flight (Fig. 7). An individual should use the wind more consistently if it is favorable, whereas individuals that encounter unfavorable winds should alter course when possible (Fritz et al. 2003). Low wind-use consistency in flight was associated with high wind speeds, which may force tacking motion if individuals must travel upwind (Sachs 2016; Richardson et al. 2018). Alternatively, individuals that successfully find food may have higher wind-use consistency because they do not need to change course to target more prey patches (Weimerskirch et al. 1997c). Regardless, greater wind-use consistency led to more successful foraging, suggesting this mode of flight is associated with favorable conditions.

Difference in cost choice and wind use between species, stage, and behavioral states

Cost choice scores were higher in Campbell albatrosses during the guard stage compared to the incubation stage; however, when stages were contrasted within the same year, cost choice scores were equivalent. This suggests differences in flight path choices were related to annual differences rather than stage-specific differences, perhaps due to differences in wind speed or location of ocean productivity (Trathan et al. 2007; Bost et al.

2009; Raymond et al. 2010). Additionally, cost choice scores were greater for incubation-stage grey-headed albatrosses compared to incubation-stage Campbell albatrosses. Grey headed albatrosses during incubation experienced a higher proportion of strong headwinds than incubating Campbell albatrosses but spent a greater proportion of flight in area restricted search, which should be less flight-path efficient than transiting given frequent turning angles irrespective of the wind (Louzao et al. 2014). Indeed, incubation-stage grey-headed albatrosses had mean cost choice scores closest to 0.5, indicating flight irrespective of wind (Felicisimo et al. 2008). Incubation-stage Campbell albatrosses where the only group among species and stages that did not have greater inbound relative to outbound transiting cost choice scores. Inbound flight path efficiency is expected to be higher as many central place foraging seabirds return with tailwinds to minimize total costs of foraging trips (Liechti 1995; Alerstam et al. 2019). Lower total flight cost may make it less imperative to return with flight efficient tailwinds (Suryan et al. 2008) and incubation-stage Campbell albatrosses were the only group to primarily travel to destinations north of the breeding colony (Fig. 1), where wind speeds are lower overall (Young et al. 2011). Differences in least cost path choices across stages suggest flexibility in foraging strategies may be afforded by lower wind speed.

Given the more uniform westerly wind fields heavily utilized by grey-headed albatrosses (Chapter 3; Phillips et al. 2004; Fig. 1), it is surprising that their wind-use consistency was lower than for incubation-stage Campbell albatrosses. Incubation-stage Campbell albatrosses can pass through more wind fields on their wide ranging and variable trips (Fig. 1), increasing variability in wind directions on the birds. This variability did appear to reduce wind-use consistency relative to short-trip guard-stage Campbell albatrosses. Less aerial foraging will result in higher wind correlations and Campbell albatrosses performed less area restricted search and spent more time on the water, likely employing more sit-and-wait strategies (Catry et al. 2004; Weimerskirch and Pinaud 2007; Louzao et al. 2014; Conners et al. 2015). However, the same differences in wind-use consistency were evident in transit states suggesting wind speed contributed to the observed differences. Indeed, lower wind speeds experienced by Campbell albatrosses correlated with higher wind-use consistency in flight relative to grey-headed albatrosses.

Guard stage individuals from both species that had longer trip durations in 2011 (when overall mass gain was lowest) had lower wind-use consistency, potentially because less success finding prey leads to more targeted areas and extended foraging trips (Weimerskirch et al. 1997c; Cornioley et al. 2016). Furthermore, wind-use consistency was lower during outbound transit than inbound transit, except for guard stage Campbell albatrosses that experienced lower windspeeds on outbound transit than inbound and also had the lowest relative mass gains. Wind-use consistency reveals differences in foraging strategy that are nonlinearly influenced by wind speed and may have consequences for foraging success (Weimerskirch et al. 2012). However, lower foraging success associated with different wind-use and flight patterns does not necessarily equate to lower foraging efficiency as overall energy balance and total foraging trip costs must be considered. Guard stage Campbell albatrosses spend more time foraging on the Campbell Plateau which may require more targeting more locations (Weimerskirch et al. 1997c) in low winds and be less effective as an energy acquisition strategy but enable more frequent chick feedings (Weimerskirch 1998; Shaffer et al. 2003).

Cost choice and wind-use consistency

Individuals that fly irrespective of the wind should have cost choice scores centered near 0.5 because they should be equally likely take high and low-cost trajectories (Felicisimo et al. 2008). As expected, this relationship was observed in individuals of both species that use more tortuous flight during foraging (Fig. 4). In contrast, when individuals are in transit, those that use the wind less consistently should have higher cost choice scores (i.e., less efficient flight paths) than those that use the wind more consistently. An individual that navigates into a high cost area may alter course to a more energy-efficient direction; however, because birds likely navigate to known and preferred foraging regions and then back to the nest, individuals may have to recalibrate trajectories into potentially high cost regions to reach their intended destination, thus reducing the wind correlation (Weimerskirch et al. 2000; Weimerskirch 2007; Goto et al. 2017). Sachs (2016) describe this pattern in albatrosses as individuals use lower-cost dynamic soaring to tack upwind and reach foraging destinations. During incubation-stage trips that are longer than guard-stage trips, higher cost choices and lower wind-use consistency in transit may be likely if (a) wind fields are variable or unpredictable en route to preferred foraging destinations and/or (b) less experienced birds make poor navigational decisions. In the case of the former, individuals should have greater foraging success and in the case of the latter, less foraging success (Limmer and Becker 2009, but see Nevoux et al. 2007).

As expected, the results of this study showed that in transit, cost choice scores and wind-use consistency were negatively correlated for both species during incubation. Moreover, males obtained less food than females for the same cost choices, lending support to cases A and B above where males may have been more inexperienced breeders. Because males take the first incubation shift, and less experienced breeders have been shown to lay eggs earlier (Weimerskirch 1992), it is feasible that males sampled around the same period as females were less experienced breeders particularly given that adults were not sampled from the same pairs. Alternatively, males may have had lower food acquisition if productivity was abnormally low in their preferred foraging locations in 2013 (Phillips et al. 2004; Wakefield et al. 2014).

When transit was parsed to outbound and inbound components, incubation-stage Campbell and grey-headed albatross showed a negative correlation between cost choice scores and wind-use consistency during inbound transiting only. In Figure 5a, I show a grey-headed albatross returning into a strong headwind requiring high-cost choice tacking movements upwind to return home. Grey-headed albatrosses may navigate to frontal upwelling regions south of the breeding colony for predictable resources, but the cost of flying into strong headwinds on return with heavy food loads may offset outbound travel speeds and energy gains (Weimerskirch et al. 2000; Weimerskirch 2007; Alerstam et al. 2019). Unlike wandering albatrosses, grey-headed albatrosses with lower wing loading may be less likely to benefit from climate-driven intensification of poleward winds (Weimerskirch et al. 2012). I also show an example of a Campbell albatross individual using a different inbound strategy (Fig. 5b), moving with high flight path efficiency (low cost choice score) utilizing a consistent cross-tailwind. Thus, there are clear differences in available strategies used by grey-headed and Campbell albatrosses to return to the nest during the incubation stage which may have implications for population dynamics if poleward wind speeds continue to intensify (Gillet and Thompson 2003).

In contrast to the incubation stage, individuals transiting in the guard stage may be more likely to make high cost choices with high wind-use consistency if they are attempting to acquire high reward food quickly for their young chicks at the expense of self-maintenance. In this stage, individuals may forgo avoiding costly strong headwinds as has been observed in wandering albatross (Weimerskirch et al. 2000). Indeed, adults have been shown to lose mass as they devote more energy toward chick-rearing (Weimerskirch et al. 1997a; Weimerskirch and Lys 2000). Additionally, guard-stage individuals may be more likely to utilize tailwinds to increase flight speed and reduce overall trip duration (Wakefield et al. 2009). Typically, Procellariiformes do not use tailwinds as frequently as other wind angles, potentially because flight speeds are too fast to search for food (Houston 1986; Spear and Ainley 1997; Weimerskirch et al. 1997, but see Catry et al. 2004) or because they may be costly at high speeds before food loads have been acquired (Chapter 3), but this relationship does not apply to low wind speed locations or species with lower wing loading (Spear and Ainley 1997; Awkerman et al. 2014).

Guard-stage individuals showed no relationship between wind use measures on return to the breeding colony but showed similar strategies across species during the outbound portion of their trips. As expected, outbound transiting revealed a positive association between cost choice scores and wind-use consistency. Individuals with high cost choice scores and high vector correlations coefficients head straight for their foraging destinations using cross- to cross-headwinds (Fig. 6a, b). However, when utilizing low-cost tailwinds on outbound transit, they appear to tack in the wind thus lowering vector correlations (Fig. 6c, d). Individuals may travel with direct tailwinds to gain speed (Alerstam et al. 1993; Richardson et al. 2018) but need directional corrections to reach the preferred destination. Alternatively, strong direct tailwinds may be too destabilizing for birds that have not acquired food loads, thus the need for tacking (Alerstam et al. 2019, Chapter 3). Guard-stage individuals that made higher outbound cost choices had higher proportional mass gain, suggesting a beneficial trade-off of high cost choices for high food reward using a direct route strategy (Shaffer et al. 2003; Wakefield et al. 2009). This trade-off may only be beneficial during the guard stage when total incurred flight costs are lower than during incubation (this study, Salamolard and Weimerskirch 1993). However, in 2011 when mass gain was lowest and flight costs were highest, albatrosses that flew costlier routes also had the lowest mass gains. This finding indicates that individuals are more willing to take high-cost routes when productivity is high enough to offset costs.

Implications and future directions

When validated, flight cost functions can be applied to estimate flight costs during less accessible breeding stages with less disturbance to animals. Flight cost models may be further improved by correction factors for variable take-off windspeeds and the potential impact of strong tailwinds based on findings of Chapter 3. Nonetheless, flight cost estimates were illuminating with respect to life history differences, where greater estimated flight cost during the incubation stage in grey-headed albatrosses may help explain why this species breeds biennially compared to the annually breeding Campbell albatross. More sustained transit tacking upwind for grey-headed albatrosses may increase total flight costs as westerly winds intensify with climate change (Gillett and Thompson 2003). In contrast to grey-headed albatrosses, Campbell albatrosses flew with greater consistency to the wind and had lower flight costs with similar foraging success; thus, it appears that greater wind-use consistency is a favorable foraging strategy enabled by lower wind speeds. Individuals utilizing low wind areas could make higher cost choices without increasing total costs; however, take-off costs from the water will be higher, which may increase total foraging trip costs relative to grey-headed albatrosses. Compared to the incubation stage, guard-stage Campbell albatrosses utilize more mid/higher latitudes where consistent wind-use patterns may be impacted by strengthening winds. Male Campbell albatrosses that travel farther south (Fig. 1) toward intensifying winds may be disproportionately impacted. Finally, incubation-stage males within each species demonstrated lower food acquisition, but it is unclear if this was due to relative inexperience, differing wind fields, or low productivity. Future studies that examine wind-use consistency in known-age individuals would improve our understanding of foraging strategy differences and sex-specific vulnerabilities. Together flight cost choices and wind-use consistency reveal different foraging strategies and provide clues as to how different species, stages, or sexes may tolerate forecasted atmospheric changes within their foraging habitat.

References

Adams J. and S. Flora. 2010. Correlating seabird movements with ocean winds: linking satellite telemetry with ocean scatterometry. Mar Biol 157:915–929.

Agostinelli C. and U. Lund. 2017. R package 'circular': Circular Statistics (version 0.4-93). URL https://r-forge.r-project.org/projects/circular/

Alerstam T., J. Bäckman, and T.J. Evans. 2019. Optimal central place foraging flights in relation to wind. J Ornithol.

Alerstam T., G. A. Gudmundsson, and B. Larsson. 1993. Flight tracks and speeds of antarctic and atlantic seabirds: radar and optical measurements. Philos Trans R Soc B Biol Sci 340:55–67.

Antolos M., S.A. Shaffer, H. Weimerskirch, Y. Tremblay, and D.P. Costa. 2017. Foraging behavior and energetics of albatrosses in contrasting breeding environments. Front Mar Sci 4:1–12.

Arnholt A. T. and B. Evans. 2017. BSDA: Basic Statistics and Data Analysis. R package version 1.2.0. https://CRAN.R-project.org/package=BSDA

Bost C.A., C. Cotté, F. Bailleul, Y. Cherel, J.B. Charrassin, C. Guinet, D.G. Ainley, et al. 2009. The importance of oceanographic fronts to marine birds and mammals of the southern oceans. J Mar Syst 78:363–376.

Breaker L.C., W.H. Gemmill, and D.S. Crosby. 1994. The application of a technique for vector correlation to problems in meteorology and oceanography. J Appl Meteorol 33:1354–1365.

Cai W., G. Shi, T. Cowan, D. Bi, and J. Ribbe. 2005. The response of the Southern Annular Mode, the East Australian Current, and the southern mid-latitude ocean circulation to global warming. Geophys Res Lett 32:1–4.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516-519

Catry P., R.A. Phillips, and J.P. Croxall. 2004. Sustained fast travel by a gray-headed albatross (*Thalassarche chrysostoma*) riding an antarctic storm. Auk 121:1208–1213.

Catry P., R.A. Phillips, B. Phalan, J.R.D. Silk, and J.P. Croxall. 2004. Foraging strategies of grey-headed albatrosses *Thalassarche chrysostoma*: integration of movements, activity and feeding events. Mar Ecol Prog Ser 280:261–273.

Chapman J.W., R.H.G. Klaassen, V.A. Drake, S. Fossette, G.C. Hays, J.D. Metcalfe, A.M. Reynolds, et al. 2011. Animal orientation strategies for movement in flows. Curr Biol 21:R861–R870.

Cherel Y. and N. Klages. 1997. Chapter 10: A Review of the food of albatrosses. Pp. 113–136 in Albatross Biol Conserv.

Conners M.G., E.L. Hazen, D.P. Costa, and S.A. Shaffer. 2015. Shadowed by scale: subtle behavioral niche partitioning in two sympatric, tropical breeding albatross species. Mov Ecol 3:1–20.

Cornioley T., B. Luca, A. Ozgul, and H. Weimerskirch. 2016. Impact of changing wind conditions on foraging and incubation success in male and female wandering albatrosses. J Anim Ecol 85:1318–1327.

Costa D.P. and P.A. Prince. 1987. Forgaing energetics of Grey-headed Albatrosses

Diomedia chrysostoma at Bird Island, South Georgia. Ibis (Lond 1859) 129:149–158.

Cribari-Neto F. and A. Zeileis. 2010. Beta Regression in R. Journal of Statistical Software 34:1-24. URL http://www.jstatsoft.org/v34/i02/.

Crosby D.S., L.C. Breaker, and W.H. Gemmill. 1993. A proposed definition for vector correlation in geophysics: theory and application. Am Meteorol Soc 10:355–367.

Elliott K., L.S. Chivers, L. Bessey, A.J. Gaston, S.A. Hatch, A. Kato, O. Osborne, et al. 2014. Windscapes shape seabird instantaneous energy costs but adult behavior buffers impact on offspring. Mov Ecol 2:17.

Fagan W.F., M.A. Lewis, M. Auger-Méthé, T. Avgar, S. Benhamou, G. Breed, L. Ladage, et al. 2013. Spatial memory and animal movement. Ecol Lett 16:1316–1329.

Felicisimo A.M., J. Munoz, and J. González-Solís. 2008. Ocean surface winds drive dynamics of transoceanic aerial movements. PLoS One 3:1–7.

Fritz H., S. Said, and H. Weimerskirch. 2003. Scale-dependent hierarchical adjustments of movement patterns in a long-range foraging seabird. Proc R Soc B Biol Sci 270:1143–1148.

Gillett N.P. and D.W.J. Thompson. 2003. Simulation of recent southern hemisphere climate change. Science 302:273–275.

Goto Y., K. Yoda, and K. Sato. 2017. Asymmetry hidden in birds' tracks reveals wind, heading, and orientation ability over the ocean. Sci Adv 3:1–9.

Houston, A. I. 1986. The optimal flight velocity for a bird exploiting patches of food. J Theor Biol, 119:345-362.

Jouventin P. and F.S. Dobson. 2002. Why breed every other year? The case of albatrosses. Proc R Soc Lond B 269:1955–1961.

Kroeger C., D.E. Crocker, D.R. Thompson, L.G. Torres, P.M. Sagar, and S.A. Shaffer. 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 92:702656.

Kuhn, M. 2008. Building Predictive Models in R Using the caret Package. Journal of Statistical Software 28:1-26.

Liechti F. 1995. Modelling optimal heading and airspeed of migrating birds in relation to energy expenditure and wind influence. J Avian Biol 26:330–336.

______. 2006. Birds: blowin' by the wind? J Ornithol 147:202–211.

Limmer B. and P.H. Becker. 2009. Improvement in chick provisioning with parental experience in a seabird. Anim Behav 77:1095–1101.

Long J. A. 2019. interactions: Comprehensive, User-Friendly Toolkit for Probing Interactions. R package version 1.1.0, URL: https://cran.r-project.org/package=interactions.

Louzao M., O. Aumont, T. Hothorn, T. Wiegand, and H. Weimerskirch. 2013. Foraging in a changing environment: Habitat shifts of an oceanic predator over the last half century. Ecography 36:057–067.

Louzao M., T. Wiegand, F. Bartumeus, and H. Weimerskirch. 2014. Coupling instantaneous energy-budget models and behavioural mode analysis to estimate optimal foraging strategy: an example with wandering albatrosses. Mov Ecol 2:1-15.

Lovenduski N.S. and N. Gruber. 2005. Impact of the Southern Annular Mode on Southern Ocean circulation and biology. Geophys Res Lett 32:1–4.

Masson-Delmotte V., P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, et al. 2018. IPCC Special Report 1.5 - Summary for Policymakers. IPCC.

Nel D.C., J.R.E. Lutjeharms, E.A. Pakhomov, I.J. Ansorge, P.G. Ryan, and N.T.W. Klages. 2001. Exploitation of mesoscale oceanographic features by grey-headed albatross *Thalassarche chrysostoma* in the southern Indian Ocean. Mar Ecol Prog Ser 217:15–26.

Nevoux M., H. Weimerskirch, and C. Barbraud. 2007. Environmental variation and experience-related differences in the demography of the long-lived black-browed albatross. J Anim Ecol 76:159–67.

Oke P.R. and M.H. England. 2004. Oceanic response to changes in the latitude of the Southern Hemisphere subpolar westerly winds. J Clim 17:1040–1054.

Phillips R.A., J.R.D. Silk, B. Phalan, P. Catry, and J.P. Croxall. 2004. Seasonal sexual segregation in two *Thalassarche* albatross species: Competitive exclusion, reproductive role specializaion or foraging niche divergence? Proc R Soc B Biol Sci 271:1283–1291.

Pennycuick, C. J. 1975. Mechanics of flight. Avian biol 5:1-73.

Quintana F., G.C. Lopez, and G. Somoza. 2008. A cheap and quick method for DNA-based sexing of birds. Waterbirds Int J Waterbird Biol 31:485–488.

Warham J. 1977. Wing loadings, wing shapes, and flight capabilities of procellariiformes. New Zeal J Zool 4:73–83.

Warham J ed. 1990. The petrels: their ecology and breeding systems. London, Academic Press.

Raymond B., S.A. Shaffer, S. Sokolov, E.J. Woehler, D.P. Costa, L. Einoder, M. Hindell, et al. 2010. Shearwater foraging in the Southern Ocean: The roles of prey availability and winds. PLoS One 5.

Richardson P.L., E.D. Wakefield, and R.A. Phillips. 2018. Flight speed and performance of the wandering albatross with respect to wind. Mov Ecol 6:1–15.

Rykaczewski R.R. and D.M. Checkley. 2008. Influence of ocean winds on the pelagic ecosystem in upwelling regions. Proc Natl Acad Sci U S A 105:1965–70.

Sachs G. 2016. In-flight measurement of upwind dynamic soaring in albatrosses. Prog

Oceanogr 142:47–57.

Sachs G., J. Traugott, A.P. Nesterova, G.D. Omo, F. Ku, W. Heidrich, A.L. Vyssotski, et al. 2012. Flying at no mechanical energy cost: disclosing the secret of wandering albatrosses. PLoS One 7:e41449.

Sagar P. 2014. Population estimates and trends of Campbell and grey-headed albatrosses at Campbell Island: Campbell and grey-headed albatross population estimates. NIWA report prepared for Department of Conservation.

Sage E., W. Bouten, B. Hoekstra, K.C.J. Camphuysen, and J. Shamoun-Baranes. 2019. Orographic lift shapes flight routes of gulls in virtually flat landscapes. Sci Rep 9:9659.

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

Shaffer S.A., D. Costa, and H. Weimerskirch. 2003. Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. Funct Ecol 66–74

Shaffer S.A., D.P. Costa, and H. Weimerskirch. 2001. Behavioural factors affecting foraging effort of breeding wandering albatrosses. J Anim Ecol 70:864–874.

______. 2004. Field metabolic rates of black-browed albatrosses *Thalassarche melanophrys* during the incubation stage. J Avian Biol 35:551–558.

Shaffer S.A., H. Weimerskirch, and D.P. Costa. 2001. Functional significance of sexual dimorphism in wandering albatrosses, *Diomedea exulans*. Funct Ecol 15:203–210.

Shepard E.L.C., A.N. Ross, and E.L.C. Shepard. 2016. Moving in a moving medium: new perspectives on flight. Philos Trans R Soc B Biol Sci 371:20150382.

Speakman J.R. 1997. Doubly Labelled Water: Theory and Practice. Chapman & Hall.

Spear L.B. and D.G. Ainley. 1997. Flight behaviour of seabirds in relation to wind direction and wing morphology. Ibis (Lond 1859) 139:221–233.

Suryan R.M., D.J. Anderson, S.A. Shaffer, D.D. Roby, Y. Tremblay, D.P. Costa, P.R. Sievert, et al. 2008. Wind, waves, and wing loading: Morphological specialization may limit range expansion of endangered albatrosses. PLoS One 3.

Sztukowski L.A. 2015. *Foraging ecology of the Campbell albatross: individual specialisation and fishery interactions*. Unpublished. Plymouth University.

Tew Kai E., V. Rossi, J. Sudre, H. Weimerskirch, C. Lopez, E. Hernandez-Garcia, F. Marsac, et al. 2009. Top marine predators track Lagrangian coherent structures. Proc Natl Acad Sci 106:8245–50.

Thompson D.W.J. and J.M. Wallace. 2000. Annular modes in the extratropical circulation. Part II: Trends. J Clim 13:1018–1036.

Thorne L.H., M.G. Conners, E.L. Hazen, S.J. Bograd, M. Antolos, D.P. Costa, and S.A. Shaffer. 2016. Effects of El Niño-driven changes in wind patterns on North Pacific albatrosses. J R Soc Interface 13:20160196.

Torres L.G., R.A. Orben, I. Tolkova, and D.R. Thompson. 2016. Classification of Animal Movement Behavior through Residence in Space and Time. PLoS One 12:e0168513.

Trathan P.N., J. Forcada, and E.J. Murphy. 2007. Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability. Philos Trans R Soc Lond B Biol Sci 362:2351–65.

Wakefield E.D., R.A. Phillips, and J. Matthiopoulos. 2014. Habitat-mediated population limitation in a colonial central-place forager: The sky is not the limit for the black-browed albatross. Proc R Soc B Biol Sci 281.

Wakefield E.D., R.A. Phillips, J. Matthiopoulos, A. Fukuda, H. Higuchi, G.J. Marshall, P.N. Trathan, et al. 2009. Wind field and sex constrain the flight speeds of central-place foraging albatrosses. Ecol Monogr 79:663–679.

Warham J. 1977. Wing loadings, wing shapes, and flight capabilities of procellariiformes. New Zeal J Zool 4:73–83.

Waugh S.M., H. Weimerskirch, Y. Cherel, and P.A. Prince. 2000. Contrasting strategies of provisioning and chick growth in two sympatrically breeding albatrosses at Campbell Island, New Zealand. Condor 102:804–813.

Waugh S.M., H. Weimerskirch, Y. Cherel, U. Shankar, P.A. Prince, and P.M. Sagar. 1999a. Exploitation of the marine environment by two sympatric albatrosses in the Pacific Southern Ocean. Mar Ecol Prog Ser 177:243–254.

Waugh S.M., H. Weimerskirch, P.J. Moore, and P.M. Sagar. 1999b. 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.

Weimerskirch H. 1998. How can a pelagic seabird provision its chick when relying on a distant food resource? Cyclic attendance at the colony, foraging decision and body condition in sooty shearwaters. J Anim Ecol 67:99–109.

______. 2007. Are seabirds foraging for unpredictable resources? Deep Res Part II Top Stud Oceanogr 54:211–223.

Weimerskirch H., C. Bishop, T. Jeanniard-du-dot, A. Prudor, and G. Sachs. 2016. Frigate birds track atmospheric conditions over months-long transoceanic flights Henri. Science 353:74–78.

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

Weimerskirch H., A. Gault, and Y. Cherel. 2005. Prey distribution and patchiness: factors in foraging success and efficiency of wandering albatrosses. Ecology 86:2611–2622.

Weimerskirch H., T. Guionnet, J. Martin, S.A. Shaffer, and D.P. Costa. 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. Proc R Soc B Biol Sci 267:1869–1874.

Weimerskirch H., M. Louzao, and K. Delord. 2012. Changes in wind pattern alter albatross distribution and life-history traits. Science 335:211–214.

Weimerskirch H. and P. Lys. 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., T. Mougey, and X. Hindermeyer. 1997b. Foraging and provisioning strategies of black-browed albatrosses in relation to the requirements of the chick: natural variation and experimental study. Behav Ecol 8:635–643.

Weimerskirch H. and D. Pinaud. 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.

Weimerskirch H., R.P. Wilson, and P. Lys. 1997c. Activity pattern of foraging in the wandering albatross: a marine predator with two modes of prey searching. Mar Ecol Prog Ser 151:245–251.

Ydenberg R.C., C.V.J. Welham, R. Schmid-Hempel, P. Schmid-Hempel, and G. Beauchamp. 1994. Time and energy constraints and the relationships between currencies in foraging theory. Behav Ecol 5:28–34.

Yonehara Y., Y. Goto, K. Yoda, Y. Watanuki, L.C. Young, H. Weimerskirch, C.-A. Bost, et al. 2016. Flight paths of seabirds soaring over the ocean surface enable measurement of fine-scale wind speed and direction. Proc Natl Acad Sci 113:9039–9044.

Young I.R., S. Zieger, and A.V. Babanin. 2011. Global trends in wind speed and wave height. Science 332:451–455.

Figures and Tables

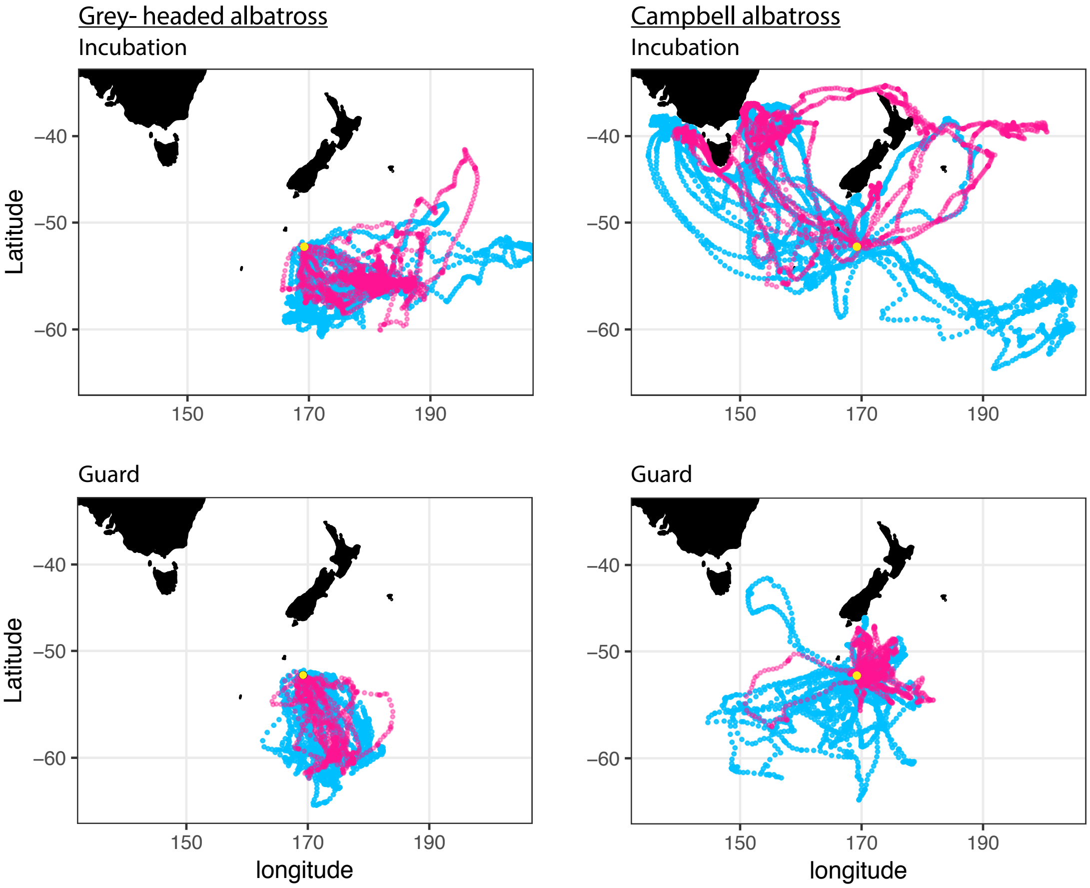


Figure 1. Movement patterns of male (blue) verses female (red) albatrosses from each species and stage (years are grouped together) to illustrate differences and similarities in area use. Yellow dot represents breeding colony.

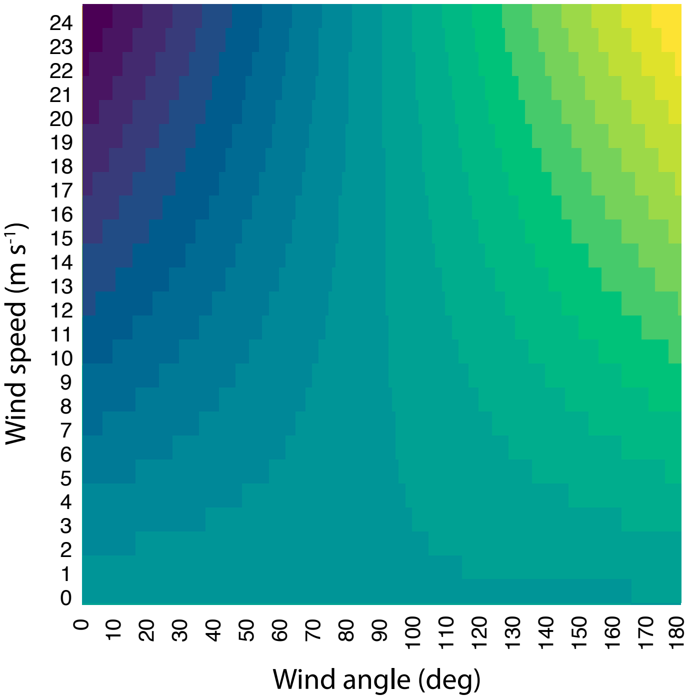


Figure 2. The flight cost function from Louzaou et al. (2014) that was applied to create instantaneous flight costs and cost choice scores. Darker colors indicate lower cost and lighter colors indicate higher cost. Tailwind is at 0° and headwind is at 180°.

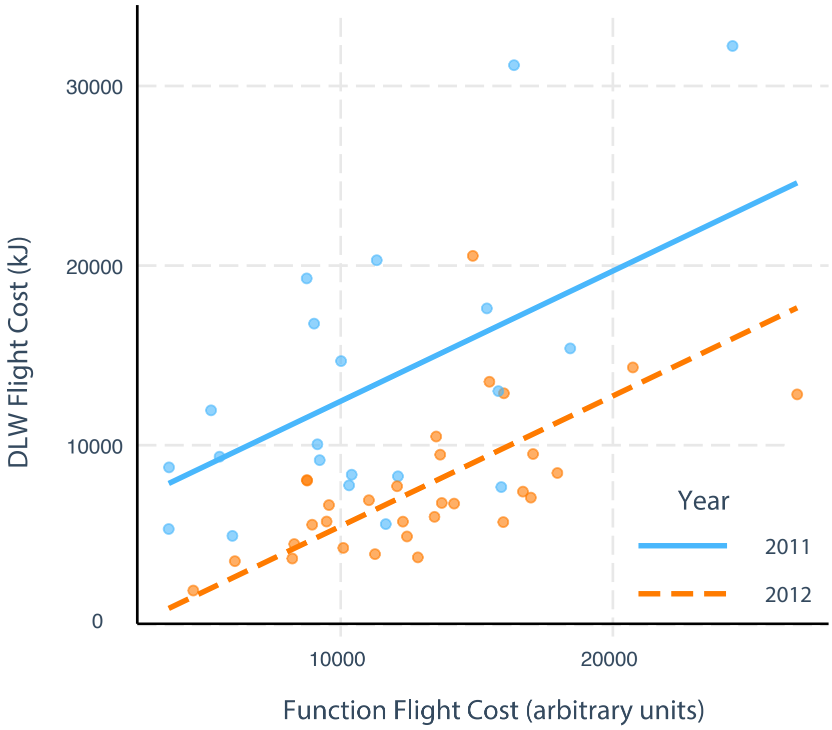


Figure 3. Relationship between flight costs measured by the doubly-labelled water method regressed on flight cost estimated with a cost function (Louzaou et al. 2014). There were no species or sex effects; however, costs were significantly greater in 2011 (blue solid line).

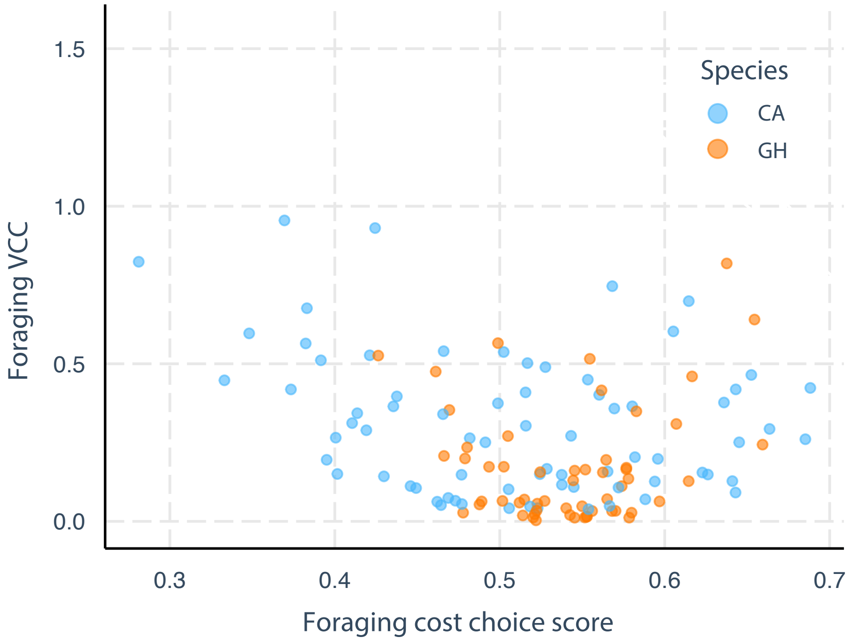


Figure 4. Relationship between foraging vector correlation coefficients (VCC) regressed on mean foraging cost choice scores. VCC values are lowest when cost choice scores are near 0.5, as expected for individuals that fly irrespective of the wind. Campbell albatrosses are indicated by blue dots and grey-headed albatrosses are indicated by orange dots.

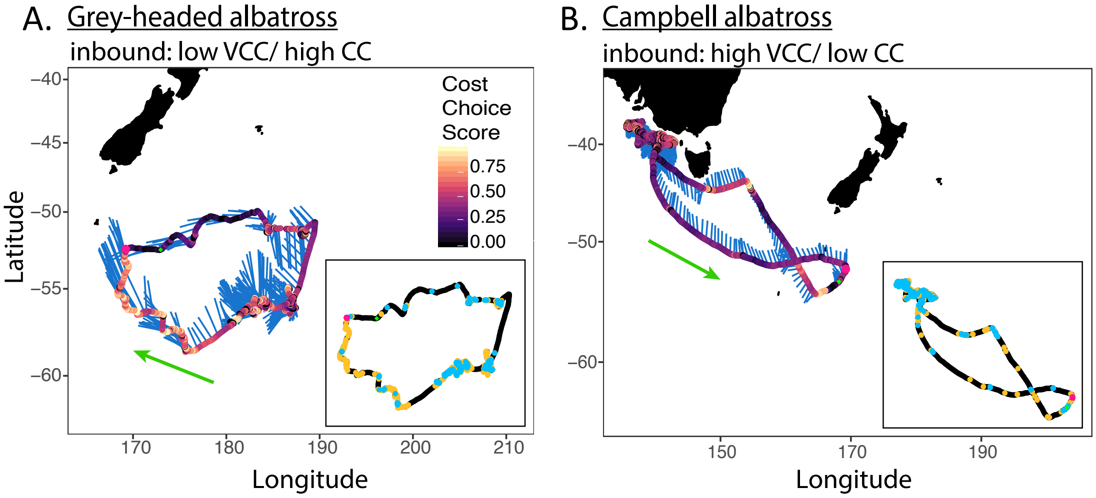


Figure 5. Tracks from one individual of each species during the incubation stage to illustrate relationships between cost choice scores (CC) and vector correlation coefficients (VCC) for the following cases: (A) high CC with low VCC during inbound transit and (B) low CC with high VCC during inbound transit. High vs. low values are determined relative to the mean CC and VCC value (0.42 and 0.63, respectively) from inbound transit for incubation-stage birds. Cost choices are shown every 10 minutes with black as the least costly choice and red to yellow as increasingly costly choices. Wind vectors in blue depict the angle of the wind on the bird at every hour (subset for visual clarity). An inset is provided of the same track, but color coded by behavioral state where black is transit, yellow is foraging (ARS) and blue is on-water. The breeding colony is indicated by a large pink dot and the green arrow indicates direction of inbound transit. Note that map boundaries are different for each track.

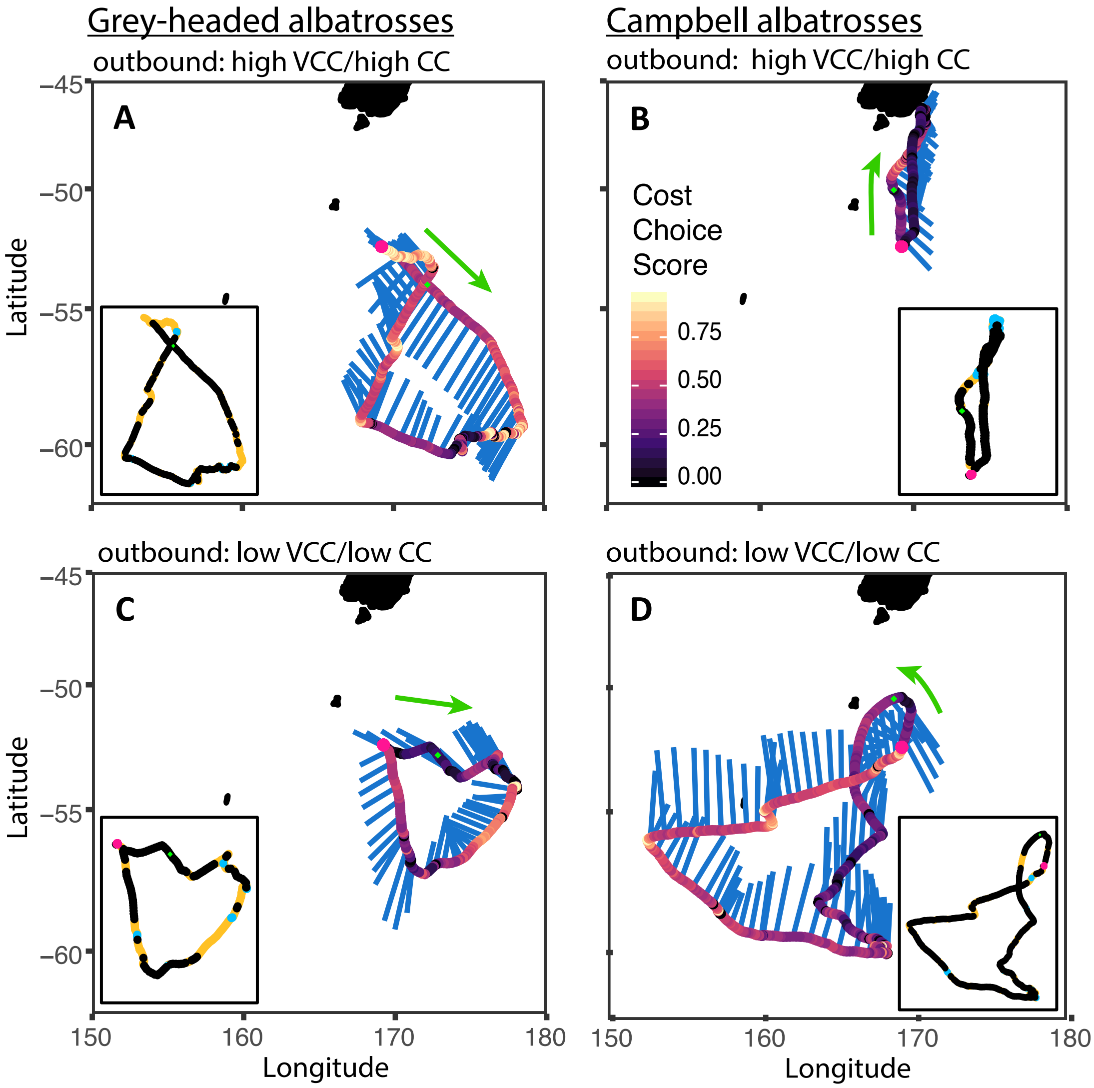


Figure 6. Tracks from two individuals of each species during the guard stage to illustrate relationships between cost choice scores (CC) and vector correlation coefficients (VCC) for the following cases: (A and B) low CC with low VCC during outbound transit states and (C and D) high CC with high VCC during outbound transit states. High vs. low values are determined relative to the mean CC and VCC value (0.35 and 0.72, respectively) from outbound transit for guard-stage birds. Cost choices are shown every 10 minutes with black as the least costly choice and red to yellow as increasingly costly choices. Wind vectors in blue depict the angle of the wind on the bird at every hour (subset to for viewing purposes). An inset is provided of the same track, but color coded by behavioral state where black is transit, yellow is foraging (ARS) and blue is on-water. The breeding colony is indicated by a large pink dot and the green arrow indicates the direction of outbound travel.

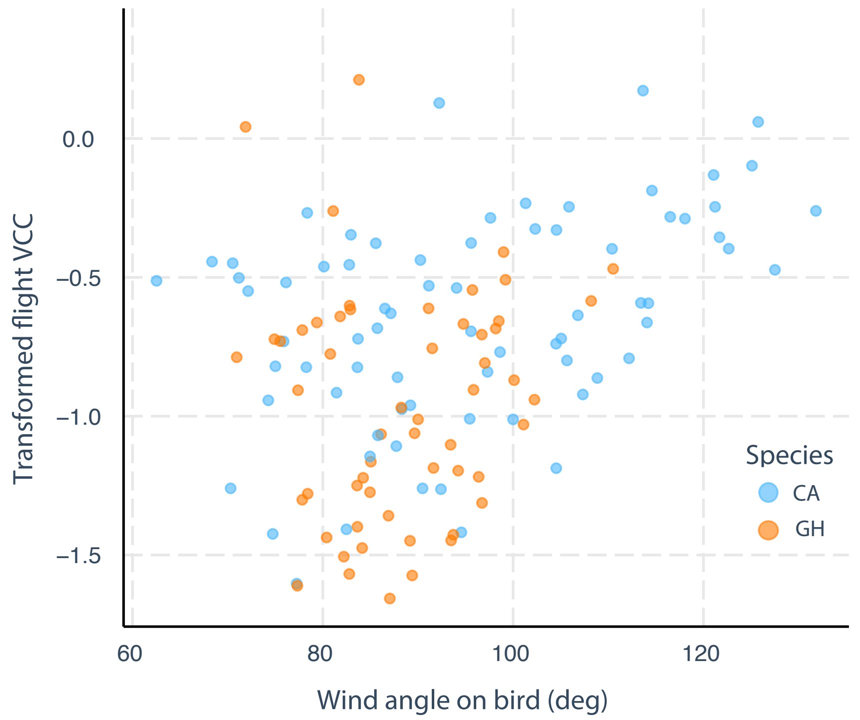


Figure 7. Box Cox transformed (λ = 0.5) flight vector correlation coefficients (VCC) regressed on circular mean wind angles incident on the bird depicting that lowest wind-use consistency values occur when birds experience wind angles near 90°. Tailwind is at 180° and headwind is at 0° (not shown). Campbell albatrosses are indicated by blue dots and grey-headed albatrosses are indicated by orange dots.

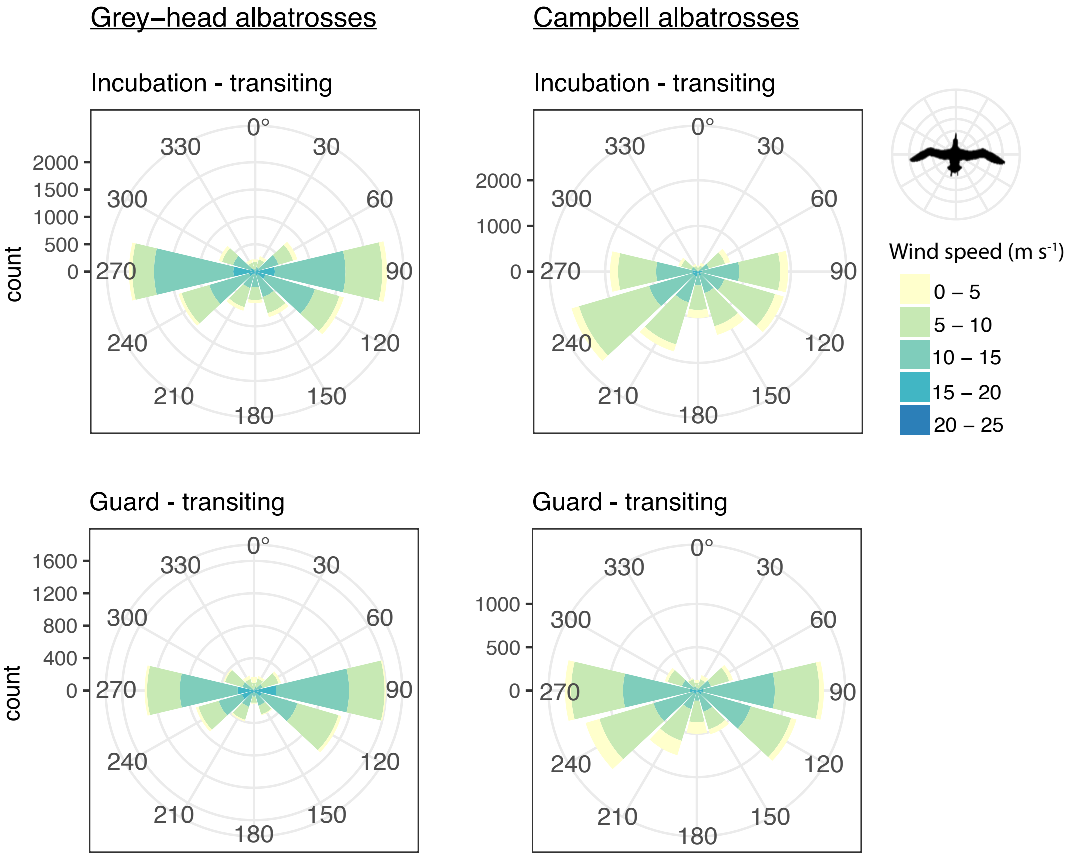


Figure 8. Rose plots illustrating the cumulative angles of the wind on grey-headed and Campbell albatrosses for transit-only periods during the incubation and guard stages. Angles are grouped in 30° bins that are centered degrees depicted on the plots. Wind speeds are represented by color intensity with higher winds speeds at darker colors. Albatross silhouette represents the direction of flight relative to all rose plot angles. Crosswinds are the most common among all groups with the exception that incubation-stage Campbell albatrosses experiencing the highest frequency of winds between 225 – 255°. Campbell albatrosses also experience a greater proportion of lower wind speeds than grey-headed albatrosses.

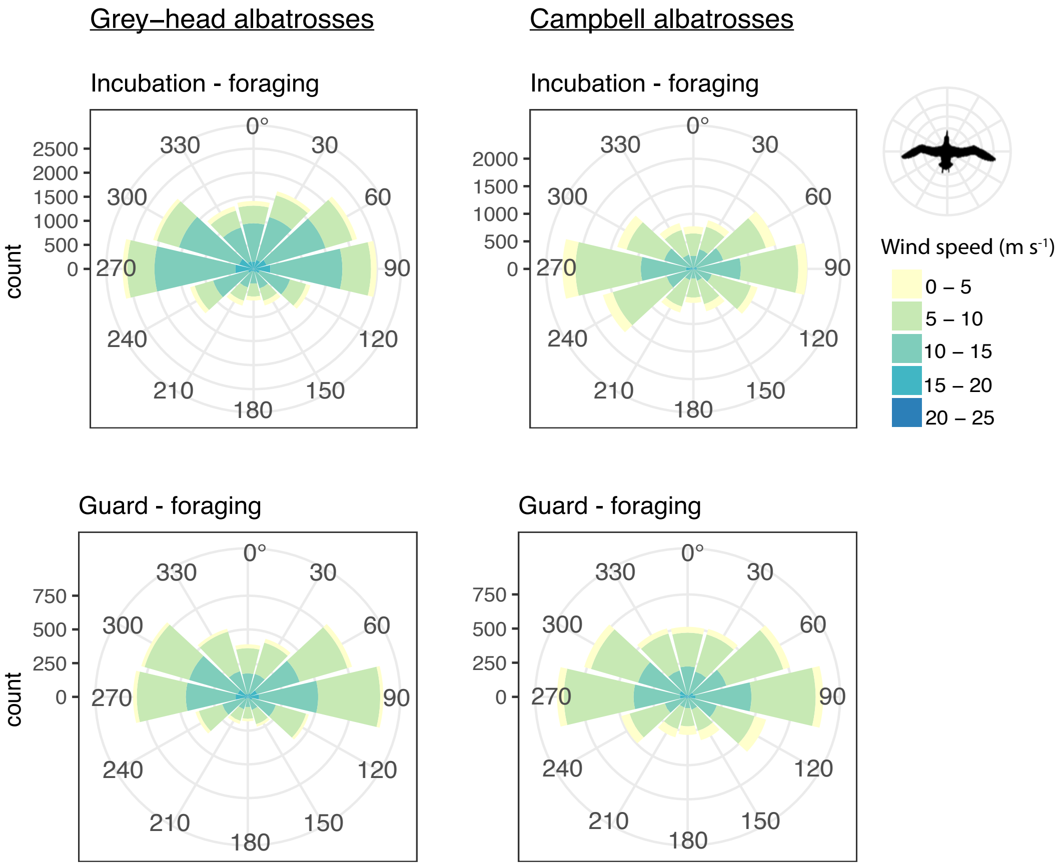


Figure 9. Rose plots illustrating the cumulative angles of the wind on grey-headed and Campbell albatrosses for foraging-only (ARS) periods during the incubation and guard stages. Angles are grouped in 30° bins that are centered degrees depicted on the plots. Wind speeds are represented by color intensity with higher winds speeds at darker colors. Albatross silhouette represents the direction of flight relative to all rose plot angles. Headwinds are more common in incubation-stage grey-headed albatrosses and guard-stage Campbell albatrosses. Campbell albatrosses from both stages and guard-stage grey-headed albatrosses experience a greater proportion of lower wind speeds than incubation-stage grey-headed albatrosses.

Table 1. Sample sizes for tracked individuals for each species, stage, and year used in analysis.

Year	Campbell albatrosses		Grey-headed albatrosses	
	incubation	guard	incubation	guard
2011	0	16 (11)	0	12 (10)
2012	0	16 (15)	0	20 (16)
2013	21	20	24	0
	21	52 (26)	24	32 (26)

Note: Numbers in parenthesis indicate the subset of individuals that also had measurements of flight cost by the doubly labeled water method. All numbers are presented as female/male. All tracks used for analysis were complete and each bird was tracked for one foraging trip. Total N = 129 (52).

Chapter 5

Conclusion

Albatrosses are long-lived birds with low annual reproductive output, which means that their rate of adaptation may become outpaced by the rate of climate change. This vulnerability is concerning as ozone depletion over much of their range has been linked to an intensification of tropospheric winds poleward and a weakening of winds toward the subtropics (Thompson and Solomon 2002). Although albatrosses use dynamic soaring to travel at low cost (Sachs et al. 2012), wind changes are still expected to have negative consequences given that they are central place foragers constrained in time and space when feeding young (Weimerskirch et al. 2012). For these reasons, it is imperative to gain a better understanding of the physiological and behaviorally flexibility of albatrosses on the individual level, as these traits will reveal tolerance to change and allow us to forecast population trajectories. The relative ability to cope with environmental stressors can be better understood if we examine species, such as the Campbell and grey-headed albatrosses, with differing foraging strategies and life history patterns that synchronously breed at the same location to reduce confounding seasonal or land-based factors. Lastly, it is valuable to have record of favorable physiological and behavioral patterns that lead to foraging success for which to measure future changes against for vulnerable species.

In CHAPTER 2, I found that despite differences in foraging strategy and life history between Campbell and grey-headed albatrosses, the metabolic stress hormone corticosterone mobilized similarly between species, sex, and stage. Unexpectedly, the body condition of individuals before foraging did not affect corticosterone concentrations during the incubation stage when individuals fasted for longer periods, but lower body condition before foraging led to higher concentrations in guard stage birds. In general, greater pre-trip corticosterone concentrations led to greater foraging success, but incubation-stage Campbell albatrosses with higher pre-trip concentrations had shorter foraging ranges, contrary to previous findings in seabird (Angelier et al. 2007; Kitaysky et al. 2001). Additionally, guard-stage individuals with less time between returning to the nest and their last at-sea feeding had reduced corticosterone concentrations. These results indicate that guard stage birds have a heightened sensitivity to fluctuations in energy reserves such that monitoring corticosterone during the guard stage, directly after foraging trips, will be most indicative of environmental conditions at sea. Among incubation-stage Campbell albatrosses with wider ranging foraging locations, pre foraging trip corticosterone may be related to factors such as foraging destination, prey preference, or age-related experience, but this requires further investigation.

In CHAPTER 3, consistent with similarities in pre and post-trip corticosterone between species and stages, I found that during early chick-rearing foraging trips, daily energy expenditure was similar between species and sexes. Costs differed across years but differed similarly for both species. Models revealed that in both species, greater daily energy expenditure was positively associated with larger proportional mass gain, lower mean wind speeds during water take-offs, strong (>12 m s^{-1}) tailwinds, and younger chicks. I also found that male grey-headed albatrosses with greater relative mass gains expended marginally more energy, probably due to a greater relative increase in wing loading. Daily energy expenditure at sea was also greater for grey-headed albatrosses relative to Campbell albatrosses when experiencing a similarly high proportion of strong headwinds at sea. I suggest that female Campbell albatrosses that primarily forage toward the subtropics may be negatively impacted by forecasted weakening winds if they are forced to use more sit-and-wait strategies that are less energy efficient (Louzao et al. 2014).

In CHAPTER 4, I more closely examined flight costs and wind use in these species during breeding and found that grey-headed albatrosses had greater mean flight costs during the incubation stage compared to Campbell albatrosses. Flight path efficiency was lowest in incubation-stage grey-headed albatrosses, as they performed more area restricted search into headwinds and performed upwind tacking to return to nests. These greater costs may be a contributing factor to why grey-headed albatrosses breed biennially rather than annually. In contrast, Campbell albatrosses exhibited greater wind-use consistency (attributed to lower windspeeds), which positively correlated with lower mean flight costs. In all individuals, greater wind-use consistency correlated with greater foraging success. However, male incubation-stage albatrosses of both species that had similar transit strategies to females had lower foraging success, potentially due to preferred foraging locations or timing. Finally, guard stage individuals that made higher cost path choices in outbound transit had greater food acquisition, suggesting that experience may play a role.

Together these chapters indicate that in addition to potential negative effects of weakened winds on Campbell albatrosses, grey-headed albatrosses that are already driven to delay breeding events may incur additional energy deficits if wind speeds continue to strengthen within their preferred foraging areas. Further investigation is required to determine if differences in foraging success between males and females when using similar strategies is driven by wind interactions or by regional differences in productivity. Moreover, in each chapter, there was a need for future research to examine how age-related experience affects foraging strategies and ultimately mediates energy balance. Finally, flight cost functions could be improved with correction factors to account for wind speeds during take-off from the water. Nonetheless, this work demonstrates that a comprehensive view of the physiological and behavioral strategies used to maintain energy balance can shape our understanding of how vulnerable species will cope with rapid environmental change.

***

The Hatter opened his eyes very wide on hearing this; but all he said was, "Why is a raven like a writing-desk?"

"Have you guessed the riddle yet?" the Hatter said, turning to Alice again.
"No, I give it up," Alice replied: "What's the answer?"
"I haven't the slightest idea," said the Hatter.

— Lewis Carroll, Alice in Wonderland

References

Angelier F., S.A. Shaffer, H. Weimerskirch, C. Trouvé, and O. Chastel. 2007b. Corticosterone and foraging behavior in a pelagic seabird. Physiol Biochem Zool 80:283–92.

Kitaysky A.S., J.C. Wingfield, and J.F. Piatt. 2001. Corticosterone facilitates begging and affects resource allocation in the black-legged kittiwake. Behav Ecol 12:619–625.

Louzao M., T. Wiegand, F. Bartumeus, and H. Weimerskirch. 2014. Coupling instantaneous energy-budget models and behavioural mode analysis to estimate optimal foraging strategy: an example with wandering albatrosses. Mov Ecol 2:1-15.

Sachs G., J. Traugott, A.P. Nesterova, G.D. Omo, F. Ku, W. Heidrich, A.L. Vyssotski, et al. 2012. Flying at No Mechanical Energy Cost: Disclosing the Secret of Wandering Albatrosses. PLoS One 7:e41449.

Thompson D.W.J. and S. Solomon. 2002. Interpretation of Recent Southern Hemisphere Climate Change. Science 296:895–899.

Weimerskirch H., M. Louzao, and K. Delord. 2012. Changes in wind pattern alter albatross distribution and life-history traits. Science 335:211–214.