AN ABSTRACT OF THE DISSERTATION OF

Peter Jürgen Kappes for the degree of Doctor of Philosophy in Wildlife Science presented on March 7, 2019.

Title: The Influence of Alternate Life History Strategies and Natal Conditions on the Reproductive Performance of Adélie Penguins Breeding on Ross Island, Antarctica.

Abstract approved: ____

Katie M. Dugger

A fundamental objective of ecology and population biology is to identify factors that drive population dynamics and determine the population-level consequences of their interaction with the environment. Studies of reproductive performance can illuminate population dynamic processes, including the links between organismal biology, the environment, and life history theory. A central tenent of life history theory is that organisms face trade-offs when partitioning limited resources among growth, maintenance, survival, and lifetime reproductive potential. For long-lived species that have multiple breeding attempts during their lifetime (i.e., iteroparous species), these trade-offs can be observed in the age-related variation in reproductive performance associated with alternate breeding strategies, namely, variation in the age of first reproduction/recruitment into the breeding population and lifetime reproductive potential. Understanding the consequences of this variation can provide insights into population dynamics and life history theory and is critical to predicting how individuals and thus populations are likely to respond to anthropogenic and natural changes in their environment.

In Chapter 2, I used generalized linear mixed models to disentangle population and within-individual processes influencing observed patterns in age-specific reproductive

performance. I tested the following five distinct patterns in breeding success as predicted by various life history hypotheses: 1) linearly increasing with breeding experience; 2) increasing with low levels of experience to a plateau; 3)increasing with low levels of experience to a plateau or peak near optimum performance with intermediate levels of experience, then increasing again in older age classes; 4) increasing with low levels of experience to a plateau or peak near optimum performance with intermediate levels of experience, then decreasing; or (5) remains constant. Overall patterns of reproductive performance were similar at all three colonies. Regardless of recruitment age, breeding success improved with post-recruitment experience at all three colonies, reaching a maximum at intermediate experience (4-8 attempts), which occurred roughly 4 years earlier for younger recruits than for older recruits. At all three colonies, improvement in breeding success was most dramatic for the youngest recruits, while the oldest recruits showed the lowest overall improvement in breeding success with additional post-recruitment experience. Together, these results support the “constraint hypothesis” and suggest that individuals face trade-offs late in life based on recruitment decisions. When controlling for selective disappearance of lower quality phenotypes, I documented pronounced declines (i.e., senescence) in breeding success for the oldest recruitment cohorts at all three colonies.

In Chapter 3 I decomposed age-related reproductive performance into its constituent processes at each colony. The selective appearance of new phenotypes contributed negatively (range: 20% - 54%) to overall age-related reproductive performance at all colonies. At the small- and medium-sized colonies improvements in age-related reproductive performance was driven by a combination of within-individual maturation (15% at both colonies) and selective disappearance (41% and 32%, respectively). At the largest colony, the majority of the improvement was due to within-individual maturation (67%). Comparisons of the relative contribution of each of the processes in early life versus late life stages at all three colonies revealed similar contributions early in life, but important differences at advanced ages. At the two smaller colonies, observed changes late in life were primarily driven by population level changes resulting from selective disappearance of individuals of lower phenotypic quality. However, at the largest colony, changes in performance were driven by a combination of decline due to within-individual maturation and the selective disappearance of individuals of higher phenotypic quality. This unexpected result may be due to a combination of potential trade-offs associated with differences between colonies of different sizes and associated differences between individual life history strategies. These results highlight the importance of accounting for the different processes contributing to reproductive performance and of incorporating replication into studies of age-related performance.

In Chapter 4 I tested the prediction from the internal predictive adaptive response (internal PAR) hypothesis that individuals raised under poor natal predictions can mitigate those conditions and have equally productive reproductive life spans as individuals raised under better natal conditions. For five years, two giant icebergs substantially altered sea ice conditions throughout the annual cycle, including preferred penguin habitat (i.e., sea ice concentrations on the foraging grounds near breeding colonies, and increased fast ice extent near breeding colonies). As a result, 5 iceberg-affected cohorts experienced significantly reduced early-life conditions from other non-iceberg-affected cohorts. In accordance with predictions from the internal PAR hypothesis, iceberg cohorts entered the breeding population earlier, exhibited higher levels of breeding success, and for individuals that met my criteria for having “died”, had shorter lifespans than non-iceberg-affected cohorts. Non-iceberg-affected cohorts recruited to the breeding population later, never achieved levels of breeding success documented for iceberg-affected cohorts, and for the individuals that met my criteria for having died, lived longer than icebergs cohorts, for individuals that met our de. At the end of their lifespan iceberg-affected cohorts were nearly able to completely mitigate the fitness costs of poor natal conditions. These results support the internal PAR hypothesis and highlight the importance of accounting for early life conditions when studying life history strategies and population dynamics.

Taken together, these results highlight the importance of long-term studies that incorporate sufficient spatial and temporal variability to understand how varying reproductive strategies drive population dynamics. Without the temporal scale of 20 years and spatial scale across three colonies, the quantitative analysis of age-related reproductive strategies (Chapter 1), the decomposition of reproductive success into constituent processes (Chapter 2), or the testing of hypotheses relating natal environment to life-time reproductive success (Chapter 3) would have been impossible. The results of these three studies will further guide and refine the next 20 years of research and contribute to our knowledge of life history theory and an ice-obligate species facing dramatic changes in sea ice conditions in the coming decades.

The Influence of Alternate Life History Strategies and Natal Conditions on the Reproductive Performance of Adélie Penguins Breeding on Ross Island, Antarctica

by
Peter Jürgen Kappes

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented March 7, 2019
Commencement June 2019

Doctor of Philosophy dissertation of Peter Jürgen Kappes presented on March 7, 2019

APPROVED:

Major Professor, representing Wildlife Science

Head of the Department of Fisheries and Wildlife

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Peter Jürgen Kappes, Author

ACKNOWLEDGEMENTS

First I would like to thank the many generous funding sources that supported my research. The Antarctic field work was funded by NSF grants OPP 9526865, 9814882, 0125608, 0440643, 0944411 and 154398 awarded to Oregon State University (OSU) and Point Blue Conservation Science, Petaluma, CA, USA and New Zealand (NZ) Ministry of Business, Innovation, and Employment Grant (C09527, C09X0510, C01X1001) and NZ's Ministry for Primary Industries (MPI17238-S01-LC), with addenda, awarded to Manaaki Whenua Landcare Research. I received additional support from the Department of Fisheries and Wildlife, OSU, via TA-ships, the Ted Thorgaard Student Research Award, Chairman's Leadership Award, Thomas G. Scott Grant Scholarship for Outstanding PhD student, Munson Wildlife Graduate Scholarship, and a Thomas G. Scott publication fund award. I also received the Savery Outstanding Doctoral Student Award from the College of Agriculture at OSU, as well as an Oregon Lottery Graduate Scholarship and Dissertation Completion award from the OSU Graduate School. I was able to present my research at several conferences thanks to the Henry Mastin Graduate Student Travel Fund, multiple Graduate Student Travel Awards from the OSU Graduate School with matching funds from the Department of Fisheries and Wildlife, a World Seabird Conference travel award, and a Pacific Seabird Group travel award.

There are so many people who have helped me through this process, but no one more than my advisor and mentor, Katie Dugger. I appreciate all of the time and energy that you have invested in my research and professional development. Whether you were on the ice or across the hall or somewhere in-between, you always were available and committed to making this experience as rewarding as possible. It may have taken me longer than expected, but I appreciate the freedom you gave me to pursue other research interests, to fully participate with non-research

related aspects of departmental and academic life, and balance that with having time for a personal life. I will miss working with you and hope that I will be able to emulate your ability to mentor, balance your professional life with your personal life, conduct high quality research, and still take time out for a cocktail and the odd safari!

I also must thank each of my committee members. I'm sure all of you weren't expecting such a long commitment, so appreciate your patience and many contributions along the way. Rob Suryan's passion for seabirds has been inspirational and I appreciate his willingness to let me participate in his lab meetings so I could further pursue that passion. Whether it has been at professional meetings or via comments on manuscripts or through comps, Rob has pushed me to continue to become a better all-around scientist. I hope that our shared passion for seabirds will allow us to work together in the future. Laurie Padman has been instrumental in helping me understand sea ice in the Ross Sea. He was extremely generous with his time and I truly appreciate the various sea ice variables that he processed for me. The third chapter wouldn't have happened without you! Nathan Schumaker was a constant voice of calm throughout the ups and downs of a PhD. Despite some changes to my PhD that made his direct contributions less than anticipated, he constantly kept my perspective about finishing and that the goal was never about this chapter or that chapter, but on developing skills I would need for my career. My Grad Council Rep, Christian Langpap, has stuck through the years and helped to ensure that I made constant progress and didn't stumble over any of the bureaucratic paperwork that comes with a graduate degree. Thank you all!

I would also like to thank the other faculty members in Fisheries and Wildlife Department for making this department such a welcoming home. Tiffany Garcia, Dave Paoletti, Lisa Ellsworth-Johnson, The Heppells, Bruce Dugger, Kelly Beidenweg, Dan Roby, Doug

Robinson, and Taal Levy all helped to make this experience more than just about getting a degree. Whether it was trail runs, birding trips, professional meetings, stimulating classes and discussions, cocktails, or a mix of all, each of you has made this a rich and fulfilling seven years, and I thank all of you for making that happen.

In addition to the contributions of my committee and the faculty in FW, I would never have been able to finish this degree without the support of all of the front office staff. From paychecks, to graduate awards, to scheduling rooms and processing all the various pieces of paperwork, Amber Algren, Nancy Allen, Brooke Amon, Leighann Auer, Gabrielle Dibble, Susie Dunham, and Ann Leen have all regularly gone above and beyond in making everything just work. The same goes for Aaron Moffett. Rebuilding computers, trouble shooting software, saving hard drives, and too many tech questions to name, Aaron was always there to assist. Even better, he did so with tasty eats, too! I will miss having such competent, professional, and genuinely friendly colleagues to work with.

None of the data I used for my research would have happened without the vision and commitment of David Ainley. He has been going to the ice since before I was born and has probably forgotten more about Adélie penguins and the Ross Sea than I'll ever know. One of the world's leading seabird ecologists, it has been an honor and privilege to get to know him and work with him. It has been a true inspiration working with someone with such a passion for the seabirds, the world's oceans, and Antarctica. His curiosity and passion for these species and places is infectious and I truly appreciate his dedication in spearheading the 20+ year data set I used for my dissertation. Thank you for helping to improve my work with your encyclopedic knowledge of all things related to Adélie penguins and the Ross Sea. I hope that my longawaited work will help you gain a better understanding of this remarkable system and iconic species.

I also must thank the other PenguinScience members for all of their hard work and contributions to my research. Drs. Grant Ballard, Amélie Lescröel, and Phil Lyver, have all spent countless hours writing research grants to fund this project, not to mention years in the field collecting the data. It has been a real pleasure to meet all of you and spend so many happy hours in the field with you. I will never forget the power of Cape Crozier or the beauty of McMurdo Sound, and the amazing people I was privileged to share them with. I would also be remiss if I didn’t thank all of the biologists who spent countless hours reading penguin bands over the past 20 years. It was truly a Herculean effort! I especially thank Annie Pollard and Annie Whitehead for their sage advice when I first embarked on this degree and support throughout.

All of the staff and contractors of the US Antarctic Program and Antarctica New Zealand provided outstanding logistic support. The pilots, techs, and other staff provided safe and efficient plane and helicopter support to remote field sites, often under challenging and dangerous conditions. All of the staff in McMurdo were vital to making each season successful and providing a community to call “home”, if even for only a few days at a time. Thanks to the radio operators at Scott Base and MacOps for keeping tabs on us while we were in the field and providing a bit of contact to the outside world. Thank you to the Robert Peyton, Kelly Goodale, and the other Fish and Wildlife staff on Midway Atoll National Wildlife refuge for generously providing me a desk and IT support while I was in the last stages of writing.

I also want thank all of the grad students and many friends I made here at OSU through the years. In particular, I’d like to thank the members of the Dugger labs for all of the great discussions, support, dinners, and parties: Scott Jennings, David Loomis, Kevyn Groot, Lizz

Schulyer, Beth Orning, Ryan Baumbusch, Catherine Engelman, Digger Anthony, Anna Mangan, Leila Duchac, Cheryl Horton, Lee Foster, Chad Marks-Fife, Kevin Buffington, and Chris Malachowski. Thanks to all the members of "Group", who offered so much good advice and unconditional support. Jake and Brittany left too quickly, but made every Packer game and HBO series that much more fun, even if Jake actually thinks Westworld is better than Game of Thrones?! Tyler Hallman, Jenna Curtis, and Jesse Laney were always up to go birding, and have helped me become a much better birder. Poo ponds just won't be the same without you all! Lizz, AJ, Loomis, Matt, Pat, and Casey were always ready for much needed dance parties. Steven Whitlock and Sean Mahaffey made every night cocktail night and full of tasty libations, stimulating conversation, and wonderful memories. I also want to thank Ed Good. I doubt he remembers writing that he thought I could finish a PhD in one of the first reference letters I ever asked for, but he planted the seed and his words have stayed with me and served as a constant source of inspiration.

This wouldn't have been possible without the love and support of my family. This past seven years has thrown a lot my way, but I knew no matter what happened, I could always count on my sister, Mo. Thank you for your constant support and encouragement to pursue my dreams both through this degree and throughout my life. You have played no small part in getting me to where I am today and I am eternally grateful for having a big sister that cares for me the way you do. While my parents are not here to celebrate this achievement with me, they were my initial inspiration and mentors. It was through their love of the outdoors and wild places that I grew to appreciate these too and wanted to learn more about them. I know that they would have enjoyed hearing about Antarctica, the penguins (and other birds), and all of the amazing people who I've been privileged work with along the way. They are missed, but are not forgotten.

I also need to thank my running wingman, Augustus “Gus the biscuit bandit” McCrea. He may have eaten more biscuits, cookies, and apples during my degree than I did, but he never missed a run and was always up for anything that meant he could sprint, crash through the forest, jump, stot, and act like a general jack-a-lope. He was a wonderful companion on many a trail mile and always ready with a tail wag at the end of every day. Finally, I must thank my wife, Linsey Arnold. I don’t know how I ever would have survived finishing this without your unwavering belief in me. You were always there to bounce ideas off of, or proof a draft, help with code, or answer a stats question. You inspire me with your passion for learning, no matter what the topic (you’re such a Reedie!). Thank you for all of the words of the encouragement, the notes left here and there, the hugs at the end of a long day, the amazing food you make for us, your laughter, and all of the moments in my life that are better because they are shared with you. I could not have done this without you.

CONTRIBUTION OF AUTHORS

Chapters 2-4: Drs. Katie Dugger, David Ainley, Grant Ballard, Amélie Lescöel, and Phil Lyver acquired funding, assisted with study design and development, and editorial review.

Chapter 2: Drs. Kerry Barton and Peter Wilson acquired funding, assisted with data collection, and proofing.

Chapter 4: Dr. Laurie Padman contributed seasonal sea ice products from the Ross Sea and Drs. Alex Fraser and Robert Massom contributed breeding season estimates of fast ice. Dr. Laurie Padman contributed to editorial review

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF TABLES

LIST OF TABLES (Continued)

LIST OF APPENDICES

LIST OF APPENDIX FIGURES

LIST OF APPENDIX TABLES

DEDICATION

I dedicate this PhD to my mother, Susan Janet Kappes. A dedicated biologist, my earliest memories are of her teaching me about the plants and animals we would find on walks and canoeing and camping trips. From science fair projects to backyard birding, she always encouraged me to learn all I could about the world and the birds around me and to seek answers to my questions about them.

INTRODUCTION

A fundamental objective of ecology and population biology is to identify factors driving population dynamics and how these mechanisms are affected by environmental variability. Estimates of a species' survival and reproductive performance and the relationship of these vital rates to environmental variation over time and space can provide important information on population dynamics (Caswell 2001) and life-history evolution (Stearns 1992), and is critical for management and conservation decisions (Jenouvrier 2013). A suite of hypotheses exists to link life history strategies and lifetime reproductive performance to population dynamics. These hypotheses attempt to explain how alternate life history strategies influence age-related reproductive success including comparing early and late life reproductive performance (Chapter 2), breaking down reproductive performance into the constituent components (Chapter 3), and relating natal environmental conditions to varying reproductive strategies (Chapter 4). Using a long-term data-set of known-age individuals from three different breeding populations, my research challenges these hypotheses with data (Hilborn and Mangel 1997) to evaluate reproductive success in a long-lived sea bird.

A central tenant of life history theory is that organisms face trade-offs when partitioning limited resources among growth, maintenance, survival, and lifetime reproductive potential (Partridge and Harvey 1988, Stearns 1992). Perhaps the most widely studied of these trade-offs is the cost of reproduction (reviewed by Harshman and Zera 2007). Central to this concept is the idea that reproduction is costly (Williams 1966). Dependent on the availability and ability to acquire and utilize limited resources, individuals are faced with trade-offs when allocating those resources between growth, cellular repair, immune function and energetically expensive reproduction (Nur 1984a, Reznick 1985, Gustafsson and Sutherland 1988, Gustafsson and Part

1990, Hanssen et al. 2003). As a result, investment in current reproductive effort is expected to result in a reduction in future survival and/or reproductive performance. In long-lived iteroparous (i.e., breed on multiple occasions) species, alternative life-history strategies result in different trade-offs between early- and late-life reproductive performance, which can be observed in age-specific variation in individual reproductive success (Clutton-Brock 1988, Newton 1989).

Numerous empirical studies on a variety of taxa have found that age-related variation in reproductive performance often follows a general pattern of early-life improvement, a maximum at middle age, followed by late-life decline or senescence (Newton and Rothery 1997, McElligott et al. 2002, Nussey et al. 2006, Aubry et al. 2009, Bouwhuis et al. 2010, Kim et al. 2011, Lemaître et al. 2015, Froy et al. 2017). Several non-exclusive hypotheses have been proposed to explain early- to mid-life improvement in performance, while a separate set of hypotheses have been proposed that address late life performance. Hypotheses explaining early- to mid-life performance include the constraint hypothesis, which posits that reproductive performance improves in relation to improvements in competency as an individual gets older, such as improved foraging ability (Daunt et al. 2007, Polito et al. 2010) or some other skill or behavior that improves with breeding experience (Curio 1983, Nol and Smith 1987, Perdeck and Cavé 1992, Forslund and Pärt 1995). The delayed breeding and selection hypothesis proposes that observed changes in age-related reproductive performance are due to the selective appearance or disappearance of individuals of different phenotypes among age classes (Curio 1983, Newton 1989, Cam and Monnat 2000b), while the “restraint hypothesis” proposes that when reproductive performance increases with age it is due to individuals optimizing their reproductive effort (Williams 1966, Clutton-Brock 1988).

Meanwhile, hypotheses addressing variation in late-life reproductive performance include the “disposable soma hypothesis”, “antagonistic pleiotropy hypothesis”, and “terminal investment hypothesis”. The “disposable soma hypothesis” posits that early investment in reproduction comes at the expense of future survival and reproduction due to the inability to invest in somatic maintenance (Hamilton 1966, Williams 1966, Kirkwood 1977). The “antagonistic pleiotropy hypothesis” suggests that individuals with genotypes that invest heavily in early-life reproduction may be able to counter heavy early-life selection with elevated levels of reproductive success that outweigh later costs (Williams 1957). Counter to these two hypothesis that imply senescence, “terminal investment hypothesis” posits that an age-related increase in reproductive effort corresponds with an increase in reproductive investment as residual reproductive value decreases, and would predict an increase in late-life reproductive performance (Williams 1966, Clutton-Brock 1984). In chapter 2 I used generalized mixed-effect models to test predictions made by early- and late-life hypotheses of reproductive performance, while accounting for individual- and population-level processes and controlling for colony size and environmental variability. I then compared these results among colonies.

Observed variation in age-specific performance can also reflect complex interactions between processes operating at both the individual- and population-level (Stearns 1992, Forslund and Pärt 1995, van de Pol and Verhulst 2006, Nussey et al. 2008). Operating at the individual-level, variation in performance is linked to heterogeneity among individuals and varies due to within-individual changes resulting from maturation. Meanwhile, selective disappearance and selective appearance operate at the population-level producing changes in the composition of the population. Selective disappearance results from emigration or mortality events, such that these events disproportionately remove high or low performing individuals from the population. For example, if low performing individuals suffer higher mortality or disproportionately emigrate from the population early in life, the resulting population would be composed of more high-performing individuals. Thus, an observed pattern of improved reproductive performance early in life in this population would be due to the population being composed of more high-performing individuals and not from within-individual improvement due to maturation (Cam et al. 2002). Meanwhile, selective appearance refers to the changes in the population composition if individuals of higher or lower performing individuals disproportionately immigrate or recruit into the breeding population (van de Pol and Verhulst 2006). For example, if higher performing individuals recruit to the breeding population when they are older, than the observed pattern of improved reproductive performance with increasing age in this population would be due to the compositional change to the population, such that the population is composed of more high performing individuals. Thus, to fully understand what is driving patterns of observed population variation in performance, it is essential to disentangle the contributions attributable to intrinsic individual change from processes that influence the population composition or population-level change (i.e., selective appearance and disapperance of different phenotypes; Vaupel and Yashin 1985, van de Pol and Verhulst 2006, Rebke et al. 2010). In chapter 3 I decomposed estimates of age-specific reproductive success into the constituent processes comprising those estimates and compared differences between early and late life stages and among colonies, to better understand which processes are contributing to age-related reproductive performance and if differences among colonies reflect alternate life history strategies.

The evolution of life history traits and adoption of different strategies, and population dynamics by extension, can also be influenced by environmental conditions (Sæther 1997, Lindström 1999, Beckerman et al. 2002, Lindström and Kokko 2002). This is driven by variation in lifetime reproductive success of individuals adopting alternative life history strategies and among-cohort variation in fitness-related traits (i.e., "cohort effects"; Sæther 1997, Lindström 1999, Gaillard et al. 2000, Gaillard et al. 2003, Monaghan et al. 2008). The general theory behind the effects of environmental conditions on lifetime performance is the “silver spoon” hypothesis (Grafen 1988, Monaghan 2008), which posits that adverse environmental conditions early in life impose severe constraints on individual development resulting in poorly performing individuals and vice versa. However, individuals might be able to mitigate the impacts of poor early-life conditions via various behavioral, morphological, and/or reproductive adaptations (Bateson et al. 2004, Nettle et al. 2013). According to the internal predictive adaptive response (internal PAR) hypothesis, individuals “predict” the state of their future adult condition and physiology, not on their future environment, but on their early environment, which means they adopt life history strategies that include early age at first reproduction with elevated investment in reproduction that allow them to mitigate potential deficiencies due to poor natal conditions (Nettle et al. 2013). Several recent experimental studies in wildlife have documented individuals mitigating poor early life conditions (Auer 2010, Dantzer et al. 2013) and Douhard et al. (2016) found results consistent with internal PAR in a wild population of Svalbard reindeer (*Rangifer tarandus platyrhynchus*). Beyond this work, however, there is little other data supporting this hypothesis or work investigating the long-term consequences of early life environmental conditions in free-ranging wildlife populations. This is somewhat surprising as this hypothesis seems especially relevant to long-lived, iteroparous species that will naturally encounter variable environmental conditions during the course of their lifetime, making it unlikely that early life environmental conditions will provide a reliable indication of environmental conditions later in life (Kuzawa 2005, Wells 2006). In Chapter 4 I investigate the influence different natal sea ice conditions had on life history strategies and reproductive performance of cohorts experiencing different natal conditions, to test predictions of the internal PAR and silver spoon hypotheses, and see if Adélie penguins were able to mitigate poor natal environmental conditions.

To disentangle the processes and factors influencing life history strategies and age-related reproductive performance, one must possess long-term data encompassing the entire lifespan of more than one cohort. Unfortunately, most research relating reproductive success to population dynamics rely on cross-sectional study designs that are temporally restricted, deriving estimates of vital rates from population averages representing only a small proportion of the total lifespan. Thus, for long-lived iteroparous species, cross-sectional data typically represent a snapshot of selection (Endler 1986). Unlike cross-sectional studies, long-term longitudinal studies summarize vital rates of known-aged, uniquely identifiable individuals that are observed repeatedly over the course of their lifespan (Clutton-Brock 1988, Newton 1989, Ainley 2002a, Black et al. 2007). The value of this approach is two-fold. First, the study period typically encompasses large amounts of temporal variation, which is incorporated into estimates of vital rates. Second, following known-aged individuals over their entire lifespan allows for closer inspection of the survival and reproductive trade-offs associated with alternative life-history strategies (Conroy 2009) and the evolution of demographic parameters (Cam 2009). After all, it is individuals that encounter and manage environmental variability, and not all individuals are equally successful at adapting to this variability (e.g., Fox et al. 2006, Lescroël et al. 2009). Thus, estimates from longitudinal studies that involve marking and following known-aged individuals not only allow us to identify individuals, but also assess how measures of their fitness, like survivorship and fecundity, vary in relation to alternate life-history strategies (e.g., age of recruitment), age, and environmental stochasticity, which ultimately drive population dynamics.

The Adélie Penguin

The pagophilic (ice-loving) Adélie Penguin (*Pygoscelis adeliae*) is a relatively long-lived (c. 20 years; Ainley 2002a), migratory, obligate sea-ice associated marine bird (Ribic and Ainley 1988/1989, Ainley et al. 1994). Truly marine, Adélie penguins spend only an estimated 10% of their life on land (Ainley 1980), where they breed in colonies ranging in size from only several pairs to 100,000's of pairs (Ainley 2002a). Because Adélie penguins need to nest on bare ground, colonies are distributed around the Antarctic coast and offshore islands in locations that are free from snow and/or ice during the breeding season (Ainley et al. 1983) and offer access to nearby pack ice (Ainley et al. 1998).

Like many long lived seabirds, Adélie penguins exhibit delayed maturation, such that recruitment or age at first reproduction ranges between 3-7 years for females and 4-8 years for males (Ainley and Demaster 1980, Ainley 2002a). In the Ross Sea population, breeders typically arrive at the colonies in late October, usually lay 2 eggs in mid-November and provision chicks between mid-December and early February (Taylor 1962, Spurr 1975, Ainley et al. 1983). For the initial 15-30 days after chicks hatch one parent remains at the nest to guard the chicks. However, in most situations, at some point during this period both parents must forage simultaneously in order to meet the energetic requirements of growing chicks. When chicks are left unattended they frequently gather into groups called crèches, which provide protection from predation and adverse weather (Ainley and Schlatte 1972, Davis 1982). Once chicks enter the crèche, it becomes extremely difficult to determine their fate without causing high levels of disturbance, but chick mortality during this period is believed to be low (Davis and McCaffrey

1986; but see Jennings 2015). Most chicks fledge approximately 55 days after hatching (Ainley 2002a).

The Importance of Sea Ice

Sea ice is arguably the single most important environmental factor affecting Adélie penguins. It forms an important substrate for primary productivity that serves as the base of the entire Ross Sea food web (Arrigo and Thomas 2004, Smith et al. 2007, Smith et al. 2012). Furthermore, sea ice concentration (SIC) has been shown to influence migration (Davis et al. 1996, Davis et al. 2001, Ainley 2002a, Ballard et al. 2010b), foraging ecology (Ainley et al. 1998, Ballard et al. 2010a, Lescroël et al. 2010), reproductive performance (Taylor 1962, Yeates 1968, Ainley and Leresche 1973, Spurr 1975, Irvine et al. 2000, Olmastroni et al. 2004, Emmerson and Southwell 2008), survival (Ainley 2002a, Dugger et al. 2006, Ballerini et al. 2009b, Emmerson and Southwell 2011), and population size (Fraser et al. 1992, Wilson et al. 2001, Ainley 2002a, Ainley et al. 2005b). Even during the non-breeding season Adélie penguins are dependent on pack ice (Fraser et al. 1992). When they are on their at-sea wintering grounds, they utilize areas with high concentrations (between 75% and 85%) of sea ice (Ballard et al. 2010b). Given these limitations suitable winter habitat for Adélie penguins is likely only a couple of hundred kilometers wide and likely explains why most adult mortality occurs during the non-breeding season (Spurr 1975, Ainley et al. 1983, Wilson et al. 2001).

Predictions of climate-induced environmental change indicate that high latitude Polar ecosystems, like the Ross Sea, are likely to experience some of the most dramatic changes this century (Hughes 2000, IPCC 2007). These changes are likely to be particularly pronounced in regards to sea ice dynamics (IPCC 2007) which will have associated impacts on the Ross Sea ecosystem and the Adélie penguin population (Smith et al. 1999, Arrigo and Thomas 2004, Smith et al. 2007, Ainley et al. 2010a, Smith et al. 2012). In fact, climate-induced changes are already affecting the physical environment of the Ross Sea in profound ways, including the production of sea ice, and extent and duration of cover (Parkinson 2002, Stammerjohn et al. 2008b, Comiso et al. 2011, Smith et al. 2012, Stammerjohn et al. 2012).

Study sight location and integration with ongoing research program

Lying within the Pacific sector of the Southern Ocean, the Ross Sea is one of the southern-most reaches of ocean on the planet. Despite the reduction of cetacean populations and current illegal, unregulated, and unreported fishing, the Southern Ocean, and particularly the Ross Sea, is widely considered one of the least altered marine systems on the planet (Ainley 2002b, Blight and Ainley 2008, Halpern et al. 2008, Ainley 2010). With the largest continental shelf system in the Southern Ocean, the Ross Sea is one of the most biologically productive systems in the region (Smith and Gordon 1997, Arrigo et al. 1998, Arrigo et al. 2002, Smith et al. 2007, Ballard et al. 2011, Smith et al. 2012) and spatial and temporal variability in SIC are arguably the most important factors influencing the Ross Sea biological communities (Smith et al. 2007, Smith et al. 2012). This productivity supports approximately 33-38% of the world’s breeding Adélie penguin population and the Southeastern Ross Sea metapopulation that is the focus of my research, represents the southern-most breeding population of the species (LaRue et al. 2013, Lyver et al. 2014). This metapopulation is composed of a cluster of three relatively easy to access colonies on Ross Island, Cape Royds (77˚34’S; 166˚11’E), Cape Bird (77˚13’S, 166˚28’E), and Cape Crozier (77°31’S, 169°23’E), and a more remote and less well studied colony on nearby Beaufort Island (Ainley 2002a).

The research presented here is part of a larger ongoing research program conducted by an international team of researchers studying the Adélie penguins breeding at the aforementioned colonies (go to: www.penguinscience.com for more information and a list of publications). Because penguins are relatively easy to census, capture, mark, and observe during the breeding season they make ideal subjects for long-term studies on demography and population dynamics. Due to the inaccessibility of Beaufort Island it is not regularly monitored but opportunistically banded known-aged birds that emigrated from this colony to any of the three Ross Island colonies are regularly monitored. Banding for the development of a known-aged population began in the 1994-1995 breeding season (hereafter 1994). Initial work investigated population trends among the four colonies (Ainley et al. 2004) and has gone on to include foraging behavior and diet relative to colony size, intra- and inter-specific competition, and sea ice conditions (Ainley et al. 1998, Ainley et al. 2003, Ainley et al. 2004, Ainley et al. 2006). There have also been methodological studies on the effects of instrument and flipper band attachment on population demographics (Ballard et al. 2001, Dugger et al. 2006). This team has also examined the role Adélie penguins play in the overall Ross Sea ecosystem (Ainley et al. 2005a, Ainley et al. 2006, Ainley et al. 2007, Ballard et al. 2011) along with studies of movement, survival, diet, and chick growth related to colony size and environmental variability (Ballance et al. 2009, Dugger et al. 2010, Dugger et al. 2014, Whitehead et al. 2015, Jennings et al. 2016, Ainley et al. 2018, Ballard et al. 2019). They have also studied winter migration and habitat use (Ballard et al. 2010b) and differences in vital rates related to individual quality and environmental variability (Lescroël et al. 2009, Lescroël et al. 2010, Lescroël et al. 2014).

During the course of this research program the three colonies on Ross Island have varied considerably in size: Cape Royds decreased from 4000 to 2300 breeding pairs; Cape Bird increased from 35,000 to 75,000 pairs; and Cape Crozier increased from 118,000 to 305,000 pairs (Lyver et al. 2014). Elucidating the mechanisms responsible for this variation is a central research question for our PenguinScience team, which I joined in 2011, and my dissertation research is focused on understanding how individual processes scale up to drive the different population trends we see at the different colonies and the mechanisms maintaining the differences in colony sizes.

I am seeking to improve our understanding of how reproductive performance varies in the Ross Island metapopulation and how alternate life history strategies influence life time performance. My research provides a deeper understanding of the reproductive trade-offs associated with alternate life history strategies, how alternate life history strategies can be influenced by environmental conditions, and how those trade-offs and strategies contribute to population dynamics and demography, both in this population of Adélie penguins as well as other long-lived iteroparous species. Ideally this improved understanding of basic life history theory will provide insights into population dynamics, facilitating improved management for the iconic Adélie penguin and other managed wildlife populations.

2 - AGE-RELATED REPRODUCTIVE PERFORMANCE OF A LONG-LIVED SEABIRD REVEALS SIMILAR OUTCOMES FOR ALTERNATE LIFE HISTORY STRATEGIES

Peter J. Kappes, Katie M. Dugger, Amélie Lescroël, David G. Ainley, Grant Ballard, Kerry J. Barton, Phil O’B. Lyver, Peter Wilson

Abstract

Variability in age-related reproductive performance is a well-documented characteristic of long-lived iteroparous vertebrate populations. Various life history strategies, particularly age of recruitment, have different trade-offs associated with early and late-life performance. Most research has focused either on improved performance early in life or late life declines, but both should be considered to fully understand life history trade-offs. The “selection,” “constraint,” “restraint,” and “senescence” hypotheses have been proposed to explain this variability. Using a 19-year data set of Adélie penguins (*Pygoscelis adeliae*) breeding at three colonies in one meta-population and differing in size by orders of magnitude, we tested predictions from the four hypotheses to understand patterns in age/experience-related reproductive effort and success, while accounting for both individual and population-level changes, and the influence of population size and growth. Overall patterns of performance were similar among colonies, such that regardless of recruitment age, success improved with early post-recruitment experience, peaking in the mid reproductive lifespan, before declining. Regardless of recruitment age, success was lowest for the initial breeding attempt, though affected subsequently by recruitment age. These results support the constraint hypothesis, indicating that pre-recruitment experience had a positive effect on birds that delayed recruitment. Overall success was highest, and recruitment earliest at the largest, growing colony and lowest at the smallest colony, which was barely growing if at all. Improvement in success was most dramatic for youngest recruits, contrasting oldest recruits, who were already successful, indicating further support for the constraint hypothesis. When controlling for selective disappearance of poor performing phenotypes, we documented pronounced declines (i.e., senescence) in success after intermediate breeding experience for all recruitment categories. Short lifespans prevented the documentation of declines for the youngest recruitment age, but rates of late-life decline were most pronounced for 4 year recruits, indicating alternative life history strategies result in different reproductive trade-offs, as well as support for the disposable soma hypothesis of senescence. These results highlight that differences in recruitment age can result in trade-offs in time of senescence later in life, but did not result in differences in the overall number of breeding attempts or successful attempts. This serves to highlight the importance of accounting for alternate life history strategies when investigating age-related reproductive performance and considering both early- and late-life performance to fully understand the evolutionary processes responsible for different life history strategies driving population change.

Introduction

A central tenent of life history theory is that organisms face trade-offs when partitioning limited resources among individual growth, maintenance, survival, and lifetime reproductive potential (Partridge and Harvey 1988, Stearns 1992). In long-lived iteroparous species, the results of these trade-offs and individual decisions can be observed in the age-related variation in probability of successful reproductive performance (Clutton-Brock 1988, Newton 1989). Understanding the drivers of this variation is important because of the consequences for both population dynamics (Caswell 2001) and life history evolution (Stearns 1992). Variation in the level of success of reproductive performance is not simply a product of varying trade-offs, but is also driven by complex interactions between processes operating both within- and among-individuals (Forslund and Pärt 1995, van de Pol and Verhulst 2006, Nussey et al. 2008). Thus, to fully understand what is driving patterns of variation in breeding success, it is essential to disentangle intrinsic individual change (i.e., improvement, senescence) from population-level change (i.e., selective appearance and disappearance of high/low quality individuals; van de Pol and Verhulst 2006, Rebke et al. 2010). This has been highlighted in a number of recent studies that pertain to age-related breeding success (Cam et al. 2002, van de Pol and Verhulst 2006, Reed et al. 2008, Aubry et al. 2009, Rebke et al. 2010, Kim et al. 2011, Hayward et al. 2013, Froy et al. 2017).

Studies of free-ranging populations have found that variation in the outcome of reproductive performance generally follows a trajectory in which breeding success increases during early levels of breeding, usually reaching a plateau/peak with intermediate experience, and then declines near the end of an individual’s reproductive lifespan (Clutton-Brock 1988, Forslund and Pärt 1995, McElligott et al. 2002, Balbontín et al. 2007). Several non-exclusive hypotheses operating at both the individual- and population-level have been proposed to explain these patterns. Hypotheses explaining early- to mid-life performance include the “constraint hypothesis”, which posits that breeding success improves with increased competency as individuals age, such as improved foraging ability (Daunt et al. 2007, Polito et al. 2010), or other skill acquired with experience (Curio 1983, Nol and Smith 1987, Perdeck and Cavé 1992, Forslund and Pärt 1995). The “delayed breeding and selection hypothesis” proposes that observed changes in average age-related breeding success are due to the selective appearance or disappearance of individuals of different phenotypes (Curio 1983, Newton 1989, Cam and Monnat 2000b), while the “restraint hypothesis” proposes that when breeding success increases with age it is due to individuals optimizing their reproductive effort, i.e. breeding successfully more often (Williams 1966, Clutton-Brock 1988).

Support for the “constraint hypothesis” comes from multiple studies finding that breeding success increases with age because individuals experience age-related improvements of competence that positively affect outcomes (Ainley et al. 1983, Curio 1983, Nur 1984b, Sydeman et al. 1991, Forslund and Pärt 1995, Aubry et al. 2009, Polito et al. 2010). Thus, we would predict that for any given age, breeding success should be higher for individuals with more rather than less breeding experience. However, it should be noted that a critical assumption of this hypothesis is that there is no association between the age at first reproduction (AFR) and individual phenotypic quality. If an association exists, then it is possible that individuals of high phenotypic quality may recruit earlier than individuals of low quality and be able to achieve higher breeding success, regardless of breeding experience (Forslund & Pärt 1995). For example, in Adélie penguins (*Pygoscelis adeliae*) the individuals that recruited early and survived, went on to be most productive individuals (Ainley et al. 1983). Thus, it is essential to account for AFR and subsequent successful breeding experience when testing this hypothesis.

Empirical data from multiple species also support the “selection” and “delayed breeding” hypotheses (Barbraud and Weimerskirch 2005, Bregnballe 2006, Aubry et al. 2009, Lescroël et al. 2009). The selection hypothesis posits that average breeding success increases with age in a population because some individuals experience higher annual breeding success and survival owing to phenotypic variation among individuals in the breeding population. Thus, average or age-specific breeding success should increase with age because poor-quality breeders die young leaving only high quality individuals to breed at older ages. If this hypothesis is true we would predict a positive correlation between breeding success and lifespan (i.e., longevity). A variation in the selection hypothesis is the “delayed breeding hypothesis” (Forslund and Pärt 1995), which postulates that the proportion of highly successful individuals (breed more frequently, more offspring per attempt) increases with increasing age because individuals that delay recruitment are of higher phenotypic "quality" and therefore exhibit increased breeding success compared to individuals that recruited early (e.g., Ollason and Dunnet 1988, Perdeck and Cavé 1992, Forslund and Pärt 1995). If this is true, we would predict a positive correlation between AFR and increased age-related breeding success.

The "restraint hypothesis" (Williams 1966, Curio 1983), is based on the life history theory that individuals optimize their reproductive effort (Stearns 1992). This hypothesis assumes a positive relationship between effort and success and suggests that as an individual ages, the frequency of and effort in reproduction should increase for one of the following two reasons. First, if the frequency of success or probability of survival decreases late in life due to senescence, formally described as decreased residual reproductive value (Williams 1966, Curio 1983), then it does not pay to anticipate future reproductive success because of the diminishing likelihood for future successful reproductive attempts. In this scenario it is assumed that there is a cost of reproduction in terms of future survival or fecundity/breeding success (Nur 1984a, 1988). Thus, investment in reproductive effort or frequency should gradually increase throughout the life of the individual as the residual reproductive value decreases. Alternatively, if we assume an individual's reproductive potential increases with age, because of improvement in competence (see above), we would expect to see that breeding success for older individuals would be higher than young individuals, i.e. more offspring, more often. Thus, we would predict individuals would delay recruitment until they have achieved the size, status, or experience necessary to be successful (Curio 1983, Forslund and Pärt 1995) and thereafter experience high success upon entering the breeding population.

A central concept underlying most hypotheses of late-life reproductive performance is the idea that reproduction is costly (Williams 1966). Dependent on the availability of resources and their ability to acquire them, individuals are faced with trade-offs when allocating those resources between growth, cellular repair, and immune function or energetically expensive reproductive effort (Nur 1984a, Reznick 1985, Gustafsson and Sutherland 1988, Gustafsson and Part 1990, Hanssen et al. 2003). If true, individuals that invest heavily in reproduction early experience costs later in life, including decreased longevity and/or reduced probability of breeding success. A number of hypotheses have been proposed to explain this pattern. The “disposable soma hypothesis”, posits that early investment in reproduction comes at the expense of future survival and due to the inability to invest in somatic maintenance (Hamilton 1966, Williams 1966, Kirkwood 1977). A number of studies have attributed individual senescence to this process (Reed et al. 2008, Hammers et al. 2013, Jankowiak et al. 2018), but at the population-level this pattern could also result from changes in the phenotypes represented in the population (Cam and Monnat 2000a, Reid et al. 2003, Descamps et al. 2006). For example, individuals of low phenotypic quality may delay recruitment, which can mask within-individual improvements with age (van de Pol and Verhulst 2006). These same individuals may also have shorter lifespans, which means older age classes may be disproportionately composed of individuals having high phenotypic quality, potentially masking senescent declines (Aubry et al. 2009). Meanwhile the “antagonistic pleiotropy hypothesis” suggests that traits selected to improve reproduction early in life have deleterious effects later in life (Williams 1957). Counter to the hypotheses of senescence is the “terminal investment hypothesis” which posits an age-related increase in reproductive effort that corresponds with an increase in reproductive investment as residual reproductive value decreases, and would predict an increased late-life probability of breeding successfully (Williams 1966, Clutton-Brock 1984).

By taking into account life history factors like AFR, breeding experience, breeding success, longevity (i.e., lifespan), and individual identification, we can see how different strategies employed by individuals of different phenotypic quality result in variable probability of breeding success with age (Descamps et al. 2006). For example, individuals who invested heavily in reproduction early, suffered from the cumulative costs of that reproduction later in life, exhibiting earlier and more rapid declines in success compared to individuals that delayed breeding (Nussey et al. 2006, Reed et al. 2008, Aubry et al. 2009). Meanwhile, Reid et al. (2003) documented a similar decline in average performance late in life, but in this case, decline was attributed to the selective disappearance of individuals from the population.

It is important to note that the predictions made from by each of these hypotheses is inextricably linked to AFR. Yet, in systems where resources are limited (e.g., larger colonies resulting in elevated competition for prey, nesting material and/or breeding sites), only individuals of high quality may be able to recruit early (Barbraud and Weimerskirch 2005). Thus, it is possible that success level with age may differ among populations ranging in levels of resource competition (e.g., higher breeding density) and should therefore be accounted for when investigating age-related reproductive performance.

We used data from a longitudinal study (1994-2013) of an Adélie penguin meta-population breeding at Cape Bird, Cape Crozier, and Cape Royds (Ross Island, Antarctica) to investigate the influence of colony size, i.e. resource availability, on age-related reproductive performance and test several hypothesis proposed to explain patterns in early and late life reproductive success. In particular, we were interested in understanding the cumulative costs of reproduction that results from differences in AFR and subsequent breeding experience (i.e., the number of reproductive attempts). Therefore, we used a combination of AFR and breeding experience, post-recruitment, to model the observed patterns in age-specific breeding success observed at each colony. Our motivation for this work stemmed from our interest in understanding the possible drivers of population changes at these colonies over two decades and augmenting the paucity of published data on how resource availability influences age-specific reproductive performance. The smallest colony, Cape Royds, decreased from 3500 to 3000 breeding pairs, while Cape Bird increased from 33,000 to 67,000 pairs, and Cape Crozier, one of the largest Adélie penguin colonies (Lynch and Larue 2014), increased from 121,000 to 281,000 pairs (see Lyver et al. 2014, Figure 2 and Antarctica New Zealand unpublished data: http://www.landcareresearch.co.nz/resources/data/adelie-census-data for more information on population trends). The study was aided by a “natural experiment” in which ocean access was inhibited for a few years by unusually extensive sea ice, thus increasing walking rather than swimming distance between colony and sea, disrupting pairs’ synchrony, and negatively affecting most greatly breeding success at the smallest colony (Dugger et al. 2014).

We used 18 years of breeding histories from >3000 known-aged individuals to disentangle trade-offs between different recruitment and breeding outcomes and their influence on early- and late-life breeding success. We controlled for within- and among-individual variation, to better understand the demographic mechanisms shaping age-specific breeding outcomes at each colony. We were particularly interested in identifying and describing any differences among colonies, which may help us to better understand the reproductive processes driving observed population changes. Because different combinations of pre- and post-recruitment experience across recruitment groups can produce different shapes of the curve describing age-related variation in breeding success we tested the following hypotheses for different AFR groups. It is important to note that this list is not exhaustive. Trade-offs between AFR and early- and late-life reproductive performance combined with complex interactions between within- and among-individual effects can produce a multitude of possible predictions, including contradictory or similar predictions driven by different processes, regarding the predicted shape of this curve.: reproductive success (i.e., Y/N) (1) linearly increases with number of years of breeding, i.e. experience (maturation or progressive selection of more efficient individuals, with no trade-off), with no senescence; (2) increases with low levels of breeding attempts then reaches a plateau where frequency remains relatively consistent (pseudo-threshold response with no senescence); (3) increases with low levels of breeding attempts, reaches a plateau or peak near optimum performance with intermediate frequency of breeding, then increases in older age classes, regardless of AFR (terminal investment; see Stearns 1992, Descamps et al. 2007); (4) increases with few early attempts, reaches a plateau or peak near optimum success with intermediate breeding frequency, then decreases (senescence), regardless of AFR; or (5) remains constant. Ultimately our objective was to fully understand the complex patterns of age-related breeding success by disentangling the various processes and strategies to better identify trade-offs associated with resource availability (function of colony size) that might influence demographic mechanisms that affect population growth rates.

Methods

Study species, study site and data collection

We used a 19-yr data set of uniquely banded known-aged Adélie penguins breeding at three colonies (Cape Bird 77˚13’S, 166˚28’E; Cape Crozier, 77˚31’S, 169˚23’E, Cape Royds 77˚34’S;

166˚11’E) on Ross Island, Antarctica, which act as a metapopulation (Dugger et al. 2010, LaRue et al. 2013) to investigate the relationship between age and reproductive performance. We attached uniquely numbered stainless steel bands on the left flipper of chicks at each colony (Dugger et al. 2006) beginning in the austral spring-summer (late October through January) of 1994-1995 (hereafter season 1994) through 2013. Each season past 1994, we searched for banded birds at 2 to 7-day intervals (depending on colony) throughout the entire season. All bands were read using binoculars from a distance of 5-10 m. Upon finding a known-aged on a nest with eggs, we marked the location (cattle ear tag on a nail driven into the permafrost) and recorded it with GPS. We subsequently monitored nest outcomes to determine reproductive performance. We determined age of first reproduction as well as breeding histories of each known-aged for as many seasons as they were present.

Adélie penguins exhibit delayed maturity with most individuals recruiting to the breeding population between the ages of 3 to 8 years (Ainley 2002a). In our study we did not observe Adélie penguins breeding at <3 years of age. Multi-state mark-recapture estimates of age-specific survival probabilities of this population found differences in survivorship among subadults (0-1), 2-3, 4, 5-8, and 9+ year olds (Dugger unpublished data). Because we were interested in understanding age-related reproductive outcomes, we grouped our sample breeding population into these age categories based on AFR (i.e., 3 = 3 years old; 4 = 4 years old; 5 = 5-8 years old; 6 = 9+ years old). This allowed us to study trajectories of breeding success within each recruitment group.

Adélie penguin chicks are typically left unattended when their growth rate can only be maintained if both parents forage simultaneously. Unattended chicks seek the company of other chicks, forming groups referred to as “crèches” (Ainley and Schlatte 1972, Davis 1982). Due to the high levels of disturbance required to monitor unmarked chicks in large crèches and that mortality of chicks that enter crèches is believed to be relatively low (Davis and McCaffrey 1986; but see, Jennings 2015), we followed the methodology of Lescroël et al. (2009) and categorized individuals observed feeding at least one chick after mean crèche date each year (about the first week of January) as "successful" (breeding success = 1) and individuals observed early in the season with an egg(s) and/or chick(s) that were not observed feeding a chick after mean crèche date as "unsuccessful" (breeding success = 0).

Modelling age-related variation in breeding success

Analyses were necessarily restricted to banded individuals that entered the breeding population (i.e., recruits) and their subsequent breeding history (3089 individuals, 9606 observations; see Table 2.1 for samples sizes). Since breeding success is a binary response variable (i.e., success or failure), we used GLMM with binomial errors and a logit link (i.e., logistic regression; see Agresti 2003) to assess age-related effects on the probability of raising at least one chick in a given season.

We parameterized breeding experience in two ways; true experience (EXP_T) and learning experience (EXP_L). We defined EXP_T as the number of seasons an individual was previously observed breeding (i.e., observed with at least one egg or chick). Thus, at first reproduction $EXP_T = 0$ and EXP_T would increase by one following each subsequent breeding attempt. Approximately 23% of the records in breeding histories reflected sabbatical years (i.e., bird present but not observed breeding; Table 2.2), which can be an efficient way to increase residual reproduction (i.e., the expected number of offspring produced by an individual at a particular age in future reproductive events; Wooller et al. 1990, Stearns 1992). However, we didn't feel that those sabbatical years reflected true breeding experience since the highest physiological costs associated with breeding in penguins relate to individuals that laid an egg, and coordinated incubation and especially chick-rearing, gaining important experience from those activities.

Our model set of biological covariates included linear, quadratic, cubic, and pseudo-threshold effects of EXP_T or EXP_L on breeding success (Table 2.3). We included a quadratic (EXP^2) effect on both parameterizations of EXP because breeding success may increase with increasing EXP to some peak at intermediate levels of experience, after which breeding success declines. In contrast, a cubic relationship can explain a possible bi-modal pattern in breeding success, reflecting increases or decreases in breeding success as breeding experience increases. The pseudo-threshold pattern reflects the improvement in breeding success with early experience that levels off without any additional benefit of more experience. We also considered AFR as a monotonically increasing (or decreasing) trend in breeding success (i.e., continuous categories for AFR: AFR_{CC}), and as a categorical variable (AFR_C). Because it is possible that AFR could interact in different ways with EXP, in addition to the models of additive effects of these variables we also included models with interactions of all combinations of parameterizations and shapes of AFR and EXP in our model set. We also included a fixed effect of breeding colony (denoted COL) in each model, to account for differences in age-related variation in breeding success among colonies. We used the structure of age-related covariates in the model that best fitted the data to further investigate effect of extrinsic variables on breeding success trends (see *Model selection*).

Controlling for selective disappearance

While the initial model set accounted for unobserved heterogeneity in individual quality by including a random effect (RE) for individual identity (ID), we did not explicitly control for potential selective disappearance of individuals in our initial analysis, because we were concerned about sample sizes. However, heterogeneous survival across individuals, where “less fit” phenotypes die, leaving only the “robust” phenotypes, can change the composition of the sample population leading to spurious estimates of age-related breeding success (Vaupel and Yashin 1985, van de Pol and Verhulst 2006). To account for this, we re-ran the top model following the methodology outlined by van de Pol and Verhulst (2006) and added an additive effect of lifespan (LIFE, in years) to the top model from our initial candidate set (i.e., model 1 in Table 2.4) to account for the “selective disappearance” of these individuals from the breeding population. Because many of the birds in our study were still alive at the end of the study period, we removed all records of these individuals from the data set used for this analysis, which reduced the data set to 2054 individuals and 5588 breeding attempts (Table 2.1). For the remaining birds, we calculated lifespan based on the last year it was observed, assuming that permanent disappearance indicated a mortality event or that they had emigrated from the study metapopulation. We assume that selective disappearance from the metapopulation primarily reflects mortality rather than emigration to elsewhere than Royds, Bird or Crozier because movement rates of breeders is very low except at Royds during the natural experiment (Dugger et al. 2010). Detection rates were not 100% each year, and this ongoing study has confirmed that Adélie penguins live and breed into their 20’s (DGA, GB, KMD unpubl. data). However, even birds taking a “sabbatical” year return to the colony. Only 5% of birds in our data set had an interruption of at least 1 season in their re-sighting history, before being subsequently re-sighted (Table 2.5).

Using this reduced data set, we then compared our best model from the previous analysis with the two models including an additive effect of LIFE parameterized either as a categorical or a continuous trend on breeding success. This approach allowed us to explicitly account for heterogeneity in appearance (i.e., variation in AFR) and disappearance (i.e., variation in lifespan) from the breeding population. If lifespan has an effect on breeding success, it indicates an association between breeding performance and lifespan. This indicates that changes in mean performance associated with AFR are the result of population-level changes driven by selective disappearance of "less fit" phenotypes. If AFR has an effect after accounting for lifespan it indicates that a portion of change in performance is due to within-individual maturation. The results of the models including lifespan should be interpreted with caution as the reduced data set created small sample sizes for some of the late-life experience levels at some colonies.

Modelling Extrinsic Temporal Change in Breeding success

To investigate extrinsic variation in breeding success (e.g., environmental driven changes) we removed SEASONS as a random effect and included it in the base model as a fixed effect, parameterized as either a log-transformed continuous variable (SEASONS) or a categorical variable (SEASONS_C), while retaining individual ID as a random effect to control for heterogeneity in individual quality. Because the study colonies were impacted by extensive sea ice, thus blocking access to the sea, by a mega-iceberg during part of the study (i.e., 2001-2005; Dugger et al. 2010, 2014), we also evaluated a model that included temporal variation as a binomial response reflecting the presence or absence of the iceberg (BERG; 1 = iceberg present, 0 = iceberg absent). In addition, colony/population density can influence reproductive performance (Hunt et al. 1986), and because previous work found evidence of density-dependent energetic constraints and increase in foraging effort at capes Crozier and Bird (Ballance et al. 2009), we also evaluated models that included the effect of colony size (SIZE; centered and scaled following EXP above) or the percent change in colony size relative to the population size in 1996 (CHANGE) when banding efforts at all three colonies was initiated.

Model Selection

We evaluated all models using an information-theoretic approach (Burnham and Anderson 2002) and Akaike's Information Criterion corrected for small samples sizes (AIC_c) to determine the model from our *a priori* model set that best explained variation in patterns. Models with the lowest AIC_c and highest Akaike weight (w_i) were generally considered the best models, but models within 2 AIC_c units ($AIC_c \leq 2.0$) were still considered competitive (Burnham and Anderson 2002). We assessed the direction and strength of evidence for each estimated slope parameter ($ß_i$) that appeared in the top performing model based on the extent that the 95% confidence intervals (CI) for each $ß_i$ overlapped zero (Arnold 2010). We considered covariates in the top model with 95% CI that did not overlap 0 as evidence for having the strongest effect. Covariates that "slightly" overlapped 0 (i.e., 95% CI that overlapped 0 by <10%) were considered to have less effect, and "widely" overlapping covariates (i.e., > 10% of the interval above or below 0) were considered to have no support (see Dugger et al. 2016).

We determined the best random effect structure using AIC from maximum likelihood estimates, because it is unclear how best to define and compute (i.e., integrating out the effects of fixed parameters) restricted maximum likelihood estimates (REML) using GLMMs (Bolker 2019). Our candidate model set for determining the best random effect structure included three different random effect structures, with no fixed effects (intercept-only model for fixed effects). The best structure was a crossed random effect with random intercepts for both SEASONS and ID, and this structure was used to build all fixed effect models. We then selected the best models based on the fixed effects of interest, using this random effect structure. After identifying the best overall fixed effect model structure, we used this model to rerun the analysis of random effect structure and confirmed the crossed random effect with random intercepts for both SEASONS and ID was the preferred structure.

We then used AIC_c to identify the fixed structure that best fit the “shape” of the data containing different parameterizations of the same biological covariates (e.g., models with AFR or EXP parameterized as continuous linear, quadratic, cubic, pseudo-threshold or as factors). Following that we compared GLMMs with additive or interacting effects of covariates with different biological meaning (e.g., AFR, EXP). We retained the structure of this model for further modeling of individual heterogeneity on age-specific breeding success and extrinsic changes in breeding success.

After identifying the best random effect structure, tests for multicollinearity on all competitive models containing AFR, EXP, and LIFE, all of which are closely related to age, produced VIF estimates < 1.60, indicating that multicollinearity was not a significant issue (Chatterjee and Hadi 2015).

Results

The age at first reproduction was significantly lower at Cape Crozier (5.4 ± 1.3) than it was at Cape Bird and Cape Royds (both = 6.0 ± 1.6; $F_{2,3086} = 59.75$, $p = < 0.001$). Models parameterized with EXP_L were not competitive (all $\Delta AIC_C > 14$) so are not discussed. The top performing model (Table 2.6) indicated that breeding success changed over life as a function of AFR_C, a quadratic effect of EXP_T, their interaction, and an additive effect of colony. It indicated that the mean population-level probability of breeding success was highest at Cape Crozier (Figure 2.1). Age at first reproduction (AFR_C) was positively associated with breeding success at all three colonies. The inclusion of a quadratic effect of EXP_T in the top model indicates that, regardless of AFR and EXP, the observed estimates of breeding success increased early in the breeding lifespan, as individuals gained more EXP and reached a peak before declining later in life (Figure 2.2). There was support for an interaction between AFR_C and EXP_T, with individuals in the youngest (AFR_C = 3 years old) and oldest (AFR_C > 9-17 years old) age categories having the greatest improvement in the probability of breeding success with early additional EXP compared to individuals in the other two categories. In general, birds in the older AFR categories had a higher probability of breeding successfully on their first breeding attempt and later in life. The highest maximum probability of breeding success at all 3 colonies was observed in birds that began breeding at 9+ years old, and the second highest was observed for birds that were 3 at AFR (Figure 2.3). No other model in the initial candidate set was within 2 ΔAIC_C of model 1 so we considered this as the model best fitting the data and continued further analyses of breeding success relative to lifespan using this model.

Accounting for selective disappearance of individuals

When we included an additive effect of a monotonically increasing trend in lifespan (LIFE) to our initial base model, both run using the reduced data set where we removed birds that were observed in the final year of the study (i.e., were still alive), the additive effect of lifespan was well supported (Table 2.7). With the exception of the AFR_C, all coefficients included 95% confidence limits that did not overlap zero (Table 2.8). The trajectories of breeding success produced by this model were similar to the top model discussed earlier, although the profile for the oldest recruitment category (i.e., 6) exhibited a very pronounced quadratic shape and the maximum performance shifted into intermediate experience levels versus the advanced experience levels in the previous analysis. Still, across all recruitment groups, breeding success clearly declined after reaching intermediate levels of experience, indicating reproductive senescence after achieving intermediate levels of experience. Individuals delaying recruitment reached maximum breeding success levels sooner than the 4 and 5 categories, but these categories enjoyed a longer period of elevated performance throughout intermediate levels of experience, appearing to balance trade-offs between early breeding and late life performance. Regardless of colony or AFR, overall estimates of breeding success were lower using the reduced data set than the full data set and breeding success was positively associated with longevity (Figure 2.4). Taken together, these results support the selection hypotheses, in that it appears “less fit” individuals, or individuals with overall lower breeding success and shorter lifespans were more likely to be in this sample, than the individuals that were removed (i.e., still alive and breeding). In addition, the average lifespan of birds that began breeding when they were younger was significantly shorter than birds that began breeding when they were older ($F_{3,2050}$ = 162.8, $p = < 0.001$; Figure 2.5) at each of the colonies. Despite this difference in lifespan expectancy, on average, the overall number of breeding attempts and number of successful breeding attempts was not biologically different between categories of AFR (all AFR categories = 2 and 1, respectively; Table 2.9) or between the colonies (all colonies = 2 and 1, respectively; Table 2.9), indicating that while different life history decisions impacted life expectancy, they did not result in differences in the number of reproductive opportunities and outcomes.

Extrinsic temporal effects on breeding success

Models that included extrinsic temporal effects (i.e., SEASONS, BERG, SIZE, CHANGE) on breeding success failed to converge when those covariates were added to the base model including the interaction term between AFR_C and quadratic EXP_T. Thus, we simplified our base model to include only the additive fixed effects for different combinations of AFR_C, quadratic $EXP_{T,}$ and SEASONS, while maintaining ID as a random effect. We then evaluated models that included colony effects (i.e., SIZE, CHANGE) and the influence of the BERG. The top model in this analysis (< 144 AIC_C from competing models) included the additive effects of the quadratic effect of EXP, $SEASONS_c$, and CHANGE (Table 2.10). The quadratic effect was significant in both this and the original base model, indicating that the observed decline in the probability of breeding successfully after reaching an optimum is not an artefact of extrinsic variation. The effect of CHANGE (i.e., percent change in colony size relative to 1996) was also significant, with a positive trend, indicating that the probability of breeding successfully increased as the percent change in colony size from the 1996 season increased (Figure 2.6).

Discussion

Age-related reproduction profiles

Like many other studies we found support for a quadratic trajectory of age-related reproductive performance (Clutton-Brock 1988, Newton 1989, Sæther 1990). Our analysis showed compelling evidence of an increase in breeding success as breeding experience increased in the years immediately following first reproduction, reaching a peak with intermediate experience followed by a decline in breeding success late in life. This relationship was evident regardless of recruitment age (i.e., AFR) and was consistent among all three colonies (Figure 2.2). Taken together these results indicate support for the constraint hypothesis (Curio 1983, Nol and Smith 1987, Forslund and Pärt 1995), which suggests that individuals improve in skills or behaviors early in their reproductive lifespan, which increases reproductive success. There are many potential ways individuals could increase in competency (e.g., familiarity to colony, improved foraging ability, hold higher quality nesting territories, etc.). Interestingly, a recent study of the same population of Adélie penguins found that foraging competency increases with age (Lescroël et al. in review), providing a possible mechanism explaining why birds that delay recruitment exhibit higher breeding success in their first reproductive attempt than individuals that recruit earlier. However, this trend was such that the oldest individuals were the most proficient, but similar to our study, improvement was most pronounced early in life. Another possible explanation for the observed improvement early in reproductive life is that breeding success is linked to prior breeding experience (Clutton-Brock 1988, Newton 1989, Sæther 1990). Indeed, previous work on Adélie penguins found that as females gain foraging and breeding experience, they were more likely to initiate breeding earlier, lay larger eggs, and lay two-egg clutches (Ainley et al. 1983, Polito et al. 2010). Given that there is evidence that eggs from earlier and larger clutches have higher probabilities of survival (Davis and McCaffrey 1986), even after controlling for age (Ainley et al. 1983), the observed increase in early performance may be driven by an increase in competency from age-related foraging ability and previous breeding experience. Several studies have noted that improvement after 5 to 7 years, gradually diminished or plateaued (Ainley et al. 1983, Polito et al. 2010; Lescroël et al. in review), indicating that there may be a threshold at which additional increases in age or experience do not provide further improvements or trade-offs counteract additional increases in performance.

Interestingly, the performance threshold for foraging ability and breeding experience appears to be between 5 and 7 years of age. Peak breeding success performance from our analysis at all three colonies and for all recruitment categories occurred between 4 and 8 breeding attempts, which occurred much later in life (between 9 and 17 years; Figure 2.3). Similar to Ainley et al. (1983) we documented that individuals recruiting at 3 and 4 years of age generally reached maximum performance 4 (range: 3-5) years earlier than individuals that initiated breeding as 5 years old or older. Breeding estimates for individuals that began breeding at 3 years ceased after maximum performance, indicating either a survival cost or truncated reproductive lifespan. This is likely, given these individuals have the lower survival rates, but the few individuals adopting this life-strategy that survived went to be the most productive (Ainley et al. 1983). Meanwhile those that recruited at 4 years of age reached a pronounced peak after intermediate breeding attempts before a pronounced decline. The later recruits had a less pronounced decline in breeding success later in life, possibly indicating a threshold effect or senescence being masked due to selective disappearance (but see below). Overall these results supported the general positive trend of increasing breeding success with age, observed at all three colonies (Figure 2.4). However, this analysis does not account for selective disappearance at older ages and may not fully capture the age-related performance process at extremely late ages, as our oldest observed individuals (age = 18) were still alive and actively breeding in the last year of our data set (but see below). It is interesting to note that the oldest and the youngest recruitment categories (AFR = 6 and 3) had the highest maximum breeding success and occurred late in the reproductive lifespan, respectively (Figure 2.3). This presents an interesting contrast between recruitment tactics, where individuals that recruit early optimize their probability of breeding success through rapid improvement at young ages with additional experience, as predicted by the constraint hypothesis, while the oldest recruits adopt the strategy predicted by the delayed breeding hypotheses and enter the breeding population with sufficient experience to have a high probability of success. Meanwhile individuals electing to breed at intermediate ages, balance lower probabilities of breeding success by having a prolonged reproductive lifespan, similar to what has been observed in Black-legged Kittiwakes (*Rissa tridactlyla*; Aubry et al. 2009). This may also represent a difference in life history strategies between sexes. We did not have enough data on individual sexes to investigate this, but Ainley et al. (1983) found that earliest recruits (i.e., 3 year olds) were predominately females, while males generally recruited later. Young female recruits may be able to take advantage of older, more experienced males that have lost their previous mate owing to mortality. Another possible explanation for the high probability of breeding success late in life is that this late life peak in performance is the result of terminal investment (Williams 1966), which posits an age-related increase in reproductive effort that corresponds with an increase in reproductive investment (e.g., Pärt et al. 1992, Descamps et al. 2007, Froy et al. 2013). To formally test this hypothesis, we would need to measure energy expenditure, usually on a variety of metrics (e.g., laying date, egg volume, chick weight, etc.) in addition to breeding success, and while this is not an insignificant proposition, we think that this would be a highly productive line of research.

Accounting for selective disappearance

After we explicitly accounted for variation due to selective disappearance of phenotypically less “robust” individuals we observed a similar quadratic relationship in breeding success that we documented in the initial analysis. Regardless of recruitment age, breeding success clearly declined after reaching intermediate levels of experience, indicating reproductive senescence. Individuals delaying recruitment reached maximum breeding success levels sooner than the 4 and 5 categories, but these categories enjoyed a longer period of elevated performance throughout intermediate levels of experience, appearing to balance trade-offs between early breeding and late life performance. Similar to Black-legged Kittiwakes (Aubry et al. 2009) the earliest and latest recruits had similar breeding success, but peaked earlier in their reproductive lifespan. The three year old recruits did not appear to survive their peak reproductive period and the oldest recruits had the steepest rate of declining performance (Figure 2.2). The early recruits show support for the cumulated cost hypothesis that indicates early recruits will experience the strongest senescent decline in breeding success in advanced ages (Orell and Belda 2002). In our analysis, it appears that early recruits experienced actual survival senescence, where late recruits experience reproductive senescence. Somewhat surprising, the number of breeding attempts and successful attempts did not differ between recruitment categories, despite differences in maximum breeding success and extent of reproductive lifespan. These results provide insights into the simultaneous evolution of reproductive strategies and senescence.

Accounting for extrinsic variation

Breeding success varied across years and was positively linked to increasing percent change in colony size observed at all three colonies (Figure 2.5). While this is the expected result for smaller colonies with little to no density dependence, it is a somewhat unexpected result, for Cape Crozier. At large colonies, increasing population size can create conditions where breeding success decreases due to density dependence effects (Alatalo and Lundberg 1984, Both 1998) and there is evidence of density effects at this colony. Within season foraging effort of breeding adults has been documented to increase to the greatest degree at Cape Crozier (Ballance et al. 2009) and, in later years of the study (but not early years), crèching and fledging chicks at Cape Crozier weighed less than similarly aged chicks at the two smaller colonies (Whitehead et al. 2015, Ainley et al. 2018). However, a post-hoc analysis did not support ($\Delta AIC_c = 332.57$) a model with a quadratic effect of percent change in colony size. It is possible that breeding success as a binary outcome (i.e., YES/NO chick(s) entered crèche), was too coarse a metric to capture density dependent responses like the true chicks/pair or condition of chicks entering the crèche. Additionally, the presence of unusually extensive sea ice, owing to blocking by mega-icebergs during 2001 – 2005, had profound, but expected (Ainley 2002), effects on the Ross-Beaufort

Island Adélie penguin meta-population, such that in 2001 numbers were depressed at all colonies (Lyver et al. 2014). Cape Royds, whose penguins had the longest distance to walk, experienced a near complete breeding failure, while breeding success at Bird and Crozier decreased 50% from average (Dugger et al. 2014). Despite the Royds population decreasing by half, owing to emigration (Dugger et al. 2010, 2014), the other two colonies continued to grow (Lyver et al. 2014). It is interesting to note that aside from the 2001 season, Capes Crozier and Bird colonies were relatively unaffected by the mega-icebergs (Lyver et al. 2014), which might further explain why we didn't find density dependent effects on breeding success even though Cape Crozier may be approaching thresholds for density dependence. However, we thought that was the case by the late 1990s, when previous growth had stopped (Ballance et al. 2009) but then the Crozier and Bird colonies began growing again, which has continued to the present. Not finding a density effect on breeding success makes particular sense in light of the performance-based conspecific attraction hypothesis (Boulinier and Danchin 1997, Danchin and Wagner 1997, Suryan and Irons 2001), which posits that individuals determine the suitability of breeding habitat based on the presence (Reed and Dobson 1993) and/or high reproductive success of conspecifics (Boulinier and Danchin 1997, Danchin et al. 1998). The movement of emigrants in this metapopulation is towards Crozier, and to a lesser extent to Bird. The unfavorable conditions at the two smaller colonies while the mega-icebergs were present (Kappes et al. Chapter 4), combined with our finding of consistently higher probability of breeding success and early average AFR at Cape Crozier, indicate that this is could be a mechanism for the continued and high rate of growth at this colony.

Conclusions

Our study is one of relatively few long-term, longitudinal studies of known-aged individuals that can provide insights into the various hypotheses proposed to explain age-related patterns in natural-history strategies, and appropriately control for both individual and population level changes driving these patterns. In addition, this data set is one of the first to be able to assess the influence of resource availability on these patterns. Surprisingly, colony size did not appear to be a factor influencing the adoption of alternative life history strategies, but was positively linked to overall breeding success. Future work investigating finer grain metrics (e.g., absolute chick mass at fledging; Ainley et al. 2018) than our binomial outcome of Yes/No for breeding success may be able to better assess potential signals. We found evidence of a variety of alternate recruitment life history strategies that supported the constraint, selection and senescence hypotheses depending on circumstances. Most interestingly, we were able to disentangle the costs and benefits associated with different strategies, highlighting a high degree of plasticity in life history strategies. Age at first reproduction was positively linked to longevity, but did not translate to increased reproductive attempts or successful outcomes, indicating that in this system attempting reproduction results in survival costs to the youngest but not oldest recruits, and reflecting how different strategies may be equally successful in a short, highly seasonal breeding environment, such as the south Ross Sea. Collecting data sets like this is challenging, these results highlight their importance and utility for providing deeper understanding of the evolution of fundamental life history strategies that are responsible for driving population change.

Acknowledgements

This work would not have been possible without the countless hours the following people spent re-sighting bands and following nests of known-aged birds during the past 20 years: C.

Adams, J. Adams, S. Allen, L. Ballance, G. Barclay, Q. Barr-Glintborg, L. Blight, J. Blum, E. Burke, H. Carrad, M. Coleman, W. Cook, K. Drew, P. Dilks, L. Doel, I. Gaffney, C. Gjerdrum, D. Gremillet, D. Hardesty, S. Heath, M. Hester, S. Jennings, D. Jongsomjit, D. Hyrenbach, K. Lindquist, V. Marsaudon, M. Massaro, A. Matthews, C. McCreedy, V. Morandini, H. Nevins, R. Orben, V. Patil, R. Pech, A. Pollard, E. Porzig, C. Ribic, V. Ruopollo, B. Saenz, A. Schmidt, L. Sheffield, L. Smith, I. Sutherland, Y. Suzuki, C. Thomson, P. Timoti, V. Toniolo, A. Varsani, S. Webb, D. Wilson, A. Whitehead, J. Whitehead, S. Winquist, S. Zador. Logistical support for the field work was provided by the US Antarctic Program, through Antarctic Support Contractors, and Antarctica New Zealand. Permits were provided under the Antarctic Conservation Act, National Science Foundation Office of Polar Programs (2006-010, 2011-002, 2017-005) and Landcare Research Animal Ethics Committee Permit (0509/01). Data collection protocols were also approved by Moss Landing Marine Lab and Oregon State University respective Institutional Animal Care and Use Committees. Funding for this work was provided by National Science Foundation Grants OPP 9526865, 9814882, 0125608, 0440643, 0944411 and 154398 (to K.M.D., D.G.A., and G.B.) and New Zealand Ministry of Business, Innovation, and Employment Grant (C09527, C09X0510, C01X1001) and NZ’s Ministry for Primary Industries (MPI17238-S01-LC), with addenda (to P.O’B.L., K.B. and P.W.). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This is Point Blue Conservation Science Contribution xxx. L. Arnold, V. Morandini, R. Suryan, and S. Whitlock provided useful discussion and comments that greatly improved this work.

Table 2.1. Sample sizes for different recruitment ages (i.e., age at first reproduction) of known-aged individuals banded between 1994 and 2013 at Cape Bird, Cape Crozier, and Cape Royds, Ross Island, Antarctica (*n* = 42,183 individuals banded). The reduced data set was used for the modeling the influence of lifespan, the full data set was used for all other analyses.

Full data set:				
AFR_C (years old)	Cape Bird	Cape Crozier	Cape Royds	Total
3	21 (1.7%)	34 (2.1%)	2 (0.8%)	57 (1.8%)
4	173 (13.7%)	364 (22.9%)	38 (14.7%)	575 (18.5%)
5 (5-8)	981 (77.5%)	1158 (72.7%)	202 (78.3%)	2341 (75.1%)
6 (≥9)	91 (7.2%)	36 (2.3%)	16 (6.2%)	143 (4.6%)
Total	1266	1592	258	3116
Reduced data set used in lifespan analysis all bands observed in 2013 season removed:				
3	19 (2.4%)	21 (1.8%)	1 (0.7%)	41 (2.0%)
4	101 (12.6%)	268 (23.5%)	20 (15.1%)	389 (18.8%)
5 (5-8)	609 (76.1%)	824 (72.3%)	102 (77.3%)	1535 (74.1%)
6 (≥9)	71 (8.9%)	27 (2.4%)	9 (6.8%)	107 (5.2%)
Total	800	1140	132	2072

Table 2.2. Summary of the number of individuals observed breeding that did and did not take sabbatical years during their reproductive lifespan, based on their breeding experience (i.e., number of breeding seasons) after entering the Ross Island, Antarctica Adélie penguin breeding population between 1994 and 2013.

Experience (# seasons)	Breeding	Percent	Sabbatical	Percent
1	1465	15.3%	809	8.4%
2	1280	13.3%	664	6.9%
3	1008	10.5%	414	4.3%
4	840	8.7%	196	2.0%
5	790	8.2%	85	0.9%
6	732	7.6%	36	0.3%
7	469	4.9%	21	0.2%
8	376	3.9%	0	0
9	225	2.3%	0	0
10	130	1.4%	0	0
11	66	0.7%	0	0
Total	7381	76.8%	2225	23.2%

Table 2.3. Acronyms and description of life history and environmental variables used to model breeding success of known-aged Adélie penguins between 1994 and 2013, at Cape Bird, Cape Crozier, and Cape Royds, Ross Island, Antarctica. Breeding success was measured as successfully feeding a chick(s) (Y/N) after mean crèche date.

Age-related covariate acronyms	Description
AFR	Age at first reproduction as a continuous variable (3 - 14).
AFR_T	Age at first reproduction as categorized into groups as a monotonically increasing trend*.
AFR_C	Age at first reproduction as a categorical variable*.
EXP_T	Breeding experience as a continuous variable.
$EXP_T{}^2$	Breeding experience if quadratic.
$EXP_T{}^3$	Breeding experience if cubic.
EXP_L	Breeding experience as a continuous variable with sabbaticals counting as experience.
$EXP_L{}^2$	Breeding experience with sabbaticals if quadratic.
$EXP_L{}^3$	Breeding experience with sabbaticals if cubic.
THRESH	Breeding experience if it were a threshold (i.e., log of breeding experience).
Extrinsic Variables	
COL	Breeding colony as a categorical variable (i.e., Cape Bird, Crozier, and Royds).
BERG	Iceberg as a categorical variable (Y/N).
SIZE	Size of colony as continuous centered and scaled variable.
CHANGE	Percent change in size of colony to 1996.
SEASONS	The log of season as a continuous variable.
$SEASONS_C$	The log of season as a factor.

*AFR_T and AFR_C levels: 3 = 3 yr old, 4 = 4 yr old, 5 = 5-8 yr old, 6 = 9+ yr old

Table 2.4. Top ten models and null model from model selection analysis for logistic regression models evaluating the probability of breeding successfully as it relates to age at first reproduction and breeding experience. Model results include, differences between model Akaike's Information Criteria adjusted for small sample size (AIC$_c$) and the AIC$_c$ from the top model (ΔAIC$_c$), AIC$_c$ weights (w_i), model deviance, and the number of parameters (K).

No.	Model structure	ΔAIC$_c$	w_i	Deviance	K
1	AFB$_c$ X (EXP + EXP^2) + COL	0	.56	9167.43	16
2	AFB$_c$ X (EXP + EXP^2 + EXP^3) + COL	2.79	.14	9162.18	20
3	AFB$_{cc}$ X (EXP + EXP^2 + EXP^3) + COL	4.40	.06	9179.87	12
4	AFB$_{cc}$ X (EXP + EXP^2) + COL	4.79	.05	9184.27	10
5	AFB$_c$ X (EXP + EXP^2) + COL	5.20	.04	9184.68	10
6	AFB$_c$ + EXP + EXP^2 + EXP^3 + COL	5.72	.03	9187.20	9
7	AFB$_c$ + EXP + EXP^2 + COL	5.74	.03	9189.22	8
8	AFB$_c$ X (EXP + EXP^2 + EXP^3) + COL	5.99	.03	9181.45	12
9	AFB$_{cc}$ + EXP + EXP^2 + EXP^3 + COL	6.83	.02	9188.31	9
10	AFB$_{cc}$ + EXP + EXP^2 + COL	6.88	.02	9190.37	8
11	Intercept-only	207.38	0	9400.89	3

Model structure display fixed effects, but include random effects of ID and SEASONS, "+" indicates an additive effect, "X" an interaction, abbreviations can be found in Table 3.

Table 2.5. Summary of number of individuals that had breaks in their resighting history (i.e., were not observed) and the number of breeding seasons between resighting events for individuals that recruited into the Adélie penguin breeding populations at Cape Bird, Cape Crozier, and Cape Royds, Ross Island, Antarctica.

Seasons not observed	Count	Percent
0	2922	94.6%
1	115	3.7%
2	33	1.1%
3	12	0.4%
4	4	0.1%
5	3	0.1%

Table 2.6. Estimates from best model relating Adélie penguin breeding success to age at first reproduction (AFR_C; categorical variable), breeding experience (EXP_T), colony (categorical), and AFR X EXP interaction at capes Royds, Bird, and Crozier, Ross Island, Antarctica, 1994-2013. Parameter estimates for variables included in the final GLMM model with binomial errors associated with age-related breeding success. Data on 3089 individuals from 7381 breeding attempts across 19 years.

Variable	Estimate	SE	*z*	*P*
Fixed effects				
Intercept	-0.6188	0.2965	-2.087	0.037
AFR_C4	0.3549	0.2118		
AFR_C5	0.4248	0.2058	2.064	0.039
AFR_C6	0.6152	0.2441	2.52	0.012
EXP_T	85.6692	5.7825	14.815	<0.001
EXP_T^2	-45.8068	4.6124	-9.931	<0.001
COL(Crozier)	0.3230	0.0559	5.766	<0.001
COL(Royds)	-0.1721	0.1064		
AFR_C4 X EXP_T	-58.1206	6.0245	-9.647	<0.001
AFR_C5 X EXP_T	-55.9530	5.9594	-9.389	<0.001
AFR_C6 X EXP_T	-29.3916	7.8303	-3.754	<0.001
AFR_C4 X EXP_T^2	24.4965	5.6118	4.365	<0.001
AFR_C5 X EXP_T^2	38.5981	4.8646	7.934	<0.001
AFR_C6 X EXP_T^2	28.2288	6.9192	4.080	<0.001
Random effects				
SEASONS	0.6261	0.0092		
ID	0.0689	0.0031		

Table 2.7. Model selection results testing the effects of age at first reproduction and experience on age-related breeding success, while accounting for selective dissapearance of individuals due to heterogeneity in individual survival (i.e., lifespan effects) for Adélie penguins breeding at Cape Bird, Cape Crozier, and Cape Royds, Ross Island, Antarctica.

No.	Model structure	ΔAIC_C	w_i	Deviance	K
12	AFB_C X (EXP + EXP^2) + LIFE + COL	0	0.98	5420.1	17
1	AFB_C X (EXP + EXP^2) + COL	8.36	0.02	5430.5	16
13	AFB_C X (EXP + EXP^2) + $LIFE_C$ + COL	21.32	0.00	5427.3	24

Table 2.8. Parameter estimates for variables included in the second GLMM model with binomial errors associated with age-related breeding success and accounting for individual heterogeneity in survival (i.e., lifespan effects) for individuals breeding at Cape Bird, Cape Crozier, and Cape Royds, Ross Island, Antarctica. Data on 2054 individuals from 5625 breeding attempts across 19 years.

Variable	Estimate	SE	*z*	*P*
Fixed effects				
Intercept	-0.9174	0.3688	-2.49	0.037
AFR$_C$4	0.1333	0.2714		
AFR$_C$5	0.0497	0.2658		
AFR$_C$6	0.2468	0.3337		
EXP$_T$	129.5680	10.5530	12.28	<0.001
EXP$_T^2$	66.5383	11.6712	5.70	<0.001
COL(Crozier)	0.4943	0.0727	6.80	<0.001
COL(Royds)	-0.4568	0.1587	-2.88	<0.001
LIFE	0.0531	0.0164	3.23	<0.001
AFR$_C$4 X EXP$_T$	-110.7187	11.3838	-9.73	<0.001
AFR$_C$5 X EXP$_T$	-117.0399	10.4872	-11.16	<0.001
AFR$_C$6 X EXP$_T$	-101.0191	13.7297	-7.36	<0.001
AFR$_C$4 X EXP$_T^2$	-71.2321	12.8021	-5.56	<0.001
AFR$_C$5 X EXP$_T^2$	-71.0925	11.7511	-6.05	<0.001
AFR$_C$6 X EXP$_T^2$	-105.8730	14.3435	-7.38	<0.001
Random effects				
SEASONS	0.6988	0.0025		
ID	0.0347	0.0111		

Table 2.9. Means and standard errors of number of breeding attempts and successful breeding attempts for different recruitment categories (i.e., age at first breeding; AFR) for Adélie penguins breeding at Cape Bird, Cape Crozier and Cape Royds (using the reduced lifespan date set).

	Bird		Crozier		Royds	
AFR$_{C}$ (years old)	Breeding attempts (*n*)	Successful attempts	Breeding attempts	Successful attempts	Breeding attempts	Successful attempts
3	1.95 ± 0.32 (19)	0.68 ± 0.29	2.42 ± 0.32 (21)	1.14 ± 0.30	NA	NA
4	1.96 ± 0.16 (99)	0.98 ± 0.12	2.28 ± 0.10 (266)	1.39 ± 0.09	1.79 ± 0.24 (19)	0.74 ± 0.21
5 (5-8)	2.17 ± 0.07 (607)	1.08 ± 0.05	2.29 ± 0.06 (822)	1.40 ± 0.05	1.75 ± 0.13 (101)	0.66 ± 0.09
6 (≥ 9)	1.72 ± 0.14 (71)	1.01 ± 0.14	1.70 ± 0.21 (27)	1.07 ± 0.22	1.56 ± 0.44 (9)	0.89 ± 0.54

Table 2.10. Top ten and intercept-only models from model selection analysis for logistic regression models evaluating the probability of breeding successfully as it relates to age at first reproduction and breeding experience and colony size and presence/absence of a mega-ice berg. Model results include Akaike's Information Criteria adjusted for small sample size (AIC_C), differences between model AIC_C and the AIC_C from the top model (ΔAIC_C), AIC_C weights (w_i), model deviance, and the number of parameters (K).

Model structure	ΔAIC_c	w_i	Deviance	K
EXP + EXP^2 + $SEASONS_C$ + CHANGE	0	1	9139.0	20
AFB_c + $SEASONS_C$ + CHANGE	144.10	0	9281.1	21
AFR_c + EXP + EXP^2 + BERG + COL	239.36	0	9398.4	10
EXP + EXP^2 + BERG + COL	248.47	0	9413.6	7
AFR_c + EXP + EXP^2 + BERG + CHANGE	254.63	0	9415.7	9
AFR_c + EXP + EXP^2 + BERG + SIZE	254.91	0	9416.0	9
EXP + EXP^2 + BERG + CHANGE	259.11	0	9426.2	6
EXP + EXP^2 + BERG + SIZE	262.53	0	9429.6	6
AFB_c + EXP + EXP^2 + SEASONS + BERG	291.20	0	9452.3	9
EXP + EXP^2 + SEASONS + BERG	294.41	0	9461.5	6
Intercept-only	863.21	0	10038.31	2

Model structure display fixed effects, but include random effect of ID, "+" indicates an additive effect, abbreviations can be found in Table 2.3.

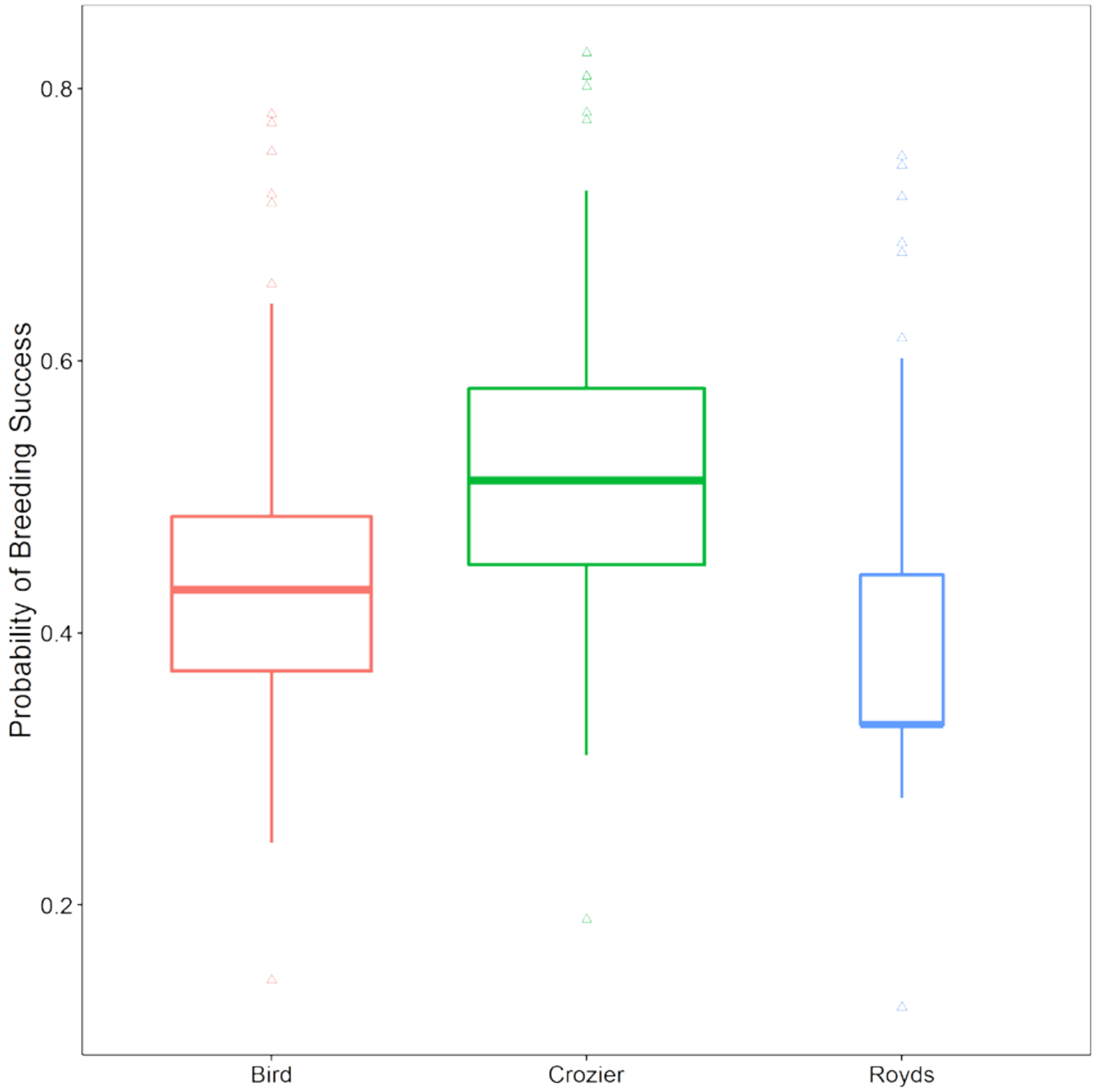
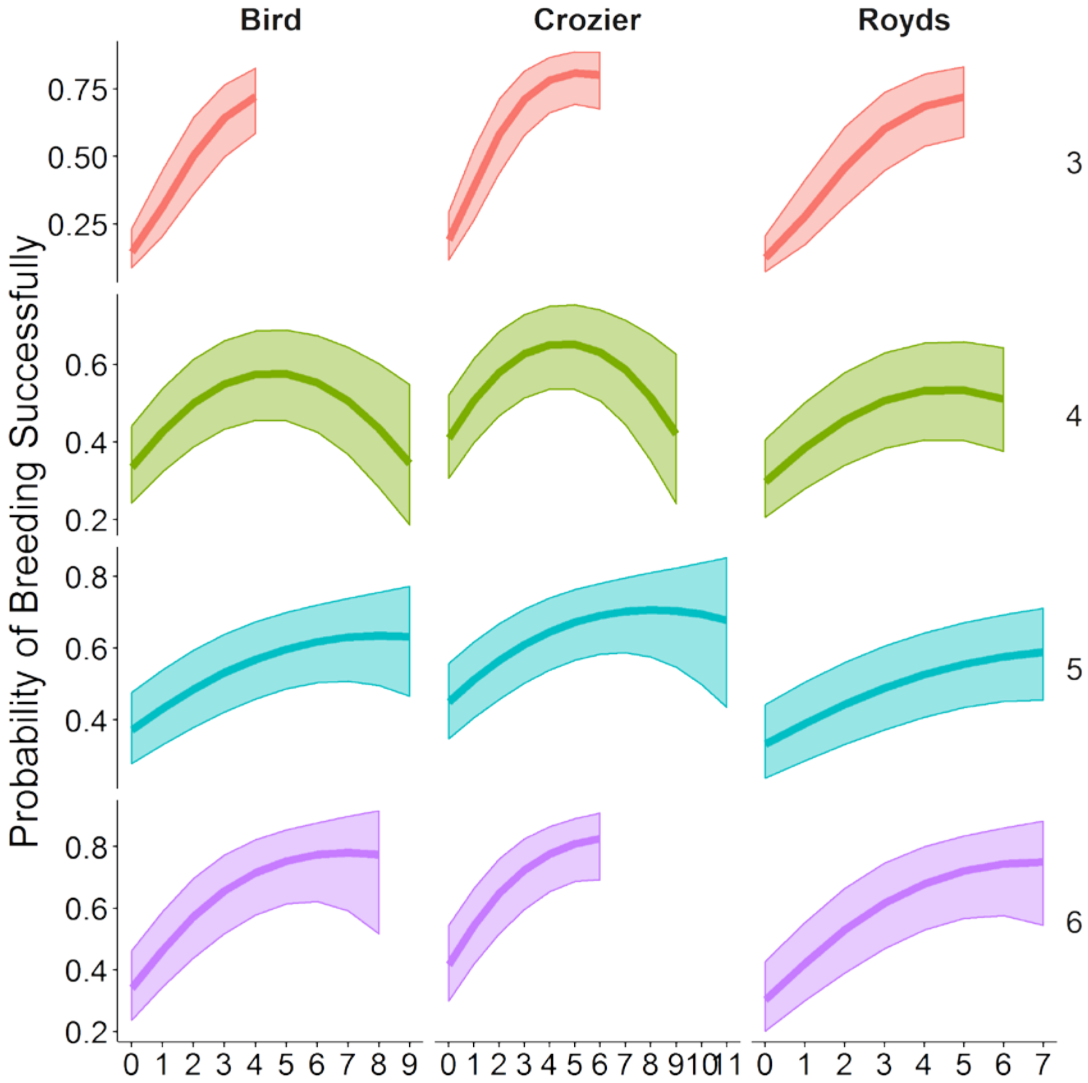


Figure 2.1. Mean population-level probability of breeding success of Adélie penguins breeding at Capes Bird, Crozier and Royds, Ross Island, Antarctica. Outliers are shown with Δ.

A)


Bird
Crozier
Royds
Probability of Breeding Successfully
0.75
0.50
0.25
0.6
0.4
0.2
0.8
0.6
0.4
0.8
0.6
0.4
0.2
3
4
5
6
0 1 2 3 4 5 6 7 8 9
0 1 2 3 4 5 6 7 8 9 10 11
0 1 2 3 4 5 6 7

B)

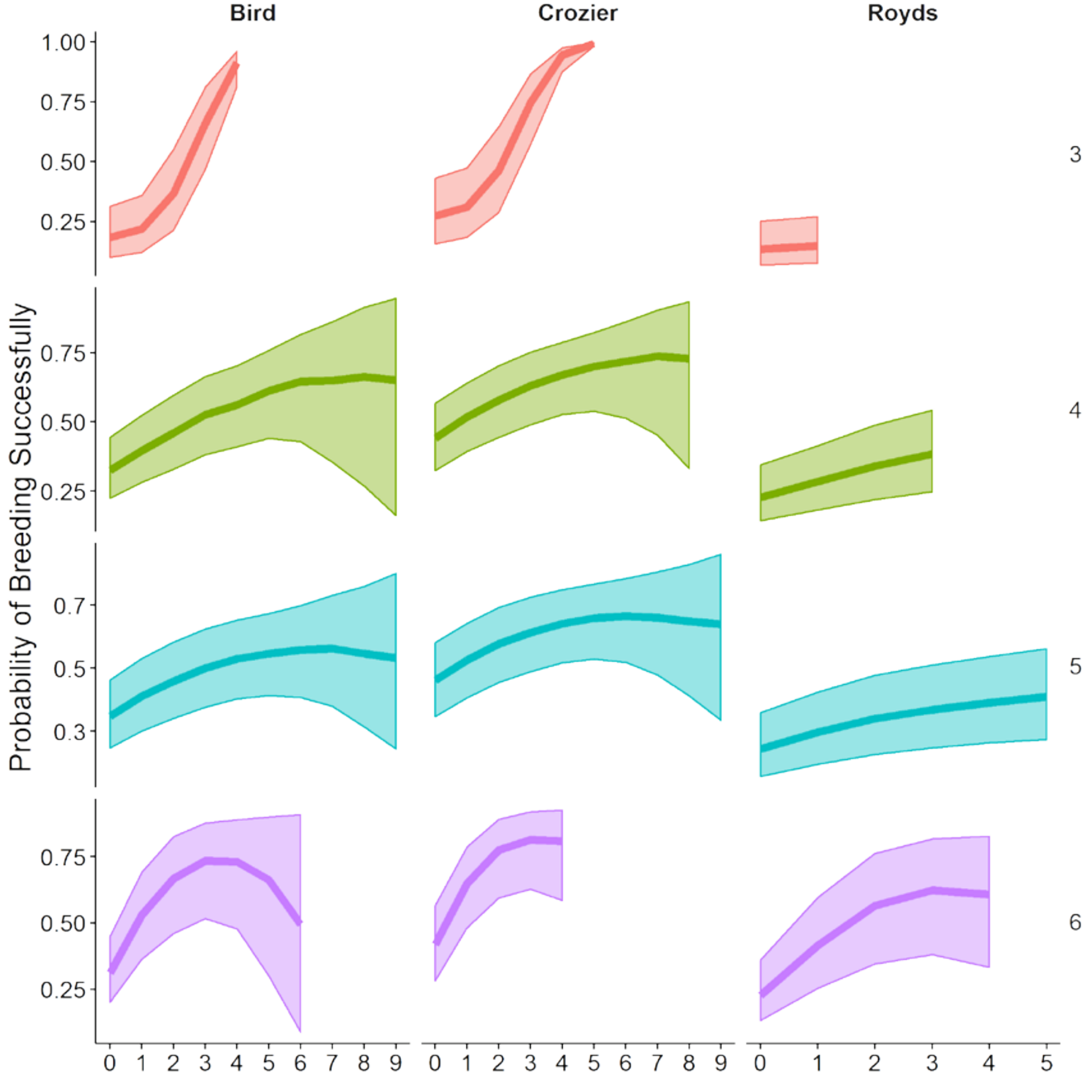


Figure 2.2. A) Trajectories of the probability of breeding successfully as it relates to categorical age at first reproduction (AFR_C; 3 = 3 years old; 4 = 4 years old; 5 = 5 - 8 years old; 6 ≥ 9 years old) and true breeding experience (EXP_T; number of breeding attempts since recruitment) using the full data set; B) using the lifespan data set, for Adélie penguins at Capes Bird, Crozier, and Royds, Ross Island, Antarctica. Mean population-level estimates and 95% confidence intervals were obtained for the fixed effects from the best performing generalized linear model and not accounting for seasonal (i.e., random effect of breeding season) and unobserved individual heterogeneity (i.e., random effect of ID).

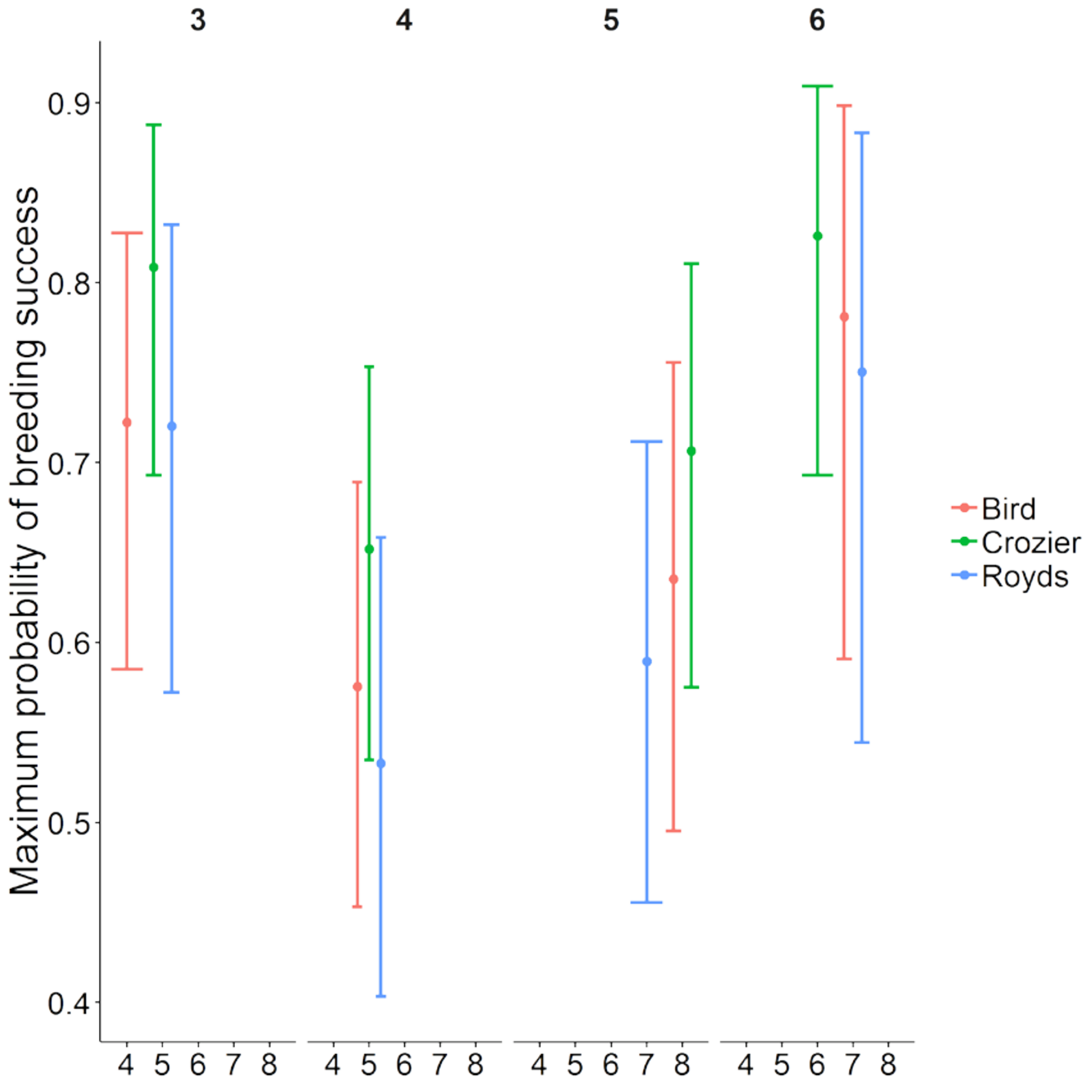


Figure 2.3. Maximum parameter estimates and 95% CI of breeding success in the final GLMM for each age at first reproduction category of Adélie penguins breeding at capes Bird, Crozier, and Royds, Ross Island, Antarctica.

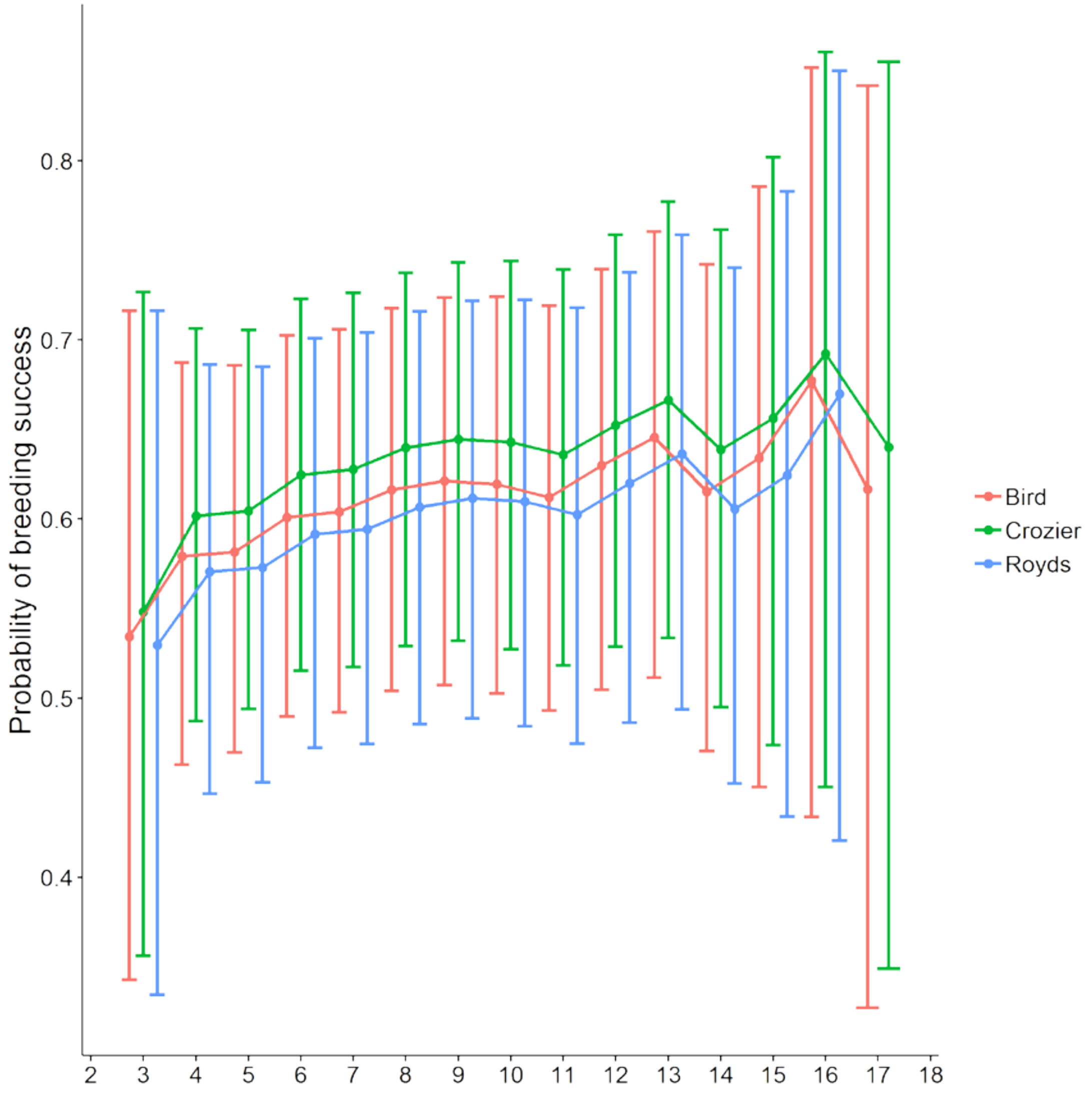


Figure 2.4. Average breeding success and 95% confidence intervals as a function of true age for known-aged Adélie penguins breeding at capes Bird (pink line), Crozier (green line), and Royds (blue), Ross Island, Antarctica. The two oldest age groups were dropped due to small sample sizes.

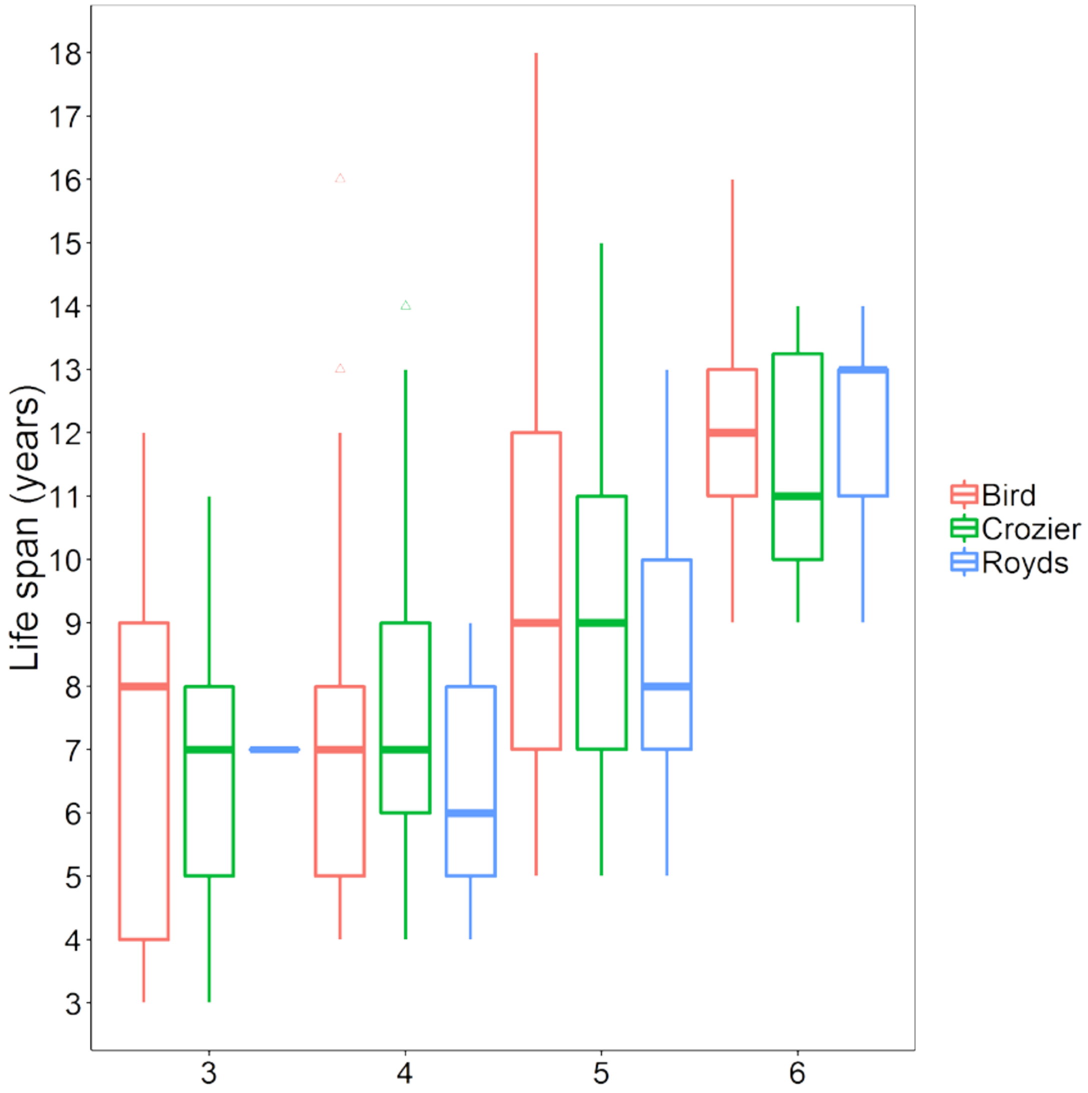


Figure 2.5. Average lifespan for age at first reproduction categories (AFR$_C$) of Adélie penguins breeding at capes Bird, Crozier, and Royds, Ross Island, Antarctica.

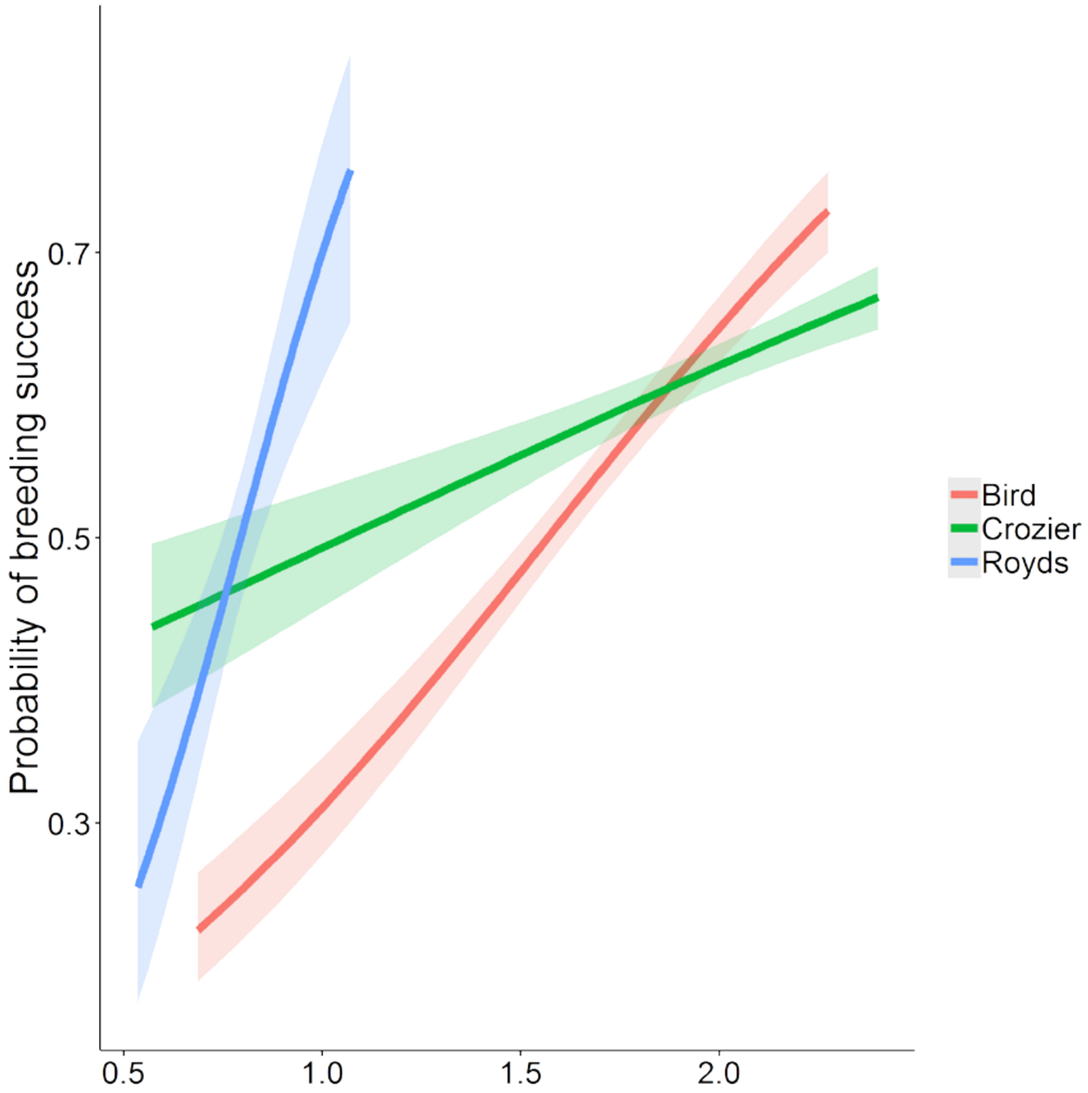


Figure 2.6. The probability of Adélie penguins breeding successfully at Capes Bird, Crozier, and Royds as a function of percent change in colony size from the 1996 season.

3 - IDENTIFYING PROCESSES RESPONSIBLE FOR AGE-RELATED REPRODUCTIVE PERFORMANCE OF A LONG-LIVED SEABIRD

Peter J. Kappes, Katie M. Dugger, Amélie Lescroël, David G. Ainley, Grant Ballard, Kerry J. Barton, Phil O'B. Lyver, Peter Wilson

Abstract

A longstanding challenge preventing deeper understanding and unlocking new directions of research of age-specific reproductive performance has been our inability to correctly attribute the processes contributing to observed population patterns that appropriately take into account both the individual-level (within individual maturation) and population-level (selective appearance and disappearance of individuals). We determined the relative contributions of each of these processes to the reproductive performance of a seabird meta-population breeding at three different sized colonies. Regardless of age, first time breeders had lower average reproductive performance than the rest of the colony. Decomposing the age-related reproductive performance into its constituent processes revealed differences in the contributions the different processes made at each colony. At all three colonies selective appearance of new phenotypes contributed negatively (range: 20% - 54%) to overall age-related reproductive performance, meaning regardless of age, first time breeders had lower reproductive performance than experienced breeders. At the small and medium sized colonies improvements in age-related reproductive performance was driven by a combination of within-individual maturation (15% at both colonies) and selective disappearance (41% and 32%, respectively). At the largest colony, the majority of the improvement was due to within-individual maturation (67%). Comparisons of the relative contribution of each of the processes in early life versus late life stages at all three colonies revealed similar contributions early in life, but important differences at advanced ages. At the two smaller colonies, observed changes late in life were primarily driven by population level changes resulting from

selective disappearance of individuals of lower phenotypic quality. However, at the largest colony, changes in performance were driven by a combination of within-individual maturation and the selective disappearance of individuals of higher phenotypic quality. This unexpected result may be due to a combination of potential trade-offs associated with differences between colonies of different sizes and differences between individual life history strategies. These results highlight that different alternative early-life history strategies, which may differ due to early-life settings, can have different consequences late in life, impacting the phenotypic composition of the population. This can have important consequences for population dynamics and highlights the importance of accounting for the different processes contributing to observed patterns in reproductive performance and of incorporating replication into studies of age-related performance.

Introduction

Age-related changes in reproductive performance is a central component of life history theory (Stearns 1992) and is well documented in long-lived iteroparous species (Clutton-Brock 1988, Newton 1989, Sæther 1990, Wooller et al. 1992). Numerous empirical studies on a variety of taxa have found that age-related changes in reproductive performance or phenotypic traits associated with reproductive performance often follow a general pattern of early-life improvement, an asymptote at middle age, followed by late-life decline or senescence (Newton and Rothery 1997, McElligott et al. 2002, Reid et al. 2003, Nussey et al. 2006, Reed et al. 2008, Aubry et al. 2009, Bouwhuis et al. 2010, Rebke et al. 2010, Kim et al. 2011, Hayward et al.

2013, Lemaître et al. 2015, Froy et al. 2017) (Kappes et al. MS1). However, a variety of factors including immigration (Bouwhuis et al. 2010), environmental stochasticity and early-life conditions (Nussey et al. 2007, Pardo et al. 2013, Panagakis et al. 2017), density-dependence (Both 1998, Rödel et al. 2004), and variation in trade-offs related to different life history decisions (Aubry et al. 2009, Limmer and Becker 2010, Bosman et al. 2013, Lemaître et al. 2015) can also influence age-related reproductive performance or associated traits. Thus, a variety of complex patterns at different life stages and within cohorts having different life histories (e.g., different ages at first reproduction, differences in number of breeding attempts) have been documented, making the interpretation of the overall observed patterns difficult. Multiple non-exclusive hypotheses have been proposed to explain the various population-level patterns observed in age-related reproductive performance and/or phenotypic traits (see Curio 1983, Clutton-Brock 1988, Newton 1989, Sæther 1990, Stearns 1992, Forslund and Pärt 1995). Because population-level changes in age-related reproductive performance can result from processes operating at both the individual- (within-individual improvement/maturation or senescence) and the population-level (selective appearance or disappearance of specific phenotypes; Vaupel and Yashin 1985, van de Pol and Verhulst 2006, Rebke et al. 2010), it is important to account for these processes to properly interpret the observed population-level patterns.

To fully understand changes in age-related reproductive performance, population level estimates need to be divided into the constituent processes that are ultimately responsible for producing the overall observed changes. Building on prior efforts to decompose change into its constituent parts (see Price 1970, Vaupel and Romo 2002, Coulson and Tuljapurkar 2008), Rebke et al. (2010) developed a simple method that aims at separating and quantifying the following three processes that are responsible for age-related changes: within-individual maturation (i.e. average change in performance), selective disappearance, and selective appearance of individual phenotypes of varying quality. Operating at the individual-level, heterogeneity refers to changes in performance or associated phenotypic traits from within-individual changes as a result of maturation. Meanwhile, selective disappearance and selective appearance operate at the population level and produce changes in the phenotypic composition of the population. Selective disappearance refers to the changes in the population composition if selective mortality disproportionately removes individuals of high or low phenotypic quality. For example, if low quality (or frail) individuals suffer higher mortality early in life, than the observed pattern of improved reproductive performance with increasing age would be due to the disappearance of low-quality individuals as opposed to a phenotypic change within a given individual (Cam et al. 2002). Selective appearance refers to the changes in the population composition if individuals of higher or lower phenotypic quality enter the population as adults at different ages due to either delayed recruitment or immigration (van de Pol and Verhulst 2006). For example, if individuals of higher phenotypic quality recruit to the breeding population when they are older, than the observed pattern of improved reproductive performance with increasing age would be due to the appearance of high-quality individuals as opposed to a phenotypic change within a given individual. These processes operate independent from one another and can interact to create observed patterns at both the individual and population level (Stearns 1992, Forslund and Pärt 1995, van de Pol and Verhulst 2006, Rebke et al. 2010). Thus, it is important to decompose these processes across a time series that encompasses the entire lifespan of ≥1 cohort.

One approach to account for the influence of population-level processes on patterns of age-related reproductive performance is to use generalized mixed-effects models with individual identities as a random effect, paired with a fixed effect of age, which acts to control for changes in individual quality (van de Pol and Verhulst 2006). The resulting parameter estimates of this approach provide a quantitative measure of the magnitude of change due to the age, but can be influenced by the choice of the fixed effect (Moyes et al. 2009, Hayward et al. 2013) and more importantly do not allow the quantification of the contributions that each process makes to observed population-level changes. As previously discussed, the Rebke et al. (2010) approach decomposes average observed population-level changes into quantifiable contributions from individual- and population-level processes responsible for those changes and can do so across the entire observed lifespan as well as at specific ages. However, it requires repeated measuring of all individuals throughout their entire lifespan to provide an accurate decomposition, something which is difficult to achieve in wild populations and for individuals at advanced ages (Nussey et al. 2008), but has become less of an issue with the maturation of more longitudinal studies following known-aged individuals through their reproductive lifespan (see Nussey et al. 2013 for review of senescences in natural populations featuring these data sets).

Here we use the decomposition method developed by Rebke et al. (2010) to investigate age-related changes in reproductive performance of known-aged Adélie penguins (*Pygoscelis adeliae*) breeding at three different colonies on Ross Island, Antarctica. We used longitudinal data collected from known-aged, uniquely banded individuals since 1994 that was collected to understand demographic processes influencing population trends at these colonies. We used breeding success for known-aged birds from all three colonies to describe population-level patterns in age-related reproductive performance while disentangling the respective contributions of within-individual maturation, selective disappearance, and selective appearance in order to better understand how these processes may contribute to, and influence observed population trends at colonies differing in size by orders of magnitude.

Methods

Since 1994, the southern Ross Sea, Antarctica, meta-population of Adélie penguins has been the focus of long-term studies of demography (Dugger et al. 2006, Lescroël et al. 2009, Dugger et al. 2010, Dugger et al. 2014) and foraging ecology (Ballard et al. 2001, Ballard et al. 2010a, Dugger et al. 2010, Lescroël et al. 2010, Lescroël et al. 2014). This meta-population is composed of 4 adjacent colonies on Ross and Beaufort Islands in the southern Ross Sea that have varied in size during the course of the study (Cape Bird: increased from 35,000 to 75,000 pairs; Cape Crozier increased from 118,000 to 305,000 pairs; Cape Royds: decreased from 4000 to 2300 breeding pairs; Beaufort Island 64000 breeding pairs in 2010; LaRue et al. 2013, Lyver et al. 2014). Starting in the 1994-1995 season (hereafter 1994) we banded chicks at three of the four colonies (Cape Bird, Cape Crozier, and Cape Royds) for the duration of the study. Banding and subsequent monitoring did not happen regularly on Beaufort Island due to logistical considerations. Chicks were banded with a uniquely numbered stainless steel band attached to the left flipper (see Dugger et al. 2006 for more information on band design). In the following seasons we searched for banded birds at 2 to 7 day intervals (depending on colony) at all three colonies. Breeding attempts and performance of these birds were recorded throughout the season.

Adélie penguins are long-lived birds that typically begin breeding between 3 and 8 years old (Ainley 2002a). On average, they lay two eggs, and because chick growth rates can usually only be maintained if both parents forage simultaneously, most chicks are left unattended at some point during chick rearing. Unattended chicks typically gather into large groups known as “crèches” (Davis 1982), at which point it becomes extremely difficult to continue to follow unmarked individual chicks without causing high levels of disturbance. Because chick mortality during the crèche stage is believed to be low (Davis and McCaffrey 1986; but see, Jennings 2015) we defined reproductive “success” as any known-aged bird observed feeding a chick after mean crèche date each year (about the first week of January) and the number of chicks crèched as the highest number (1 or 2) seen with the banded member of the pair after this date. If a known-aged bird that had previously been observed with an egg(s) and/or chick(s) was never observed with a chick after mean hatch date, we considered them to have a failed reproductive outcome for that season.

Relative reproduction is a measure of an individual's reproductive performance in relation to the average reproductive performance of the population in a given year (see Ezard et al. 2007, Limmer and Becker 2010). To assess population level performance we decomposed change in the absolute number of fledglings between age x and $x + 1$. We also decomposed change in the relative (or residual) reproduction, to account for known environmental mediated temporal variation in this population (see Dugger et al. 2014, Lescroël et al. 2014). By decomposing age-related change into its constituent components we were able to determine their overall contributions to observed population level changes, enabling comparison of the results between colonies.

Decomposition of Population-level Age-Specific Reproductive Success

We used the method developed by Rebke et al. (2010) to decompose population-level changes in age-related reproductive success with repeated measures of Adélie penguins (aged 3-17 years) breeding at three different colonies. This method can be used to extract an exact decomposition of population-level age-related change in the average of a phenotypic trait (P), into its constituent processes: within-individual change (I), change due to selective disappearance (D), and change due to selective appearance (A). Population-level changes in P are estimated as $P = I + D + A$. As defined by Rebke et al.'s (2010) method, we estimated the population-level change in reproductive success (or P) by taking the difference between the mean of reproductive success for consecutive ages measured from all individuals in the population. Within-individual change in reproductive success (RS) due to development or senescence (I_X) is estimated for all individuals (j) that survive from age x to $x + 1$ such that:

$\mathrm{RS}_{j,x} = \mathrm{RS}_{j,x+1} – \mathrm{RS}_{j,x}$

where $\mathrm{RS}_{j,x}$ is the individual phenotypic change in RS at age x. To calculate an estimate of population-level changes due to the effect of within-individual performance changes we used the mean of the differences in individual trait values between consecutive ages, for all individuals present in the population at both ages (i.e., $I_x = \Sigma(\mathrm{RS}_{j,x})/n$). The cumulative effects of within-individual change at each age can then be calculated as the sum of the mean changes up to each age (see Rebke et al. 2010 for a worked example).

To calculate an estimate for the contribution due to the effect of selective disappearance, we used the difference between mean RS at age x for the individuals that survived to age $x + 1$ and RS for the entire population at age x (i.e., $d_{j,x} = \mathrm{RS}_x – \mathrm{RS}_{j,x+1}$) and calculated the cumulative change due to selective disappearance in RS as the sum of the estimated effects at each age (i.e., $D_x = \Sigma(d_{j,x})/n$). The contribution of change in age-related performance due to selective appearance was calculated by taking the difference between the population mean at age $x + 1$ and the individuals that survived to age $x + 1$ (i.e., $a_{j,x} = \mathrm{RS}_{x+1} - \mathrm{RS}_{j,x+1}$), and cumulative effects due to selective appearance in RS is the sum of the estimated effects at each age (i.e., $A_x = \Sigma(a_{j,x})/n$).

During the course of the study, we were only able to observe approximately 95% of the banded individuals every year. This will influence estimates of within-individual performance as these individuals will not contribute to estimates in the years when they were not observed. Thus, our results represent estimates of RS. In addition, approximately 30% of all banded individuals observed in a given year at each of the colonies took a sabbatical (i.e., did not attempt to breed; Figure 3.1) during their lifetime. We assigned these individuals “NA” for their reproductive outcome because assigning them 0 impacted estimates of within-individual performance when in fact these individuals were not observed actively breeding, and therefore likely did not experience the physiologically equivalent investment (and potential associated costs) as those individuals that attempted to breed but failed. However, these individuals were kept in the breeding population “pool” throughout their sabbatical so that their future breeding attempts did not contribute to the disappearance or subsequent appearance estimates. When calculating the decomposition estimates we did not include age classes with <10 individuals (Table 3.1 and Figure 3.1 for more information) to prevent spurious interpretations due to small sample sizes in the oldest age classes at all three colonies and the 3-year old age class at Cape Royds (only 2 individuals). Our estimates for selective disappearance could not take into account individuals that emigrated from the breeding population. However, dispersal of individuals that have already recruited to the breeding population was low even during years when a mega-iceberg created extremely difficult environmental conditions (~3.5%) and under typical conditions is <1% (Dugger et al. 2010).

We also calculated the average changes arising from all individuals at all ages attributable to the different processes as a percentage (see Rebke et al. 2010 for formulas). Negative values arising from these calculations represent contributions that indicate a reduction in performance and act to reduce average observed overall performance.

Results

Ages of uniquely banded birds observed breeding during our study ranged from 3 to 19 years between the three colonies (Figure 3.1), but to avoid unreliable estimates due to small sample sizes in the oldest age classes at all three colonies we only used reproductive data from ages 3 to 17 years old. Trends of both population-level and the decompositions of reproductive performance measured as absolute and relative performance at all three colonies were similar, but for brevity we present only the relative reproductive performance here as it accounts for the temporal variation in reproductive performance we observed at all three colonies during the course of this study (Lescroël et al. 2009, Dugger et al. 2014).

Inspecting the age-specific patterns in reproductive performance (averages of all individuals at all ages) revealed an overall general increase in relative reproduction up to age 13 at capes Bird and Crozier and age 9 at Cape Royds (Figure 3.2). After this, performance patterns varied between the three colonies, but all exhibited a subsequent drop in performance between ages 9-10 and 11. At both capes Bird and Royds, this was followed by a dramatic increase in performance, such that it reached the highest level recorded at each colony in the second to last age class, before another decline in the most advance age class (17 and 13, respectively). Meanwhile, at Cape Crozier, reproductive performance continued to improve, such that performance reached its highest level in the oldest age group (i.e., 16), and still exhibited an improving trajectory. Meanwhile, the initial mean performance of the youngest age classes to recruit to the breeding population at all three colonies was not only the lowest of all age classes, but varied between colonies (one-way ANOVA: $F_{2,88} = 5.88$, $p = 0.004$), such that the residual reproductive performance of 3 year olds at Cape Crozier (-0.54 ± 0.55) was significantly lower than those at Cape Bird (-0.07 ± 0.24; Tukey: $p = 0.003$). In addition, at all three colonies, the average age-specific reproductive performance was negative (i.e., lower performance when compared to the average for the entire population) up until age 6-7, after which all subsequent age-classes outperformed their respective colony averages.

Interestingly, while the overall shape of the population level patterns in reproductive performance was similar at the three colonies, the decomposition of the constituent processes and their percent contribution to the observed age-related changes differed between the largest colony, Cape Crozier, and the two smaller colonies (Figure 3.3). At Cape Crozier both processes of selective disappearance and appearance contributed negatively to overall reproductive performance, while within-individual improvement contributed positively. Meanwhile, at the two smaller colonies, only selective appearance contributed negatively and both selective disappearance and within-individual improvement contributed positively. While nearly 70% of the observed change in age-related reproductive performance was due to within-individual improvement at Cape Crozier, it only accounted for approximately 15% at both of the smaller colonies. Meanwhile, the percent change attributed to selective appearance was negative at all three colonies, but at Cape Crozier it was responsible for approximately -21% of the observed change while it accounted for over 50%. At Cape Royds, the contributions of both selective appearance and disappearance were roughly equal, at -43.5% and 41.4% respectively.

A closer inspection of the age-specific contributions of each of the processes, revealed that the negative contribution of selective appearance was primarily confined to younger age classes. Within-individual performance improved up to age 13 at both capes Bird and Crozier, and age 9 at Cape Royds (Figure 3.4 and Figure A.1), roughly 4 years before the oldest age class. After this, within-individual contributions and population level changes trended in the same direction but exhibit different variability depending on the colony. Surprisingly, selective disappearance at Cape Crozier contributed only a little over 10% of the total observed change and was negative. Most of the contributions from this process occurred at advanced ages (i.e., after 13 at capes Bird and Crozier, and 9 at Cape Royds), suggesting that for these age classes, changes in the proportion of birds at advanced ages in the breeding population are important drivers of overall changes to age-related reproductive performance. At capes Bird and Royds, individuals with higher than average reproductive performance were more likely to remain in the breeding population, but it was reverse at Cape Crozier.

We did not make any *a priori* predictions regarding late life performance, but given the variability in the contributions of the various process to late-life performance we divided the population into two groups: “Young” (3-13 at capes Bird and Crozier; 3-9 at Cape Royds) and “Advanced” (≥ 14 at capes Bird and Crozier; ≥ 10 at Cape Royds), and compared the decomposition contributions between them. This revealed similar contribution patterns in the young age group, at all three colonies (Figure 3.5). Within the young age group, overall population level performance improved with age at all colonies and was primarily attributable to within-individual change, while selective appearance contributed negatively. In the advanced age group, contributions were similar at the small and medium sized colonies, with population level performance declining due mostly to within-individual performance, but being offset by selective disappearance of lower phenotypic quality. At Cape Crozier overall performance in the advanced age group actually continued to improve primarily due to ongoing within-individual maturation.

Discussion

All three colonies showed similar patterns of relatively consistent overall age-related improvement in reproduction until the “advanced” ages (i.e., ~4 years before the oldest age class observed in each colony) and these patterns were driven predominantly by within-individual maturation (Figure 3.4 and Figure 3.5). Selective appearance was primarily detectable at all three colonies during early life, such that birds delaying reproduction suffered lower performance on their initial breeding attempt, compared to similar-aged birds who had already recruited into the breeding population.

The initial population-level analysis, based on averages of all individuals at all ages indicated a steady improvement in reproductive performance up to advanced ages (Figure 3.2). This is a well-established pattern (Clutton-Brock 1988, Newton 1989, Sæther 1990, Forslund and Pärt 1995, Kim et al. 2011, Hayward et al. 2013, Nussey et al. 2013) even after controlling for unobserved heterogeneity (Cam et al.

2002, Rattiste 2004, Balbontín et al. 2007, McCleery et al. 2008, Aubry et al. 2009, Rebke et al. 2010; Kappes et al. ms). However, our analyses also showed that several underlying processes were contributing differently to that change and that their relative contribution was different depending on the colony (Figure 3.3). A negative effect of selective appearance was detected at all three colonies indicating that birds breeding for the first time (or immigrating into the population) had lower reproductive performance than birds of a similar age that had already recruited into the breeding population. These results suggest that regardless of an individual's age, Adélie penguins in this population have low reproductive performance the first time they breed and that previous breeding experience has a positive effect on reproductive output. First-time breeders have regularly been shown to have lower reproductive success than more experienced breeders (Curio 1983, Thomas and Coulson 1988, Weimerskirch 1990, Wooller et al. 1990, Cam and Monnat 2000a, Rödel et al. 2004, Nevoux et al. 2007, Limmer and Becker 2010, Froy et al. 2017). This could be the result of physiological maturation triggered by the first breeding attempt (Harshman and Zera 2007), or a behavioral learning effect (e.g., partner bond, ability to incubate egg or care for chicks Ollason and Dunnet 1988, Bradley et al. 2000).

Previous work on Adélie penguins supports the physiological maturation hypothesis. In the same breeding population as this study, Ainley (2002a) reported that on average, the smallest clutches were laid by three-year olds. Given we have not recorded a single bird younger than three-years-old breeding in our study, almost all of these individuals were certainly first-time breeders. Additionally, Polito et al. (2010) documented that nearly 90% of one-egg clutches were laid by first-time breeders and that declining clutch size was correlated with later laying date in first-time breeder. While Spurr (1975), did not also found that clutches laid late in the season were more likely to be a single egg. Still, it is also possible that some of the poor reproductive performance observed in first-time breeders is due to a lack of behavioral experience that can only be achieved via an active breeding attempt (Ainley 2002a, Weladji et al. 2008, Polito et al. 2010). For example, improvements in foraging ability may allow individuals to better provision and thus, successfully fledge chicks, which could also lead to measures of improved reproductive performance (Limmer and Becker 2007, 2009). In fact, foraging performance in this population of Adélie penguins improves with age (Lescroël et al. in review). Thus, it is likely that a combination of age-related physiological and behavioral maturity explain the closely related patterns of improvement in early-life reproductive performance and within-individual maturation at observed at all three colonies.

While selective appearance was negative at all three colonies, it did not contribute as much at Cape Crozier (Figure 3.3), indicating that the poor performance of new recruits relative to the rest of the breeding population at Cape Crozier does not play as big a role in age-related change as it does at the smaller colonies. However, given the overall poor initial performance of 3-year-olds at Cape Crozier (Figure 3.4), it is possible that the reproductive performance of more mature new recruits simply could not be poorer than the initial performance of 3-year olds, thereby limiting the overall contributions of this process. In turn, the overall low performance of 3-year-olds at Cape Crozier also could account for the large contribution (~70%) and rapid pattern of improvement in within-individual performance. The poor performance of

3-year old individuals at the very large Cape Crozier colony may be explained by differences in colony density-dependent processes, which can directly influence performance as individuals adjust their behavior in response to resource limitation associated with increased population density (Both 1998, Rödel et al. 2004). While density dependent processes only operate when resources are limited, several studies suggest that this might be the case at the extremely large Cape Crozier colony. Since the onset of the project in 1996 the size of both the Cape Bird and Crozier colonies has tripled, but Cape Crozier is an order of magnitude larger than Bird (~300,000 to 80,000 breeding pairs; Lyver et al. 2014). Thus, the overall number of birds at Cape Crozier is much higher and therefore may have density effects on prey resources during the breeding season. Additionally foraging expenditure studies have documented that as the breeding season progresses breeding birds at Cape Crozier travel further from the colony and/or deeper in the water column (Ballance et al. 2009) and reduced food delivery to chicks at Cape Crozier results in smaller chicks than at the other two colonies (Whitehead et al. 2015). Taken together, these results indicate that density dependent factors influencing foraging behavior might be more pronounced at Cape Crozier. This seems especially plausible given foraging performance of Adélie penguins improves with age at Cape Crozier (Lescroël et al. in review), but not at the two smaller colonies. Penguins are central place foragers when they are breeding (Ford et al. 2015) so their maximum foraging range during this period is limited to the time and energy it takes to locate and catch prey and return to the colony to provision their chicks (Ballance et al. 2009). Because penguins essentially forage whenever they are at-sea (Ford et al. 2015), during the course of a breeding season, a large colony creates a “foraging halo” devoid of prey items that slowly expands throughout the season (Ashmole 1963, Birt et al. 1987, Elliott et al. 2009, Oppel et al. 2015), forcing individuals to forage further from the colony and/or deeper in the water column (Ballance et al. 2009, Lyver et al. 2011). If intraspecific competition for prey is higher later in the season at the biggest colony, then the additional incurred costs for poorly performing 3-years-olds relative to more mature age classes could be reflected in lower reproductive performance than observed at the smaller colonies. Thus, the difference in 3-year-old performance between colonies could be due to differences in colony density-dependent processes.

Comparisons between young and advanced breeders, and process contributions for advanced breeders should be interpreted cautiously as sample sizes in the advanced group were small and resulting estimates were imprecise. On-going research on this population also suggests that the lifespan of breeding Adélie penguins can reach 20 years, which exceeds the upper age limit for the data used in this analysis (Dugger, Ainley, Ballard, unpubl. data). Only ~10%-20% of all individuals in the population reach what we defined as the advanced life stages (Table 3.1), so the processes acting in the advanced age group only impacted a small portion of the breeding population at each colony. Still we did find signs of senescence at both capes Bird and Royds, which is in agreement with numerous other studies (Rattiste 2004, Nussey et al. 2006, Balbontín et al. 2007, McCleery et al. 2008, Aubry et al. 2009, Bouwhuis et al. 2009, Rebke et al. 2010, Lemaître et al. 2015, Froy et al. 2017). However, the continued improvement in reproductive performance in the advanced age group observed at Cape Crozier was unexpected.

Most studies that account for compositional changes at advanced ages find that individuals with higher reproductive performance live longer (Nussey et al. 2006, McCleery et al. 2008, Bouwhuis et al. 2009), but at Cape Crozier, the contributions from selective disappearance were negative, indicating the selective disappearance of previously high performing individuals. However, the continued improvement from within-individual maturation masked the selective disappearance of these high quality individuals. Froy et al. (2017) found a similar pattern in grey-headed albatrosses (*Thalassarche chrysostoma*) and suggested it is the result of this species' overall low reproductive investment. However, this seems unlikely in Adélie penguins, given we do not see similar patterns at the other two colonies. Importantly, at Cape Crozier we also see continued positive contributions in reproductive performance due to within-individual change, such that they mask the compositional changes producing the net increase in population performance, indicating a trade-off between reproduction and survival. This could be due to the influence of trade-offs inherent to different life history-strategies and the resulting differences in costs producing different patterns for different cohorts at the same age (Aubry et al. 2009, Bosman et al. 2013). For example, in lesser black-backed gulls (*Larus fuscus*) individuals that delayed their first breeding attempt, had advanced arrival dates throughout their breeding lifespan (Bosman et al. 2013). Indeed, previous work in this population has shown that the shapes of age-related reproductive performance patterns differ depending on the interaction between age at recruitment and breeding experience (Kappes et al. unpublished data). Thus, it's possible that the individual improvement we see at advanced ages at Cape Crozier are from individuals that recruited later in life and are still experiencing improvement in their foraging ability, translating into improving reproductive performance as they continue to age. However, on average the age at first reproduction at Crozier is lower than the two smaller colonies, indicating the possibility that individuals at Crozier employ a variety of alternative life history strategies. Another explanation, may be the predator hypothesis. Predation rates of leopard seals (*Hydrurga leptonyx*) on Adélie penguins have been estimated to be as high as 5% of the breeding population at Cape Crozier (Penney and Lowry 1967), making breeding a potentially hazardous undertaking (Ainley et al. 1983, Ainley 2002a), particularly at medium and larger sized colonies that attract leopard seals (Ainley et al. 2005a). Over their lifetime, high performing individuals at these colonies may have to cross through waiting seals 20-30 times each season, to trade off with waiting mates and provision their chick(s), while an individual that doesn't breed has no pressure to risk going through the seals and may only transit this dangerous zone 2-4 times per breeding season (Ainley et al. 2005a). In combination, predation may be removing a disproportionate number of high performing individuals and the high levels of intra-specific foraging competition documented at Cape Crozier (Ballance et al. 2009, Lescroël et al. 2009), may explain the selective disappearance of these individuals. Meanwhile, lower quality individuals who are not breeding may be able to avoid this risk and continue to improve their foraging capabilities, which may explain the pattern we observe at Cape Crozier in the advanced breeding group. Because Cape Bird is a medium sized colony, we would expect to see a similar pattern here, but given this colony is composed of several smaller sub-colonies, each separated by several kilometers, there may not be a high enough concentration of penguins to be attractive to hunting leopard seals. Indeed, we seldom observe leopard seals at this colony (or Cape Royds), which may help to explain why we don’t see a similar pattern in the advanced age group at this colony.

Like many of the other studies investigating age-related performance and aging in wild populations, our results stress the importance of long-term uninterrupted data sets with known-aged individuals. Accounting for the different processes that influence population-level changes is difficult to do without this type of data and can lead to spurious conclusions. Unlike most studies that focus on a single population, our study included multiple colonies and revealed different patterns in performance resulting from different processes. These results highlight the importance of not only comparing results between conspecifics but also between populations, which can lead to greater understanding of the range of behaviors, life history strategies and mechanisms that affect population dynamics with a species.

Acknowledgements

This work would not have been possible without the countless hours the following individuals spent re-sighting bands and following nests of known-aged birds during the past 20 years: C. Adams, J. Adams, S. Allen, L. Ballance, G. Barclay, Q. Barr-Glintborg, L. Blight, J. Blum, E. Burke, H. Carrad, M. Coleman, W. Cook, K. Drew, P. Dilks, L. Doel, I. Gaffney, C. Gjerdrum, D. Gremillet, D. Hardesty, S. Heath, M. Hester, S. Jennings, D. Jongsomjit, D. Hyrenbach, K. Lindquist, V. Marsaudon, M. Massaro, A. Matthews, C. McCreedy, V. Morandini, H. Nevins, R. Orben, V. Patil, R. Pech, A. Pollard, E. Porzig, C. Ribic, V. Ruopollo, B. Saenz, A. Schmidt, L.

Sheffield, L. Smith, I. Sutherland, Y. Suzuki, C. Thomson, P. Timoti, V. Toniolo, A. Varsani, S. Webb, D. Wilson, A. Whitehead, J. Whitehead, S. Winquist, S. Zador. We also want to thank the US Antarctic Program, through Raytheon and Antarctic Support Contractors, and Antarctica New Zealand for logistical support for the field work. Permits were provided under the Antarctic Conservation Act, National Science Foundation Office of Polar Programs (2006-010, 2011-002, 2017-005) and Landcare Research Animal Ethics Committee Permit (0509/01). Oregon State University's Institutional Animal Care and Use Committee approved all data collection protocols. This work was funded by National Science Foundation Grants OPP 9526865, 9814882, 0125608, 0440643, 0944411 and 154398 (to K.M.D., D.G.A., and G.B.) and New Zealand Ministry of Business, Innovation, and Employment Grant (C09527, C09X0510, C01X1001) and NZ's Ministry for Primary Industries (MPI17238-S01-LC), with addenda (to P.O'B.L., K.B. and P.W.). Discussions with L. Arnold and comments from R. Suryan greatly improved this manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This is Point Blue Conservation Science Contribution #XXX.

Table 3.1. Summary information of sample populations of Adélie penguins breeding at capes Bird, Crozier, and Royds used to decompose population-level age-related change in breeding success.

Colony	Number of unique individuals	Number of observations	Observed Ages (range)	Ages used in analyses	Alive at advanced (age)
Bird	1254	3979	3-19	3-17	11% (13)
Crozier	1584	5208	3-17	3-16	7% (13)
Royds	252	635	3-16	4-13	21% (9)

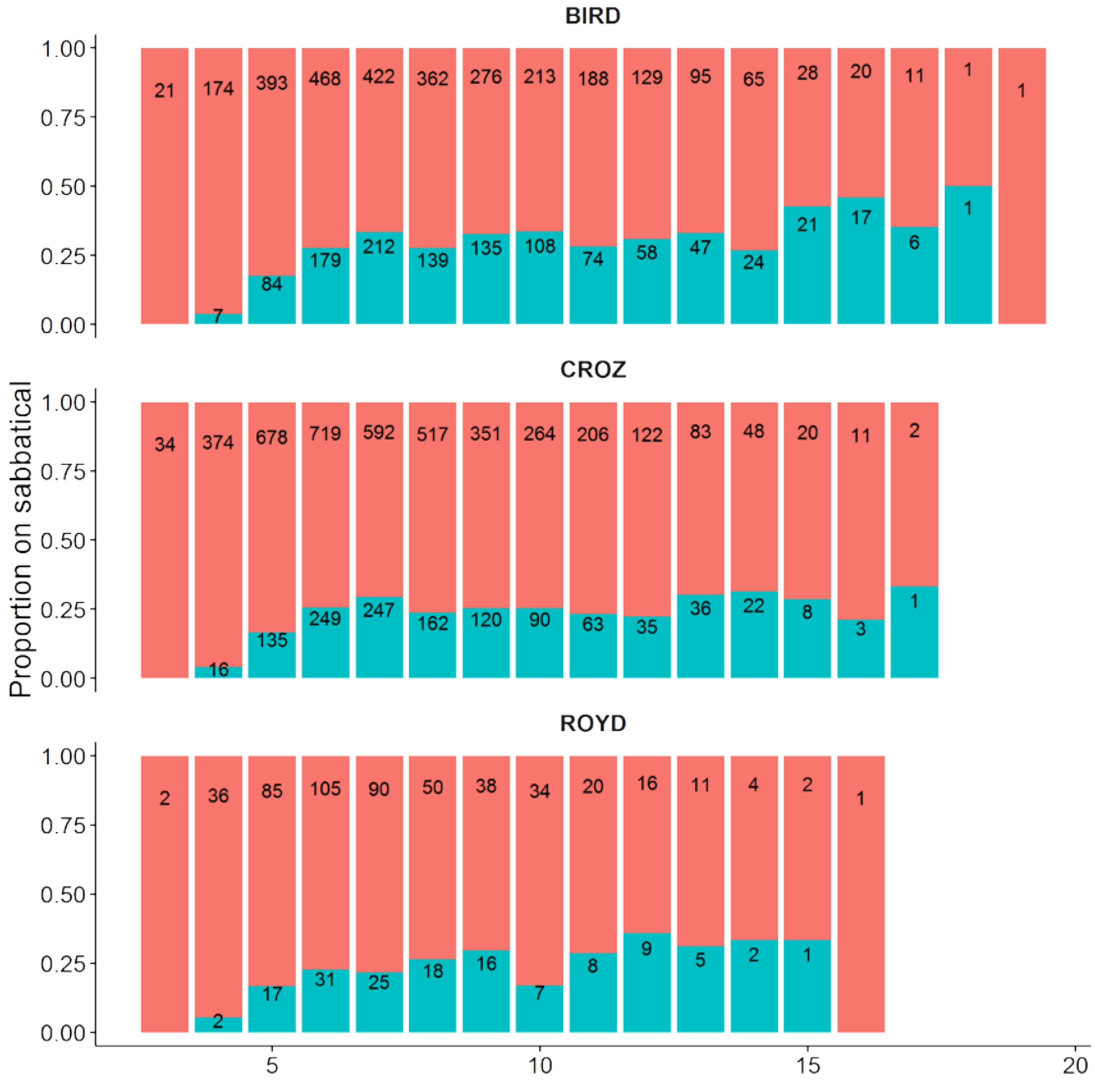


Figure 3.1. Proportions (numbers in bars represent counts of raw data) of uniquely banded known-aged birds engaged in breeding (pink shade) or sabbaticals (blue shade) for each age class observed at capes Bird, Crozier, and Royds, Ross Island, Antarctica. Age groups with fewer than 10 individuals were not used in subsequent analyses.

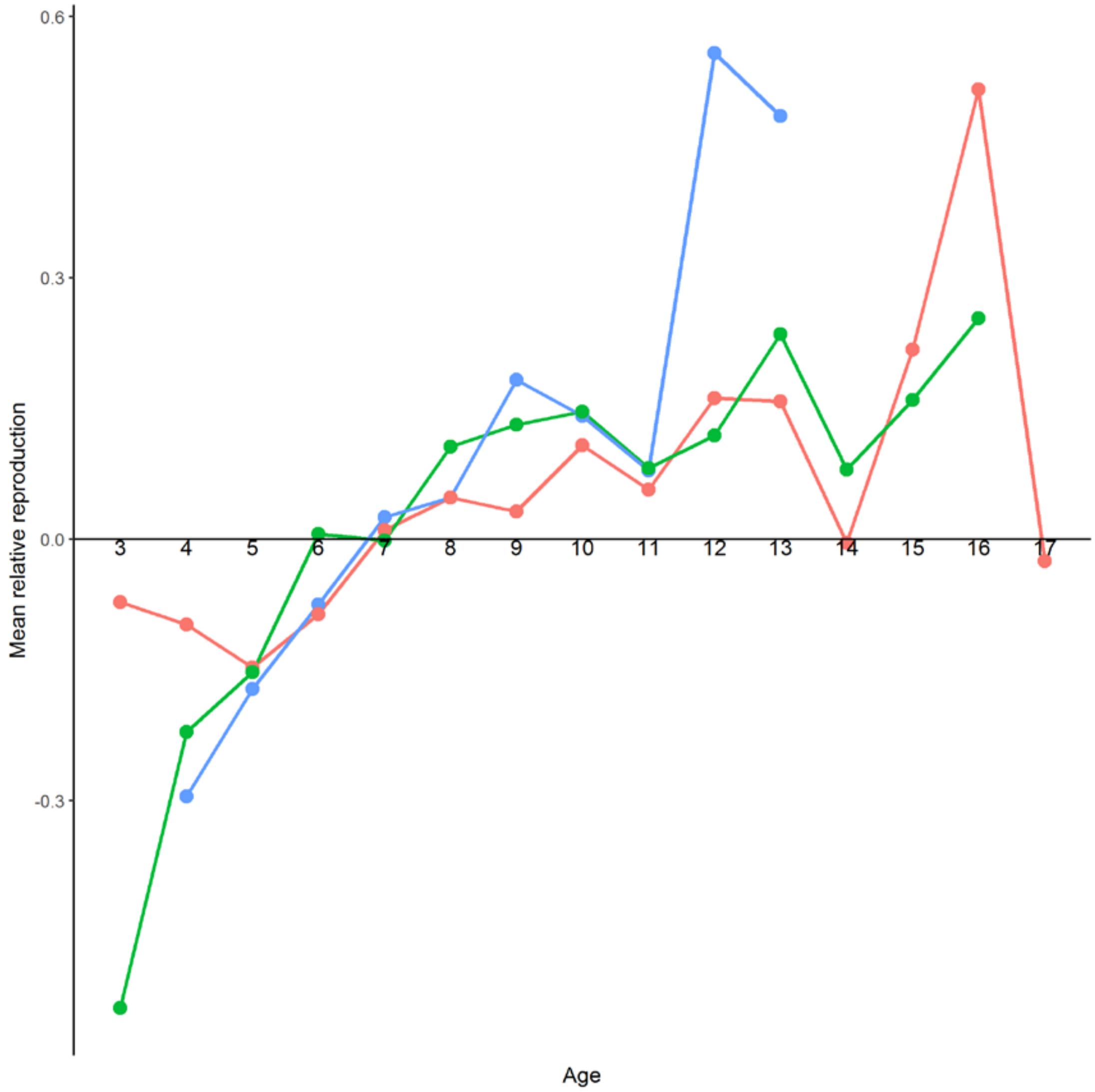


Figure 3.2. Age-specific residual reproductive performance of known-aged Adélie penguins breeding at Cape Bird (pink line and circles), Cape Crozier (green line and triangles), and Cape Royds (blue line and squares), Ross Island, Antarctica.

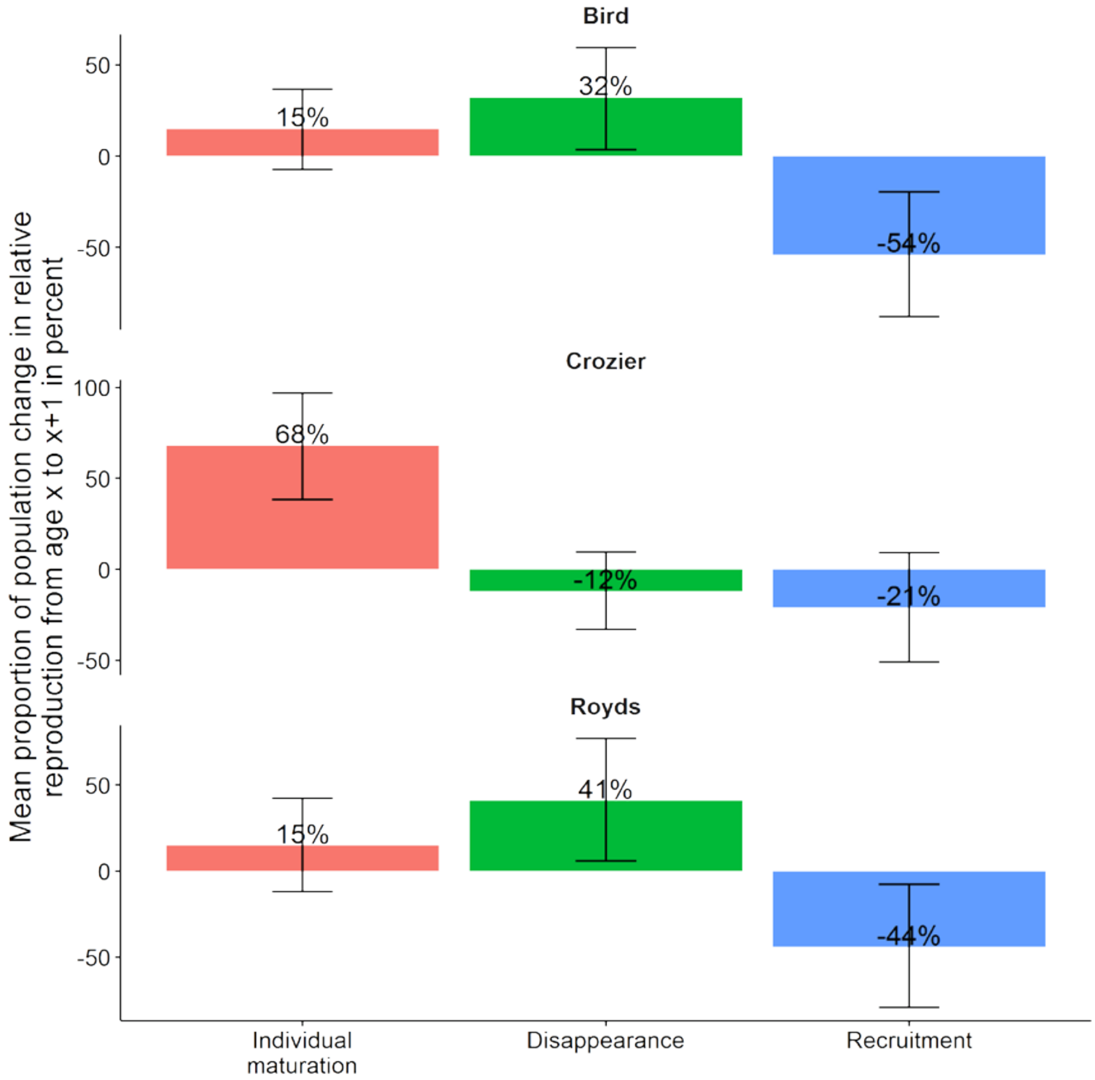


Figure 3.3. Decomposition of population change in relative reproduction from *x* to *x* + 1 into average within-individual maturation, selective disappearance, and selective appearance for all individuals in all ages in percent. The error bars represent 95% confidence intervals.

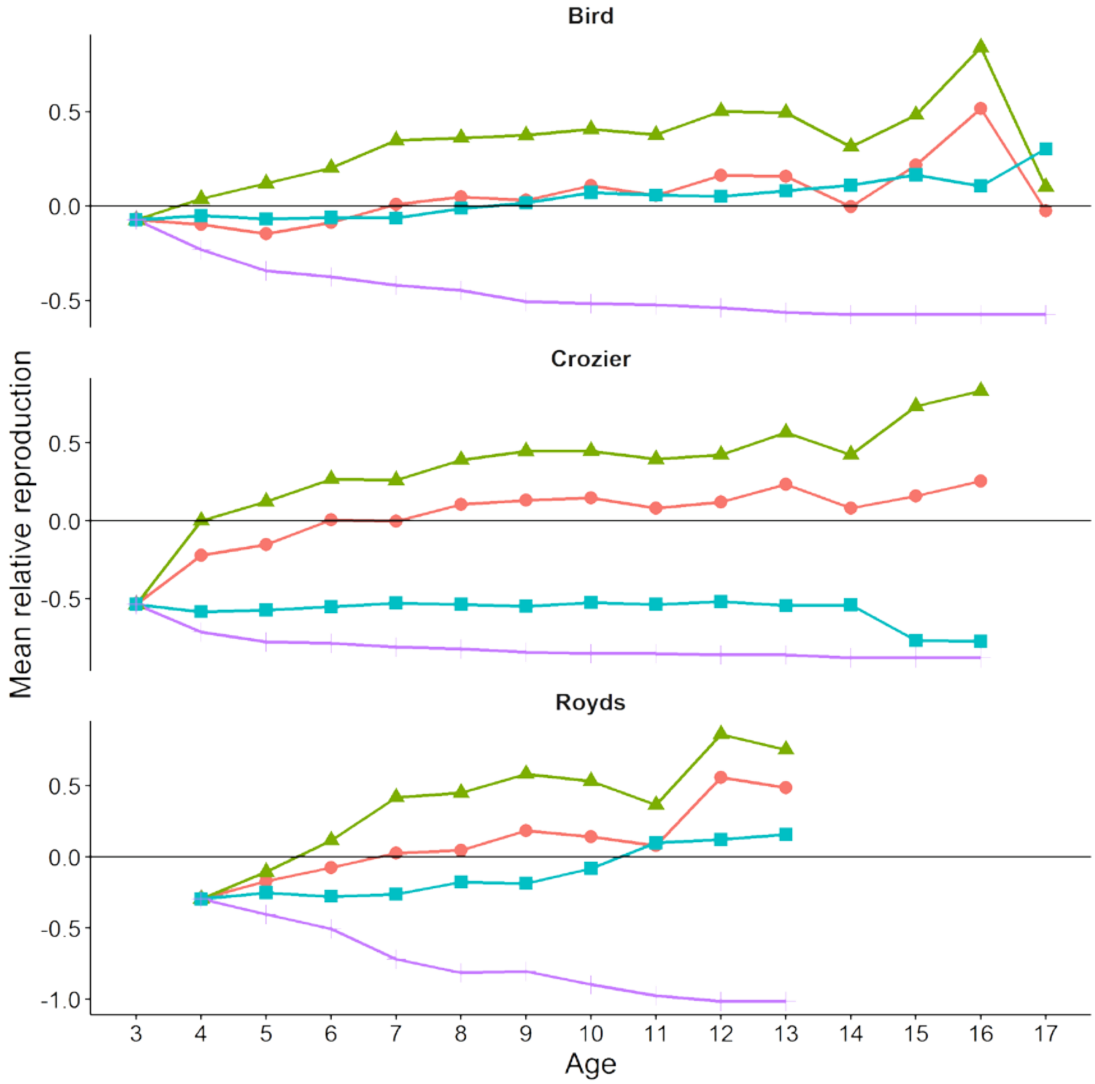


Figure 3.4. Age-specific changes in relative reproduction relative to the minimum age of recruitment due to individual- and population-level processes for Adélie penguins breeding at capes Bird, Crozier, and Royds, Ross Island, Antarctica. The pink circles and lines represent the cumulative population-level mean performance at each age; the green triangles and lines represent the age-specific pattern resulting from within-individual maturation; blue squares and lines represent the pattern resulting from changes due to selective disappearance; and the purple crosses and lines represent the pattern resulting from changes to do selective appearance, such that values at any age are the cumulative sum of average changes up to each age.

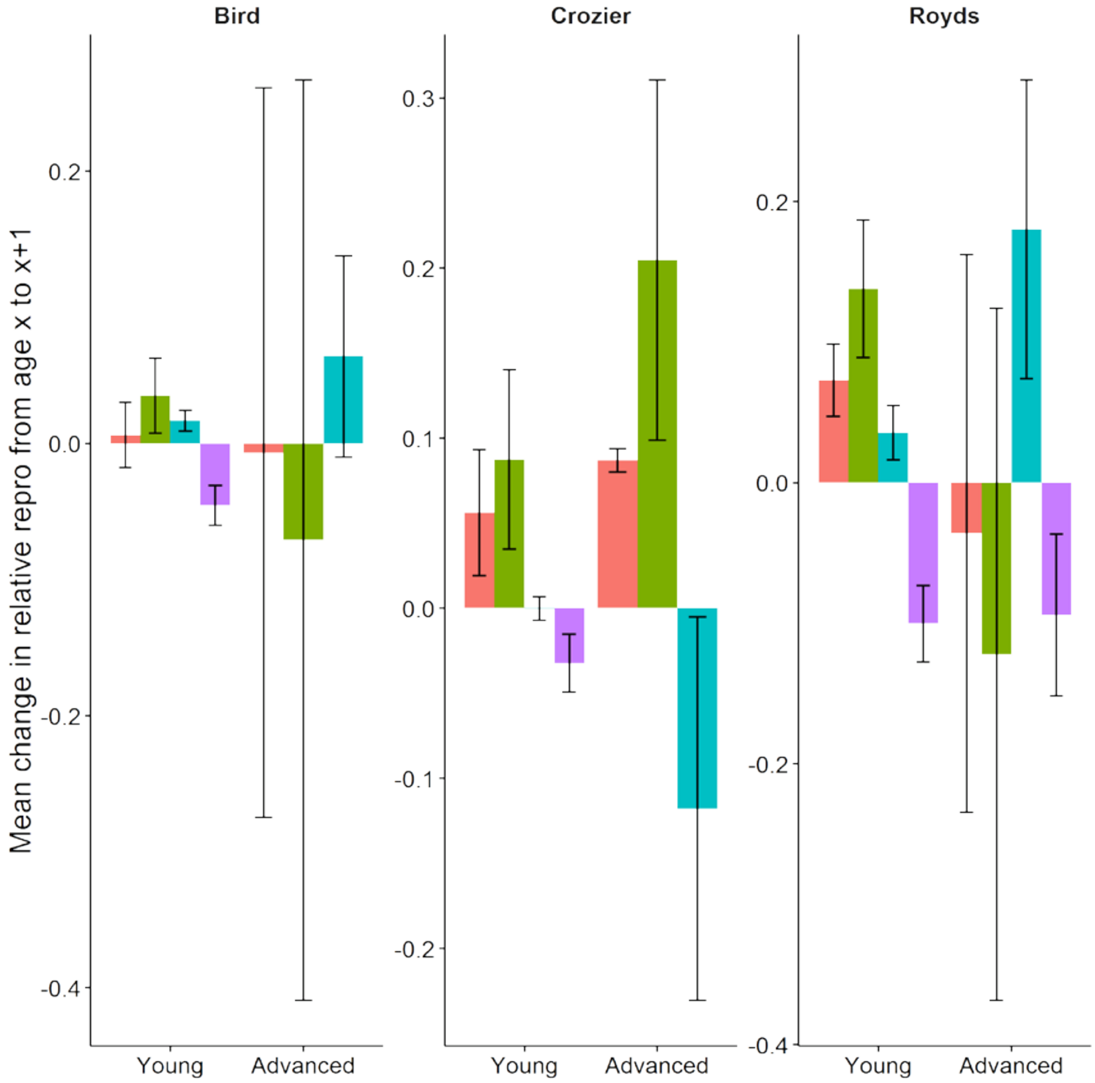


Figure 3.5. Change in relative reproduction for young age group (ages 3-13 capes Bird and Crozier; 3-9 Cape Royds) and advanced age group (ages > 13 at capes Bird and Crozier; > 9 at Cape Royds) at the population level (pink bars), and the contributions to this change due to average within-individual maturation (green bars); selective disappearance (blue bars), and selective appearance (purple bars). The error bars represent the standard error.

4 - NATAL CONDITIONS ALTER LIFE HISTORY STRATEGIES AND AGE-SPECIFIC REPRODUCTION BUT NOT LIFETIME REPRODUCTIVE PERFORMANCE IN A LONG-LIVED SEABIRD

Peter J. Kappes, Katie M. Dugger, Amélie Lescroël, David G. Ainley, Grant Ballard, Phil O’B. Lyver, Laurie Padman, Alexander D. Fraser, Kerry J. Barton, Robert A. Massom, Peter Wilson

Abstract

Poor natal environmental conditions have long been thought to impose limitations on development resulting in poorly performing individuals and is formally described by the “silver spoon” hypothesis. However, there is growing evidence that individuals can mitigate the effects of poor early-life conditions via adaptive behavioral, morphological or reproductive changes. According to the internal predictive adaptive (internal PAR) response hypothesis individuals that are expected to experience reduced performance later in life, should act to mitigate that loss in performance by breeding earlier. Here we take advantage of a “natural experiment” of two giant icebergs grounding off of Ross Island, Antarctica to investigate how natal conditions influenced age-related changes in life history responses and lifelong reproductive performance of a longitudinal data set of known-aged Adélie penguins. We show that for five years, two giant icebergs substantially altered sea ice conditions throughout the annual cycle, including preferred wintering habitat, sea ice concentrations on the foraging grounds near breeding colonies, and increased the extent of fast ice near breeding colonies. As a result, five cohorts of known-aged individuals experienced significantly altered early-life conditions from other cohorts. In accordance with predictions from the internal PAR, iceberg-affected cohorts entered the breeding population when they were younger, exhibited higher levels of breeding success, and had shorter lifespans than non-iceberg-affected cohorts. Non-iceberg-affected cohorts delayed reproduction, never achieved levels of breeding success documented for iceberg-affected cohorts, but lived longer than iceberg-affected cohorts. By the end of their lifespan non-iceberg-affected cohorts had minimally higher lifetime reproductive success, but in accordance with the internal PAR hypothesis individuals from iceberg-affected cohorts were nearly able to completely mitigate the fitness costs of poor natal conditions. Not only do these results support the internal PAR hypothesis, they also indicate that Adélie penguins have the ability to adapt to environmental changes. These results also provide evidence of demographic plasticity with minimal overall fitness costs for a k-selected species, which has important ramifications for understanding population dynamics of other long-lived species adapting to climate change.

Key words: Adélie penguin, age of first reproduction, age-specific reproduction, breeding success, cohort effects, life history strategies, lifetime reproductive performance, longevity, mitigation, natal environment, *Pygoscelis adeliae*, reproductive performance

Introduction

Environmental conditions experienced early in life can influence population dynamics and the evolution of life history traits (Sæther 1997, Lindström 1999, Beckerman et al. 2002, Lindström and Kokko 2002). This influence is driven by the resulting variation in the lifetime performance of individuals adopting alternative life history strategies and among-cohort variation in fitness-related traits (i.e., "cohort effects"; Sæther 1997, Lindström 1999, Gaillard et al. 2000, Gaillard et al. 2003, Monaghan et al. 2008). Numerous empirical studies have documented the importance of early-life environmental conditions on population-level fitness traits of adult phenotypes, including individual growth (Madsen and Shine 2000, Metcalfe and Monaghan 2001, Jensen et al. 2006, Douhard et al. 2013), age at first reproduction (Brommer et al. 1998, Millon et al. 2010), reproductive performance (Brommer et al. 1998, Reid et al. 2003, Van de Pol et al. 2006, Millon et al. 2011, Douhard et al. 2016), and survival (Albon et al. 1987, Rose et al. 1998, Forchhammer et al. 2001, Gaillard et al. 2003, Descamps et al. 2008, Hastings et al. 2011). However, we still know relatively little about how individuals respond to long-term changes induced by environmental conditions in early life.

The “silver spoon” hypothesis (Grafen 1988, Monaghan 2008), was developed to explain the effects of environmental conditions on lifetime performance. This hypothesis posits that adverse early environmental conditions can impose severe constraints on individual development resulting in poorly performing individuals relative to those raised during more favorable conditions. Despite numerous studies supporting this hypothesis (see above) it has also been hypothesized that individuals might be able to mitigate the impacts of poor early-life conditions via various behavioral, morphological, and/or reproductive adaptations (Bateson et al. 2004, Nettle et al. 2013). For example, the internal predictive adaptive response hypothesis (internal PAR) was proposed by Nettle et al. (2013) to explain accelerated reproductive timing observed in humans who experienced poor early-life conditions. Generally the internal PAR hypothesis posits that individuals born under poor conditions should start to reproduce earlier if they are likely to experience reduced performance later in life and/or faster rates of senescence compared to individuals raised under better conditions. Differing from the external PAR, in which individuals adjust their physiology in anticipation of the conditions they may encounter in their adult environment (Gluckman et al. 2005), internal PAR suggests that based on their early environment, individuals “predict” the state of their future adult condition, not the future environment. Several recent experimental studies in wildlife have documented individuals mitigating poor early life conditions (Auer 2010, Dantzer et al. 2013) and Douhard et al. (2016) found results consistent with internal PAR in a wild population of Svalbard reindeer (*Rangifer tarandus platyrhynchus*). Beyond this work, however, there is little other data supporting this hypothesis or work investigating the long-term consequences of early life environmental conditions in free-ranging wildlife populations. This is somewhat surprising as this hypothesis seems especially relevant to long-lived, iteroparous species that will naturally encounter variable environmental conditions during the course of their lifetime, making it unlikely that early life environmental conditions will provide a reliable indication of environmental conditions later in life (Kuzawa 2005, Wells 2006).

Clearly, studies investigating long-term consequences of cohort effects and evidence corroborating internal PAR require longitudinal data sets of long-lived species inhabiting systems with a relevant environmental regime that exhibits large amounts of variation among cohorts. Systems experiencing large-scale perturbations in weather systems seem particularly well-suited to explore these types of questions (Gaillard et al. 1997, Forchhammer et al. 2001), but relatively few data sets like this exist and even fewer have explored the role variable natal conditions plays on reproductive performance during adulthood.

In this paper, we use a 19 year data set (1994-2013) of known-aged, uniquely marked Adélie penguins *(Pygoscelis adeliae*) breeding in the southwestern Ross Sea (see Figure 4.1), to investigate the long-lasting effects natal conditions have on lifelong reproductive performance. A sea-ice obligate, Adélie penguins are a relatively long-lived (c. 20 years; Ainley 2002a) species that exhibits delayed breeding, with age at first reproduction averaging between 5-6 years of age in this meta-population (Ainley and Demaster 1980, Ainley 2002a; Kappes et al. Chapter 2). In most years, Adélie penguins will lay 2 eggs, but most young or inexperienced breeders are only able to successfully raise 1 chick (Ainley and Schlatte 1972).

This species nests in colonies that are free from snow and/or ice (Ainley et al. 1983) and offer access to nearby sea ice (Ainley et al. 1998), a crucial and highly dynamic component of the Antarctic ecosystem (Massom and Stammerjohn 2010) with important, often contrasting effects on Adélie penguin vital rates (Croxall et al. 2002, Forcada and Trathan 2009, Ainley et al. 2010b, Lynch et al. 2012, Hinke et al. 2014). For example, reproductive success is negatively impacted by increased summer ice concentrations near breeding colonies (Ainley 2002a, Emmerson and Southwell 2008, Dugger et al. 2014), and very high or low extremes in winter reduces survival (Ballerini et al. 2009a). Additionally, sea ice can disrupt or block polynyas, which can have significant negative impacts on reproductive performance of breeding penguins in the region (Ballard et al. 2010a, Lescroël et al. 2014). Because sea ice variability directly influences the entire Ross Sea food web (Massom and Stammerjohn 2010) and acts an important habitat, refuge, and barrier to penguins (Tynan et al. 2010), sea ice conditions can directly impact penguin foraging efficiency (Watanuki et al. 2002, Emmerson and Southwell 2008, Ballard et al. 2010a, Lescroël et al. 2010, Lescroël et al. 2014) and diet composition (Ainley et al. 2003). During periods of high SIC around Ross Island, penguins had reduced access to prey resulting in longer foraging trips and less food delivered to their chicks (Ballard et al. 2010a). Their diet also shifted from subadult silverfish (*Pleuragramma antarcticum*) to lower caloric value crystal krill (*Euphausia crystallorophias*) under high SIC conditions (Ainley et al. 2003). In turn, the combination of these factors influences chick growth and development (Whitehead et al. 2015) and changes in chick diets has been associated with post-fledging survival and recruitment (Ainley et al. 2018).

Furthermore, during the course of our study two giant icebergs grounded on Ross Island from 2001-2005, forming a physical barrier ~1.5 latitude degrees long (170 km in length; see Figure 4.1). These icebergs physically separated the eastern most colony from the western colonies and along with winter wind conditions, dramatically altered local ice conditions at all of the colonies (Arrigo et al. 2002, Robinson and Williams 2012). The presence of the icebergs trapped sea ice in McMurdo Sound preventing normal development of the McMurdo Sound Polynya. During some years (3 of 5 when the iceberg was present), this forced penguins nesting at the two western colonies to forage through a limited number of cracks in the sea ice or walk upwards 50-80 km to reach open water. Additionally, the icebergs physically occupied the entire western marginal ice zone of the Ross Sea Polynya, arguably the most ecologically important feature of the southern Ross Sea (Arrigo et al. 2002, Ballard et al. 2012), which reduced the availability of important foraging habitat (Ballard et al. 2010a, Lescroël et al. 2014) for one of the largest Adélie penguin breeding colonies in the world (Lyver et al. 2014).

This “natural experiment” provided us with the unique opportunity to investigate the impacts of a severe perturbation in the natal environmental conditions experienced by 5 cohorts of Adélie penguin chicks and compare the long-term consequences in lifetime reproductive performance with cohorts raised under more typical conditions. We were particularly interested in testing alternate predictions from the internal PAR and silver spoon hypotheses as Kappes et al. (Chapter 2) found evidence that some individuals adopt life history strategies that would allow them to overcome poor conditions early in life by recruiting early and having high levels of reproductive success, which offset a shorter life and produced fitness outcomes equivalent to individuals with delayed maturation and lived longer. We compared environmental sea ice conditions from iceberg-affected and non-iceberg-affected years to identify the ice conditions that differed during years when the icebergs were present compared to long-term averages during the rest of the study. We then tested multiple alternative predictions made by the internal PAR and silver spoon hypotheses regarding demographic plasticity and life time fitness of individuals from cohorts experiencing dramatically different natal environmental conditions (see Table 4.1 for specific predictions).

Methods

Field Site and Biological Variables

We conducted fieldwork at Cape Royds (77° 34’ S, 166°11’ E), Cape Bird (77°13’ S, 166° 28’ E) and Cape Crozier (77° 27’S, 169° 23’ E) on Ross Island, Antarctica. These colonies vary in size by multiple orders of magnitude and during the course of study the number of breeding pairs at each colony ranged between: Cape Royds 1300 to 3900; Cape Bird 23000 to 69000; Cape Crozier 67000 to 282000 (Lyver et al. 2014). The data we used for this analysis were collected as part of an on-going long-term study on Adélie penguin demography at the three different sized breeding colonies. Starting in the austral summer (mid-November to late January) of 1994-1995 (hereafter season 1994) we attached uniquely numbered stainless steel bands on chicks prior to fledging and have been band searching each breeding season to document survival and reproductive performance of known-aged banded birds through the present. Because we know the age of all banded birds, we were able to determine the age of first reproduction/recruitment (AFR) for individuals entering the breeding population. Estimates of individual reproductive success were based on nest checks of banded birds conducted every 2 to 7 days throughout the breeding season, until the nest failed or unbanded chick(s) formed crèches while both parents foraged at sea for their chicks and could no longer be easily monitored without causing high levels of disturbance (Ainley and Schlatte 1972, Davis 1982). Nest monitoring histories were categorized as “successful” for a banded parent if $\geq$1 chick crèched each year.

Because we were interested in the long-lasting effects of natal conditions, we truncated our dataset to remove all records of individuals that were still alive at the end of the study period (i.e., all records removed of any banded bird observed in the 2013 season). While band detection rates were not 100% each year, and this ongoing study has confirmed that Adélie penguins live and breed into their 20’s (DGA,GB, KMD unpubl. data), only 5% of birds in our data set had an interruption of a single season or more in their re-sighting history before being subsequently re-sighted (see supplementary material Table B.1). Because movement rates (i.e., movement of banded birds between colonies) of individuals that have entered the breeding population is very low (Dugger et al. 2010), we assumed that any interruptions in an individual’s re-sighting history of more than 1 season indicated a mortality event or that they had permanently emigrated from the breeding population. Thus, our data set only included records of the complete lifespan for all individuals, which allowed us to use the maximum age of every individual as a measure of their longevity.

We standardized age for each individual by subtracting the mean age of the banded population and dividing by the standard deviation, so that they were not biased by earlier cohorts having the opportunity to be alive longer simply because of when they were banded (Table 4.2). Because we were also interested in late-life performance, we calculated the number of years before death (YBD) for each individual, each year, such that 1 denoted the final year of life before an individual disappeared, as an alternative measure to age. This time-varying covariate allowed us to identify and compare reproductive performance during early and late life stages when ages *sensu stricto* differed as a result of alternative life history strategies. We also calculated the reproductive lifespan of each individual as longevity minus AFR, because not all penguins from the same cohort recruit at the same age.

Sea Ice Variables

We compared several measures of sea ice between iceberg-affected and non-iceberg-affected years from important periods of the Adélie penguin annual cycle to confirm if there were differences in natal conditions between cohorts that might have consequences on subsequent life history strategies and lifelong reproductive performance (Table 4.2 for detailed explanation of sea ice variables). Because maternal stress, particularly elevated glucocorticoids, during egg production has been documented to reduce growth, condition, and body size in a variety of taxa (reviewed in Breuner 2008), we investigated two sea ice metrics of winter habitat, in case winter conditions may have resulted in maternal stress effects for iceberg-affected cohorts. We defined the winter period as extending from October through November, when penguins are returning to their colonies. Additionally, we included a yearly average of the Ross Sea gyre velocity in case differences in velocity impacted the breeding condition of adults migrating back to colonies. We also investigated sea ice concentration (SIC) in the respective foraging areas of each of the colonies during the breeding season and the distance to the edge of fast ice (FI), which have been documented to impact foraging efficiency (Watanuki et al. 2002, Emmerson and Southwell 2008, Ballard et al. 2010a, Lescroël et al. 2010, Lescroël et al. 2014) and chick growth and development (Whitehead et al. 2015). These included ice conditions during the breeding season covering the entire chick rearing phase (i.e., December – January). During this period of time penguins are engaged in breeding activities and are central place foragers with a maximum foraging distance of 250km. We included a parameter for the nearest distance to the edge of fast ice (here after referred to as the fast ice), for each colony. In years that the ice bergs were present we know that leads in the fast ice were present and likely played an important role in providing access to foraging habitat, particularly at the Cape Royds colony and likely to a lesser extent at Cape Bird, but their role is unknown. We determined the spatial extent of fast ice at a resolution of approximately 1 km using 15-day Moderate Resolution Imaging Spectroradiometer (MODIS) composite imagery, following the methodology in Fraser et al. (2010, 2012). We then measured the distance from each colony to edge of the fast ice, to determine the distance to nearest open water. Estimates of SIC for wintering habitat and foraging areas were generated following the methodology and bounding described in Ballard et al. (2010a). We also generated estimates of sea ice persistence for each colony following the methodology described in Stammerjohn et al. (2008a).

Statistical Analysis

Our analysis focused on comparing abiotic and biotic factors between iceberg-affected (2001 – 2005) and non-iceberg-affected (1994 – 2001; 2006 – 2013) cohorts. Several of the sea ice related variables we investigated could be computed at several different temporal and/or spatial scales. For example, we estimated fast ice extent during the months of October, November, and December at each colony, but also combined estimates into a seasonal estimate, as well. Regardless of the scale or extent, we performed comparisons between iceberg-affected and non-iceberg-affected seasons for each variable. Because our data violated assumptions of normality (all $p \leq$

0.0001) we used the non-parametric Mann-Whitney U test with Holm adjusted significance levels to minimize Type II errors (Rice 1989) to assess if there were differences between abiotic and biotic factors of interest. Due to the number of comparisons, some tests that were initially identified as significantly different, were not significant after Holm adjustments. This was particularly pronounced for tests for Cape Royds, where small sample sizes between iceberg-affected and non-iceberg-affected cohorts (Figure B.1) reduced our power to detect differences. For brevity and to aid with interpretation, unless otherwise noted, we present results for all colonies pooled as these relationships generally were the same even for monthly comparisons at individual colonies (Table 4.3). Figures illustrating colony level differences are available in the supplemental materials (Appendix B). All data are expressed as medians ± SE unless otherwise indicated. All analyses were performed using R v. 3.4.1 (R development Core Team 2018).

Results

Differences in ice environment

We documented pronounced differences in sea ice conditions between seasons with and without icebergs present and these differences encompassed the entire annual cycle (see Figure 4.2 for trends in different sea ice metrics). The median area of preferred winter sea ice habitat, SIC between 75% - 90%, was higher (225,965 ± 6616 km^2) in iceberg-affected years than non-iceberg-affected years (168,205 ± 6656 km^2; W = 147239; $p < 0.001$; Table 4.3), but the median percent SIC was lower (84 ± 0.5% vs 88 ± 0.3%; W = 2643; $p < 0.01$; Table 4.3). Thus, in iceberg years, there was a larger extent of less concentrated, but still suitable pack ice habitat available in the Ross Sea. Annual estimates of the median velocity of the Ross Sea gyre indicated slower velocities during iceberg-affected years (-0.046 ± 0.0003) than non-iceberg years-affected (-0.051 ± 0.0004; W = 59535; $p < 0.001$; Table 4.3).

We also documented differences in sea ice conditions during the breeding season. The median extent of FI was higher (2.0 ± 1.7 km) in iceberg-affected years than non-iceberg-affected years (1.0 ± 0.4 km; W = 19331; $p < 0.001$; Table 4.3) and median SIC was higher in iceberg-affected years, as well (59.8 ± 2.2% vs. 32.8 ± 1.2%; W = 10830; $p <0.001$; Table 4.3). The median PERS of sea ice during the course of the season also differed significantly between iceberg-affected (100 ± 0.03% persistence) years and non-iceberg-affected years (75 ± 0.01%; W = 75190; $p < 0.001$), but was driven primarily by Cape Crozier, as PERS did not differ at either of the two smaller colonies (both $p > 0.1$).

Early life performance

Individuals born in cohorts when icebergs were present recruited to the breeding population earlier than cohorts born without icebergs (median AFR 5 years for iceberg cohorts versus 6 years; W=296570; p-value < 0.001; Figure 4.3). However, this relationship is driven by Cape Bird and Cape Royds. At the largest colony, Cape Crozier, AFR did not differ between cohorts (AFR = 3; $p > 0.1$). On average, over the course of their reproductive lifespan, individuals from iceberg-affected cohorts also had a higher mean breeding success (51 ± 1%) than individuals from non-iceberg-affected cohorts (43 ± 1%; W = 4124800; $p < 0.001$), particularly early in their reproductive lifespan (Figure 4.4).

Lifetime and late-life performance

While breeding success was initially very high for iceberg-affected cohorts, visual inspection of breeding success over the course of their reproductive lifespan (RLS) indicates that success generally declined thereafter. Meanwhile, cohorts born when icebergs were absent showed a classic quadratic shape in breeding success, such that they exhibited fairly consistent and rapid improvement early in their RLS, reaching peak performance a little after the middle of their RLS, before exhibiting declines late in life. However, even at peak performance, the average breeding success for non-iceberg-affected cohorts only reached the lowest average levels recorded for iceberg-affected cohorts, never approaching the initial high levels of success documented for iceberg-affected cohorts. The rates of senescent decline appeared similar between the two cohort types, but while senescence didn’t occur until three years before death in non-iceberg-affected cohorts, it started immediately after the initial breeding attempt in the iceberg-affected cohorts. A shorter median RLS of 2 years, compared to 3 years for non-iceberg-affected cohorts (W = 401720; p-value = 0.03), reflected in a statistically significant difference in median lifetime reproductive success (LRS), such that iceberg-affected cohorts fledged fewer chicks (1.71 ± 0.7) than non-iceberg-affected cohorts (1.74 ± 06; W = 476620, p-value < 0.001; Figure 4.5). Similar to breeding success, there were differences in LRS between cohorts that were driven primarily by individuals with a younger AFR fledging more chicks than individuals that delayed breeding. This pattern did not hold for the non-iceberg-affected cohorts, where LRS followed a quadratic shape, with individuals that delayed breeding until they were between 7 to 9 years old, fledging the most chicks over the course of their lifetime. Overall, the iceberg-affected cohorts did not live as long (median: 7 years ± 0.1) as the non-iceberg-affected cohorts (median: 8 years ± 0.1; $W = 316700$, $p < 0.001$), but had higher LRS compared to non-iceberg-affected cohorts that initiated breeding at the same age (Figure 4.6).

Discussion

We found that early-life environmental conditions influenced a variety of Adélie penguin life history traits with effects on both early- and late-life reproductive performance that differed between cohorts born under different environmental conditions. Cohorts born when giant icebergs dramatically altered the sea ice regimes and ecology of the Southwestern Ross Sea recruited earlier to the breeding population and had higher average levels of reproductive success than cohorts born under “normal” environmental conditions throughout their entire lifespan. However, of the individuals that met the criteria of having “died”, iceberg-affected cohorts had significantly shorter lifespans and experienced immediate declines in reproductive success that also lasted throughout their life. The rate of decline in reproductive performance matched the rate of senescence documented for late-life performance in non-iceberg-affected cohorts. In combination, these alternate life history strategies allowed iceberg-affected cohorts to nearly entirely mitigate potential fitness costs stemming from poor early life environmental conditions, as lifetime reproductive success differed only slightly between cohorts experiencing different natal conditions. In combination, these results are consistent with the internal predictive adaptive response (internal PAR) hypothesis and not the silver spoon hypothesis.

A number of studies have documented permanently reduced reproductive performance for individuals born under poor environmental conditions, regardless of the conditions they encounter as adults (Van de Pol et al. 2006, Descamps et al. 2008, Douhard et al. 2014, Lea et al. 2015), supporting the “silver spoon” hypothesis. However, several recent studies indicate that these effects are not universal, and that individuals can potentially mitigate poor early-life conditions. Auer (2010) demonstrated that juvenile female guppies (*Poecilia reticulata*) accelerated their growth rate as adults, after their diet was experimentally reduced when they were juveniles, and had similar reproductive success as individuals that experienced no dietary restrictions. Meanwhile, despite entering the breeding population and breeding throughout their early reproductive life at lower masses, female Svalbard deer born under adverse conditions had the same annual reproductive success as females born under better conditions, and lifetime fitness was similar, as well (Douhard et al. 2016). In agreement with these studies, we also found that Adélie penguins born under poor environmental conditions were able to mitigate these conditions, but unlike Douhard et al. (2016) these cohorts actually had higher reproductive performance compared to individuals in cohorts that were born under better conditions. More importantly, we also documented that these cohorts appeared to alter their reproductive strategies to offset poor natal conditions, suggesting a possible adaptive mechanism for long-lived species to deal with anthropogenic-induced changes in environmental conditions. If this is true for other long-lived, iteroparous species, this could have important ramifications for population dynamics.

Because their performance generally declined at a similar rate throughout the rest of their reproductive lifespan, it is difficult to determine if there were late-life consequences. Although, the rate of the decline did not change as they aged, indicating that “late-life” declines either began immediately after the initial breeding attempt or that late-life effects were not observed in reproductive performance. Of the individuals that met our criteria for having “died”, these cohorts did suffer shorter overall longevity than cohorts born under normal conditions, so it is possible that late-life fitness effects were expressed via mortality and not reproduction. Interestingly, individuals in these cohorts outperformed individuals of non-iceberg-affected cohorts, throughout their entire life span, despite a consistent decline in breeding success and early mortality. These fitness consequences due to early-life conditions provide a potential interesting link to the ongoing growth that we have observed in this meta-population over the past 15 years (LaRue et al. 2013, Lyver et al. 2014), as offspring produced early in life contribute more to fitness than those produced late in life (Brommer et al. 2002).

Unlike the aforementioned studies supporting the silver spoon hypothesis (Grafen 1988, Monaghan 2008) the results of our study are more in line with the internal PAR hypothesis (Nettle et al. 2013). One of the predictions of this hypothesis is that individuals experiencing poor natal conditions will speed up their physiological development and/or enter the breeding population sooner than individuals born under better conditions (Nettle et al. 2013). Sloboda et al. (2009) were able to induce early onset of puberty of offspring of Wistar rats (*Rattus norvegicus domesticus*) by experimentally restricting maternal caloric intake during gestation. Similar to their study and in accordance with predictions from the internal PAR hypothesis, iceberg-affected cohorts recruited to the reproductive population earlier than non-iceberg-affected cohorts. While we did not directly measure caloric intake in this study, foraging trips of parents were longer when the icebergs were present and there was a threshold at SIC > 15% after which forage trip duration increased, indicating the foraging was difficult under these conditions (Ballard et al. 2010a). Furthermore, chicks received over 2 kg less food per parent in iceberg-affected years than in non-iceberg-affected years and iceberg cohorts fledged nearly 800 g lighter than non-iceberg-affected cohorts. Interesting, parents feeding chicks during the iceberg-affected years also lost *c*. 2.5% more of their initial body mass than parents in non-iceberg-affected years, further indicating that both parents and chicks were likely experiencing significant caloric restrictions when the icebergs were present (Ballard et al. 2010a). Given that SIC was higher, fast ice extended further, and icebergs prevented the formation of the McMurdo polynya, altered primary productivity, and reduced assess to foraging habitat (Arrigo et al. 2002, Ballard et al. 2010a, Lescroël et al. 2014) it is extremely likely that the lighter chick weights documented in these cohorts (Ballard et al. 2010a, Dugger et al. 2014) is indicative of nutritional shortages these chicks experienced during their early development. Interestingly, Ainley et al. (2018) have found that fledging mass has declined as the Cape Crozier colony has grown, and suggest that this is due to resource competition. If true, chicks here may already be stressed early and recruit earlier than at the other colonies, which may explain why we did not detect a difference in AFR at this colony.

Contrary to the silver spoon hypothesis, individuals in the iceberg-affected cohorts, on average, had higher breeding success than their non-iceberg-affected counterparts (Figure 4.5). It is only when considering lifetime reproductive success that we documented cohorts born in good conditions out-performing the iceberg-affected cohorts. However, while statistically significant, the difference between producing 1.71 and 1.74 offspring is not likely to be biologically important.

Long-lasting effects of natal conditions are expected to affect the expression of traits in adulthood, particularly ageing or senescence (Nussey et al. 2007, Monaghan 2008). While we did document a much earlier initiation of senescence in reproductive performance for iceberg-affected cohorts, the rates of decline were similar to the senescent rate for non-iceberg-affected cohorts much later in life. Still, this could be an indication that despite attempting to mitigate early life conditions by speeding up recruitment, these individuals suffer immediate senescent declines and adopt an “all-in” approach to reproduction, such that they invest heavily in each reproductive opportunity for as long as they can. Meanwhile, individuals from normal natal conditions can adopt a more pragmatic strategy that balances early- and late-life trade-offs in performance.

In conclusion, our results showed that individuals experiencing poor natal environmental conditions bred earlier and experienced elevated reproductive success as compared to individuals born under good conditions. These results support the internal PAR hypothesis, suggesting that which individuals can mitigate the effects of poor conditions on reproductive output. Our study also highlights the importance of taking environmental conditions into account when investigating ageing and senescence, and provide a potential explanation for how poor environmental conditions may induce changes to life history strategies resulting in unexpected changes in population growth.

Acknowledgements

Funding for this work was provided by National Science Foundation Grants OPP 9526865, 9814882, 0125608, 0440643, 0944411 and 154398 (to K.M.D., D.G.A., and G.B.) and ANT-1443677 and OCE 1357522 (to L.P.) and NASA NNX17AG63G (to L.P.). New Zealand's Ministry of Business, Innovation, and Employment Grant (C09527, C09X0510, C01X1001) and New Zealand's Ministry for Primary Industries (MPI17238-S01-LC), with addenda (to P.O'B.L., K.B. and P.W.), the Australian Government's Cooperative Research Centre (CRC) through the Antarctic Climate & Ecosystems CRC (for A.F. and R.M.) and contributes to ACE CRC Project R1.3; and the Australian Antarctic Division (for R.M.) and contributes to Australian Antarctic Science Project 4166. We thank the many people who collected field data for this project over the past 20 years. Logistical support for the fieldwork was provided by the US Antarctic Program, through Antarctic Support Contractors, and Antarctica New Zealand. Permits were provided under the Antarctic Conservation Act, National Science Foundation Office of Polar Programs (2006-010, 2011-002, 2017-005) and Landcare Research Animal Ethics Committee Permit (0509/01). Data collection protocols were approved by Oregon State University's Institutional Animal Care and Use Committee (ACUP #3049, 3672, 4130). This is Point Blue Conservation Science Contribution xxx. This manuscript benefited tremendously from discussion and comments from L. Arnold. Any use of trade, firm,

or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Table 4.1. Comparison of predictions made by the internal predictive adaptive response (internal PAR) and the silver spoon hypotheses for early- and late-life reproductive performance of cohorts experiencing poor natal environmental conditions.

	Internal PAR (iceberg-affected cohorts)	Silver Spoon (non-iceberg-affected cohorts)
Age at first reproduction (AFR)	Earlier/Younger	Later/Older
Reproductive lifespan (RLS)	Shorter	Longer
Longevity (LONG)	Shorter lifespan	Longer lifespan
Lifetime reproductive success (LRS)	Equal to non-iceberg-affected cohorts	Higher than iceberg-affected cohorts
Years before death (YBD)		
Early life performance	Earlier breeding and higher success than non-iceberg-affected cohorts with steeper trajectory of improvement	Later initiation of breeding, lower success than iceberg-affected cohorts with lower trajectory
Senescence: late life performance	Earlier onset and steeper rate of decline than non-iceberg-affected cohorts	Later onset and more gradual rate of decline than iceberg-affected cohorts

Table 4.2. Acronyms and descriptions for biological and environmental to compare cohort effects in reproductive performance and sea ice conditions of Adélie penguins breeding at capes Bird, Crozier, and Royds between 1994 and 2013 on Ross Island, Antarctica during seasons with and without the presence of giant icebergs.

Acronym	Description
Biological Covariates	
AFR	Continuous variable representing the age at first reproduction.
SUCCESS	Categorical variable representing breeding success (Y/N). Measured as successfully raising chick to crèche.
AGEsc	Continuous variable representing age, centered and scaled (age –mean age)/standard deviation.
YBD	Continuous variable representing the number of years before an individual was no longer observed and is presumed to have died. The last year individual seen alive is = 1.
RLS	Continuous variable representing the number of seasons an individual was considered a breeder. Equal to an individual’s longevity minus AFR.
LONG	Continuous variable representing an individual’s lifespan.
LRS	Continuous variable representing an individual’s total number of chicks that successfully entered a crèche.
Environmental Covariates	
PERS	Persistence of ice measured as the percent time sea ice is present between the day of advance and day of retreat.
FI	Continuous variable for weekly distance (km) to edge of fast ice from each colony, averaged by month for October (FI_O), November (FI_N), December (FI_D), and all months FI.
SIC	Continuous variable for colony-specific weekly % sea ice concentration in colony specific foraging areas averaged for December (SIC-D) and January (SIC-J) and both SIC.
GYRE	Continuous variable of yearly mean Ross Sea gyre velocity based on sea ice movement.
WAice	Continuous variable for weekly % ice cover for Adélie penguin wintering areas averaged for October (WAice_O), November (WAice_N), and both (WAice).
WAhab	Continuous variable for monthly preferred wintering sea ice concentration (75% to 90%) monthly average for October (WAhab_O), November (WAhab_N), and all (WAhab).

Table 4.3. (A) summarizing comparisons of wintering and breeding season estimates of sea ice variables of interest between years when giant icebergs were present (2001 – 2005) and were absent (1997 – 2000; 2006-2013) in the southwestern Ross Sea, and (B) summarizing comparisons of biological variables of interest. Results are based on adjusted p-values of significance (significant difference between group medians = blue; non-significant difference between group medians = yellow) corrected for multiple comparisons. Monthly abbreviations: O – October; N – November; D – December; J – January. Variable acronyms and further explanations available in Table 4.2.

A)

Variables	**Ross Sea**											
GYRE	🟦											
WAsic	🟦											
WAhab	🟦											
Month	**October**						**November**					
WAsic	🟦						🟦					
WAhab	🟦						🟨					
Colony	**Bird**				**Crozier**				**Royd**			
PERS	🟨				🟦				🟨			
FI	🟦				🟦				🟦			
SIC	🟦				🟨				🟦			
Month	**O**	**N**	**D**	**J**	**O**	**N**	**D**	**J**	**O**	**N**	**D**	**J**
FI	🟦	🟦	🟦	-	🟨	🟦	🟨	-	🟨	🟦	🟦	-
SIC	-	-	🟦	🟦	-	-	🟨	🟦	-	-	🟦	🟦

B)

Variables	**Bird**	**Crozier**	**Royds**
SUCCESS	🟦	🟦	🟦
AFR	🟦	🟨	🟨
Agesc	🟦	🟦	🟨
RLS	🟦	🟦	🟨
YBD	🟦	🟦	🟨
LONG	🟦	🟦	🟨
LRS	🟦	🟦	🟦

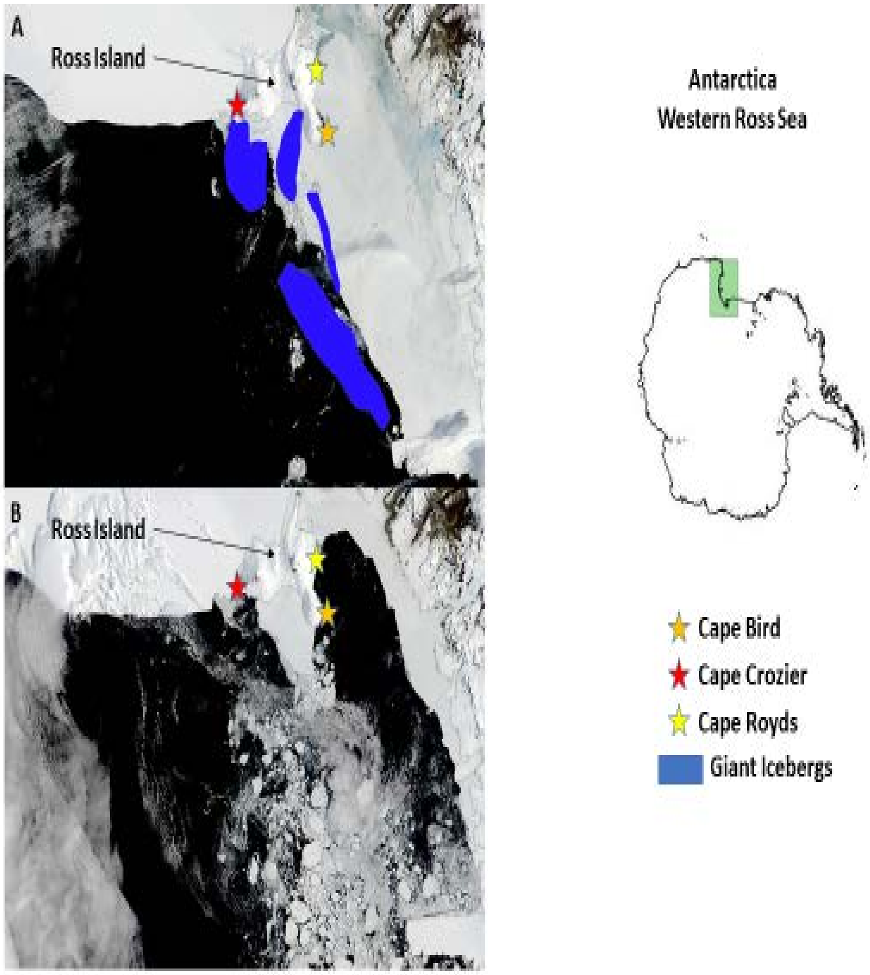
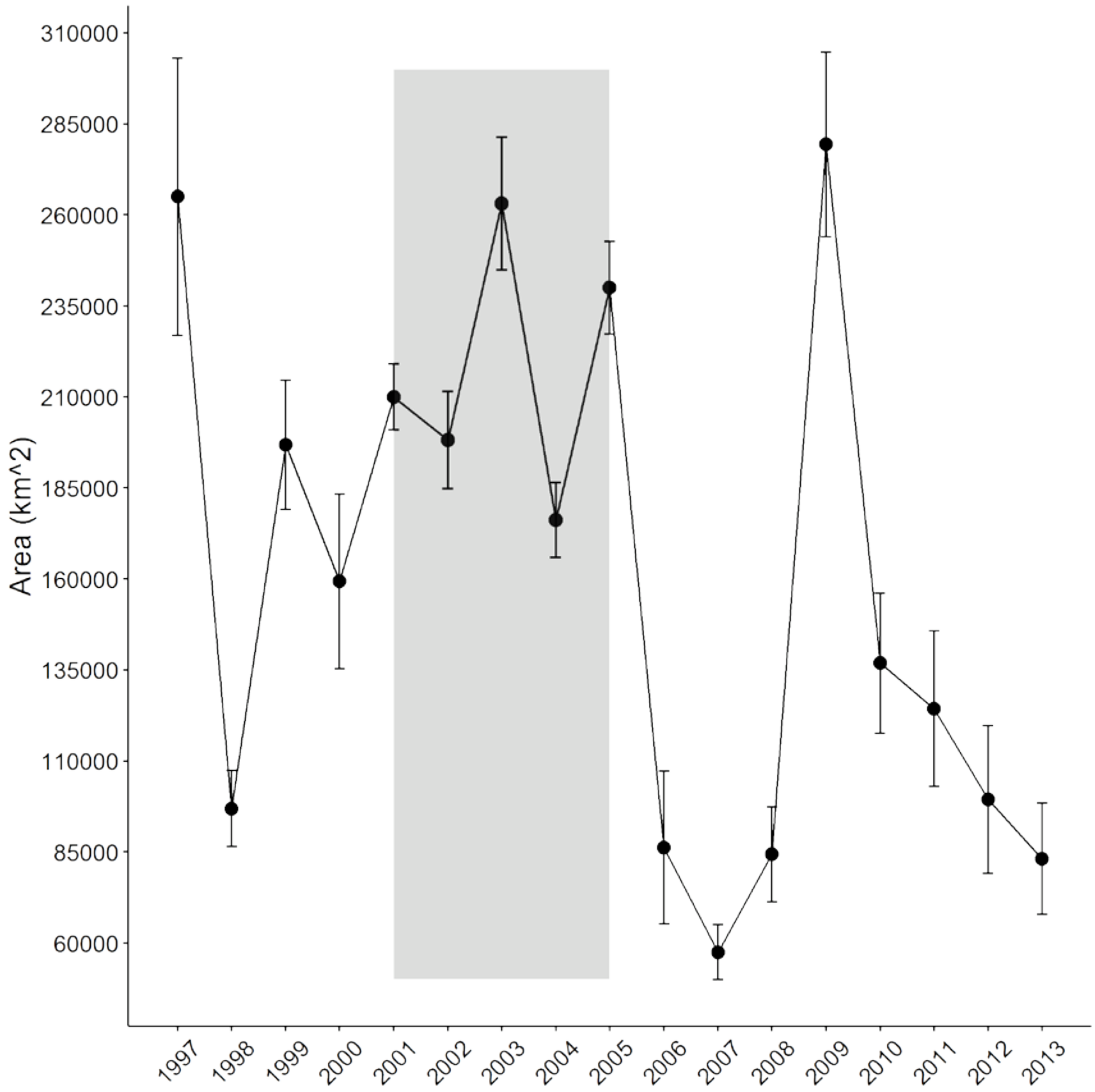
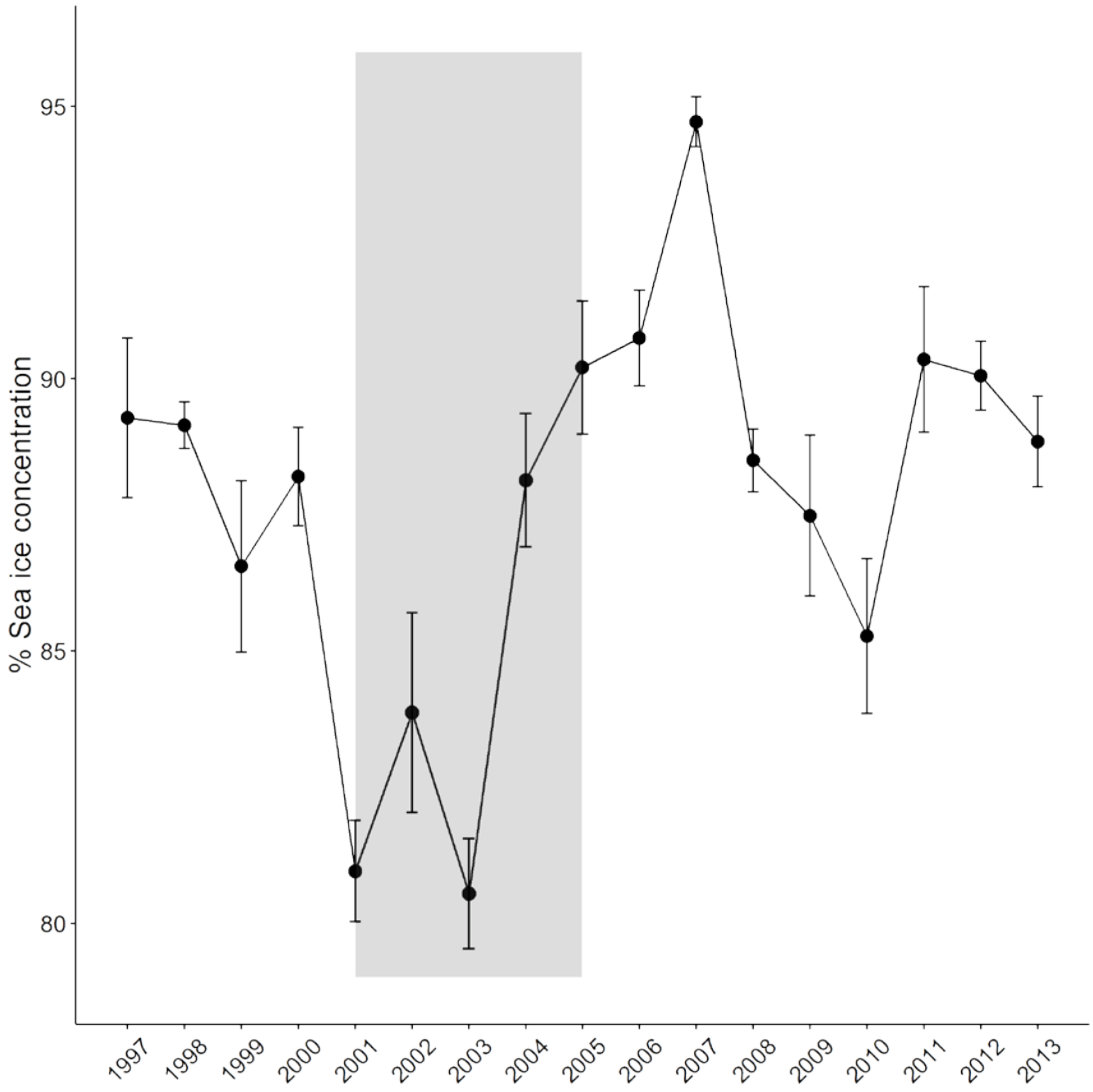


Figure 4. 1. Imagery of the Southern Ross Sea and Ross Island, Antarctica from the NASA Worldview application *(https://worldview.earthdata.nasa.gov/)*, part of the NASA Earth Observing System Data and Information System (EOSDIS) illustrating A) a typical iceberg-affected year (December 2004) showing positions of giant icebergs highlighted in blue; B) a typical non-iceberg-affected year (December 2009). Locations of Adélie penguin breeding at Capes Bird, Crozier, and Royds where reproductive performance was monitored from 1994-2013 are marked. Note in figure A that McMurdo Sound is completely covered with fast ice and the McMurdo polynya has failed to develop.

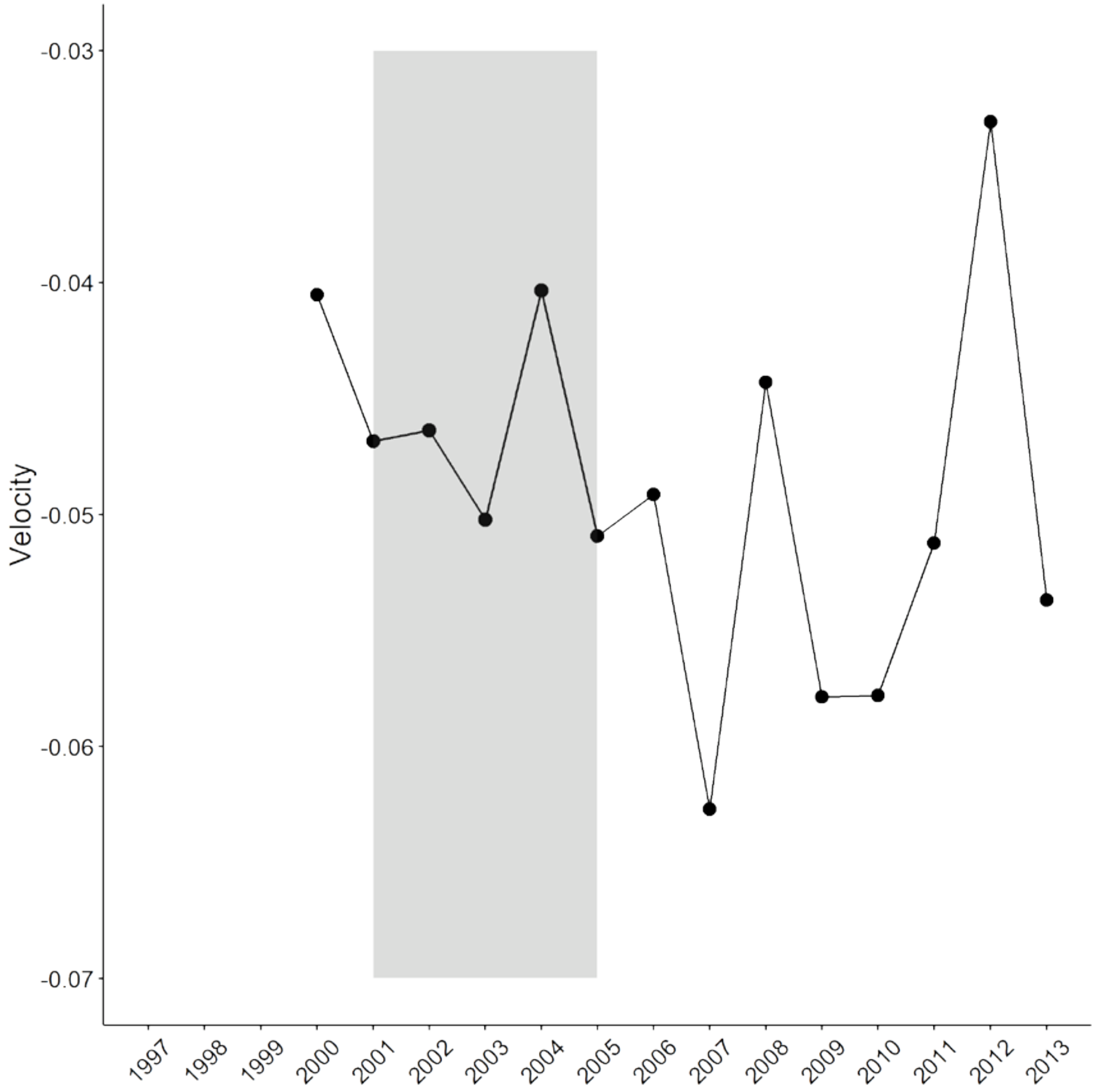
(A)


Area (km^2)
310000
285000
260000
235000
210000
185000
160000
135000
110000
85000
60000
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013

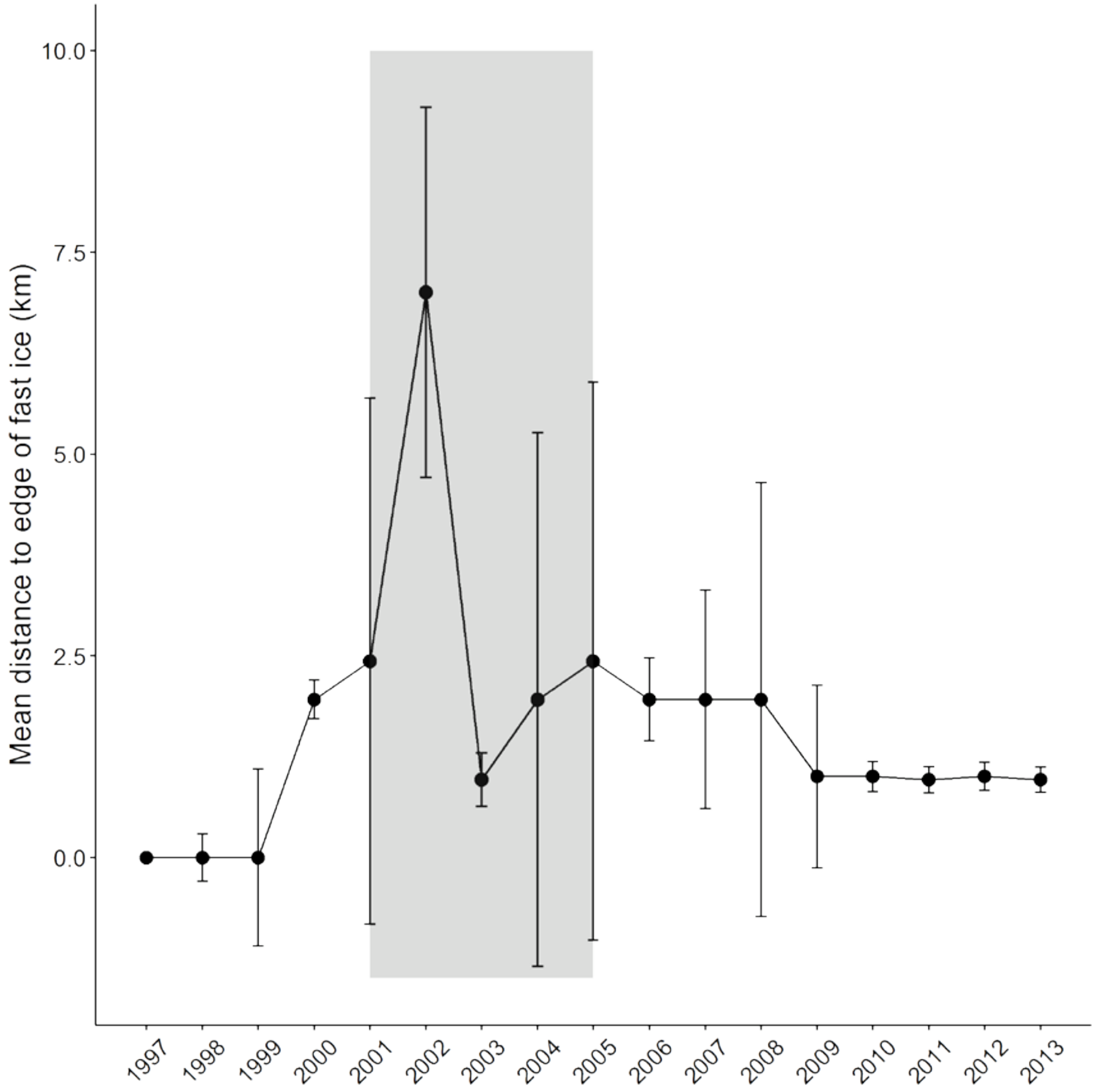
B)


% Sea ice concentration
95
90
85
80
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013

C)


Velocity
-0.03
-0.04
-0.05
-0.06
-0.07
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013

D)


Mean distance to edge of fast ice (km)
10.0
7.5
5.0
2.5
0.0
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013

E)

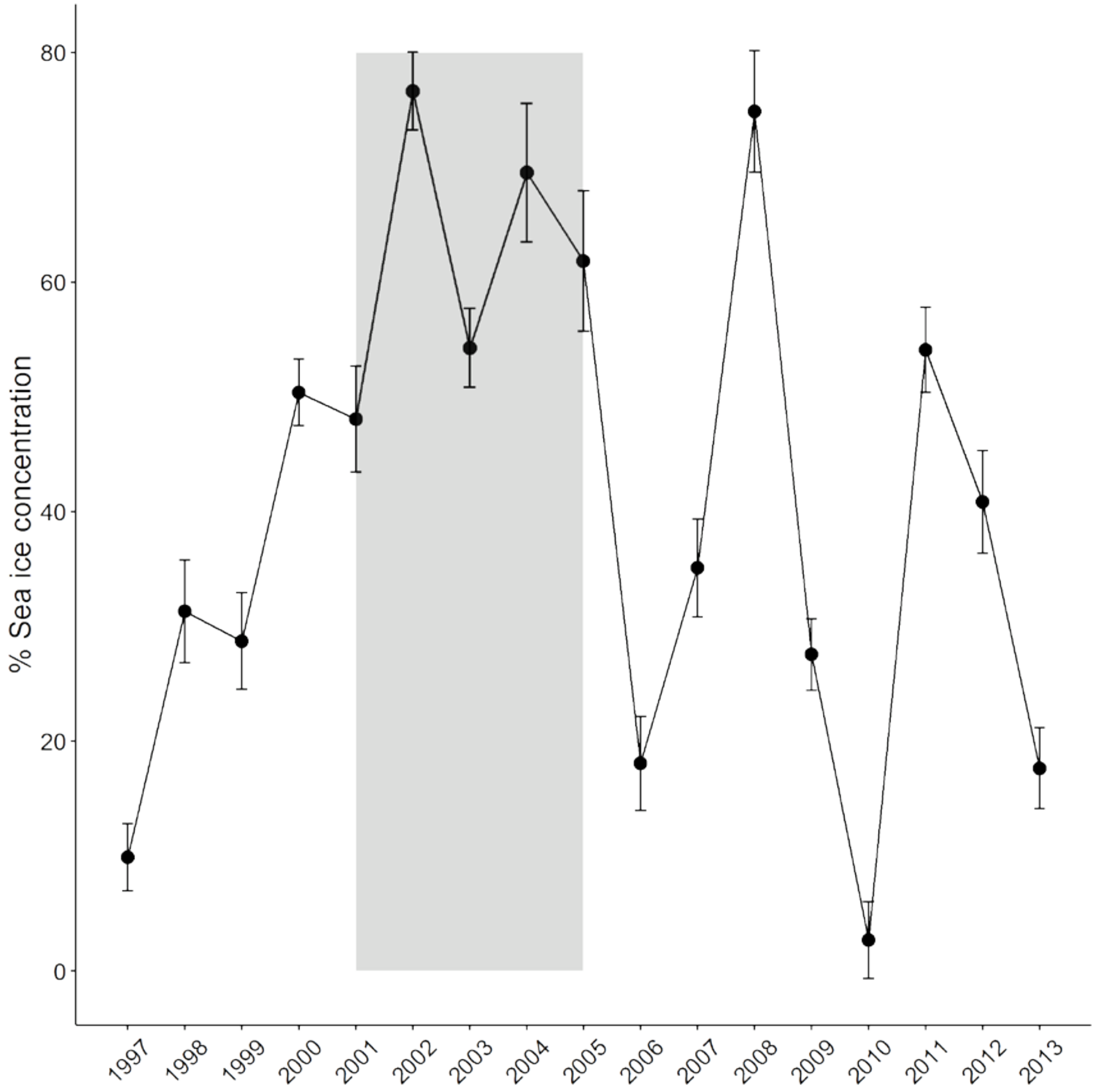


Figure 4.2. Median (± SE) annual trends in (A) the area of suitable Adélie penguin wintering habitat (sea ice concentrations between 75% and 90%, (B) sea ice concentration (SIC) on the Ross Sea wintering grounds, (C) Ross Sea gyre velocity (negative values indicate northward flow), (D) fast ice extent, and (E) SIC on the foraging grounds during the breeding season. The presence of giant icebergs is indicated by shading. More information on each metric can be found in Table 4.2.

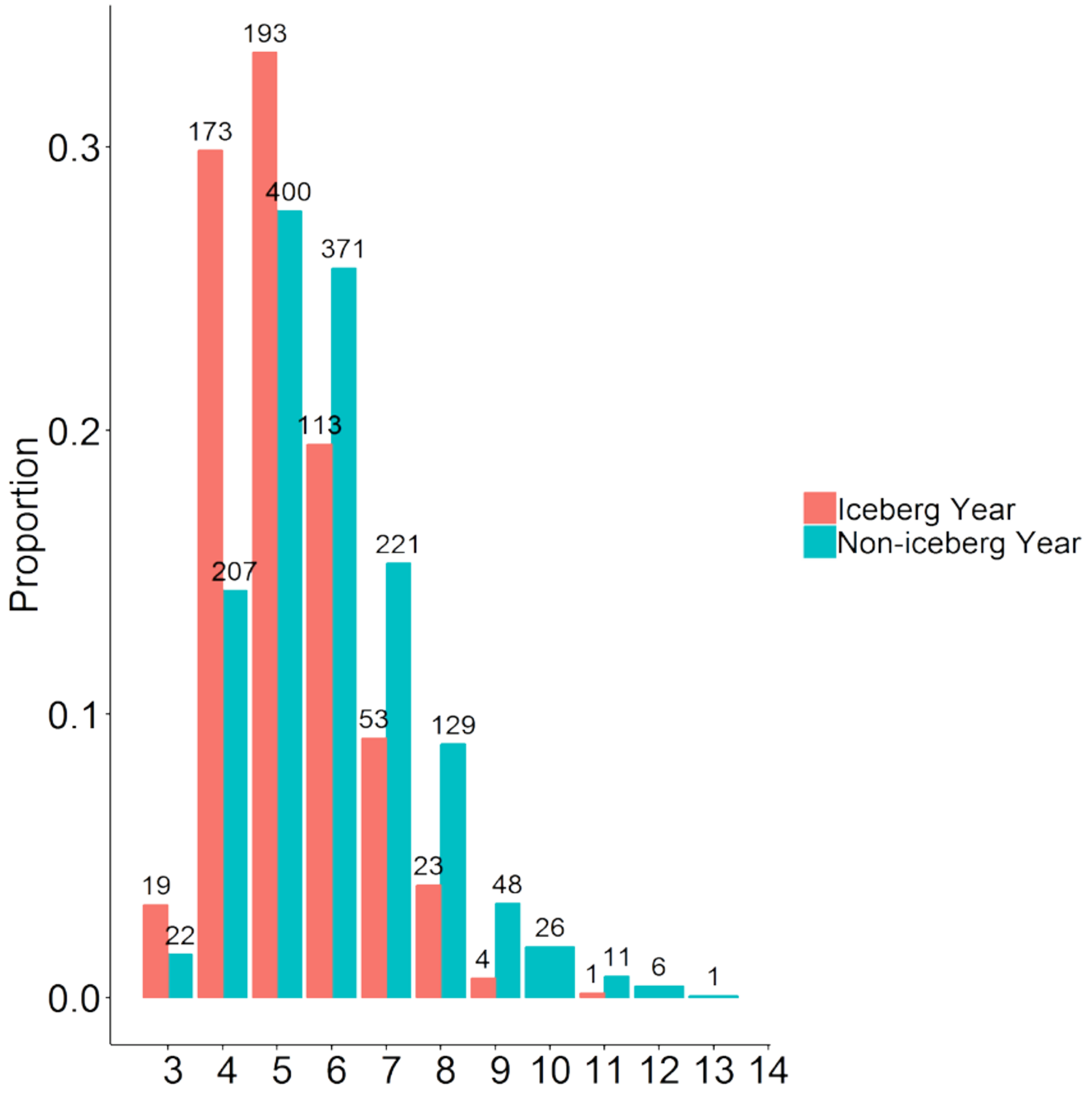


Figure 4.3. The proportion new recruits to the breeding population (i.e., age at first reproduction [AFR]) in the Ross Island Adélie penguin population, Antarctica when icebergs were and were not present. Numbers above bars indicate sample sizes for each AFR.

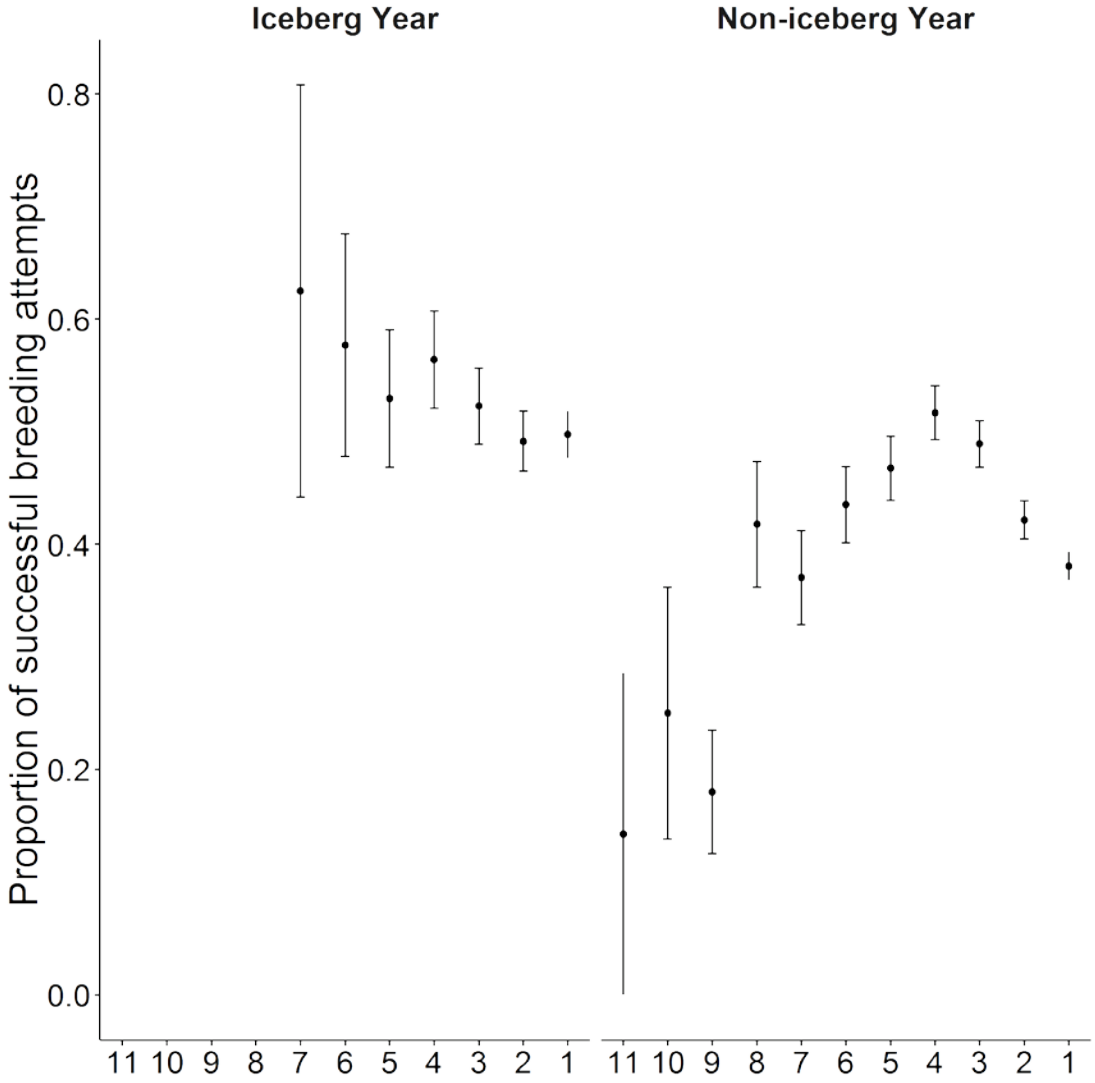


Figure 4.4. The relationship between years before death (1 being equal to the last year of life) and the proportion of successful breeding attempts (measured as the number of occasions at least 1 chick was successfully raised to enter a crèche) for cohorts born during iceberg-affected and non-iceberg-affected years. Data points are the mean ± SE; *n* = 2052 individuals.

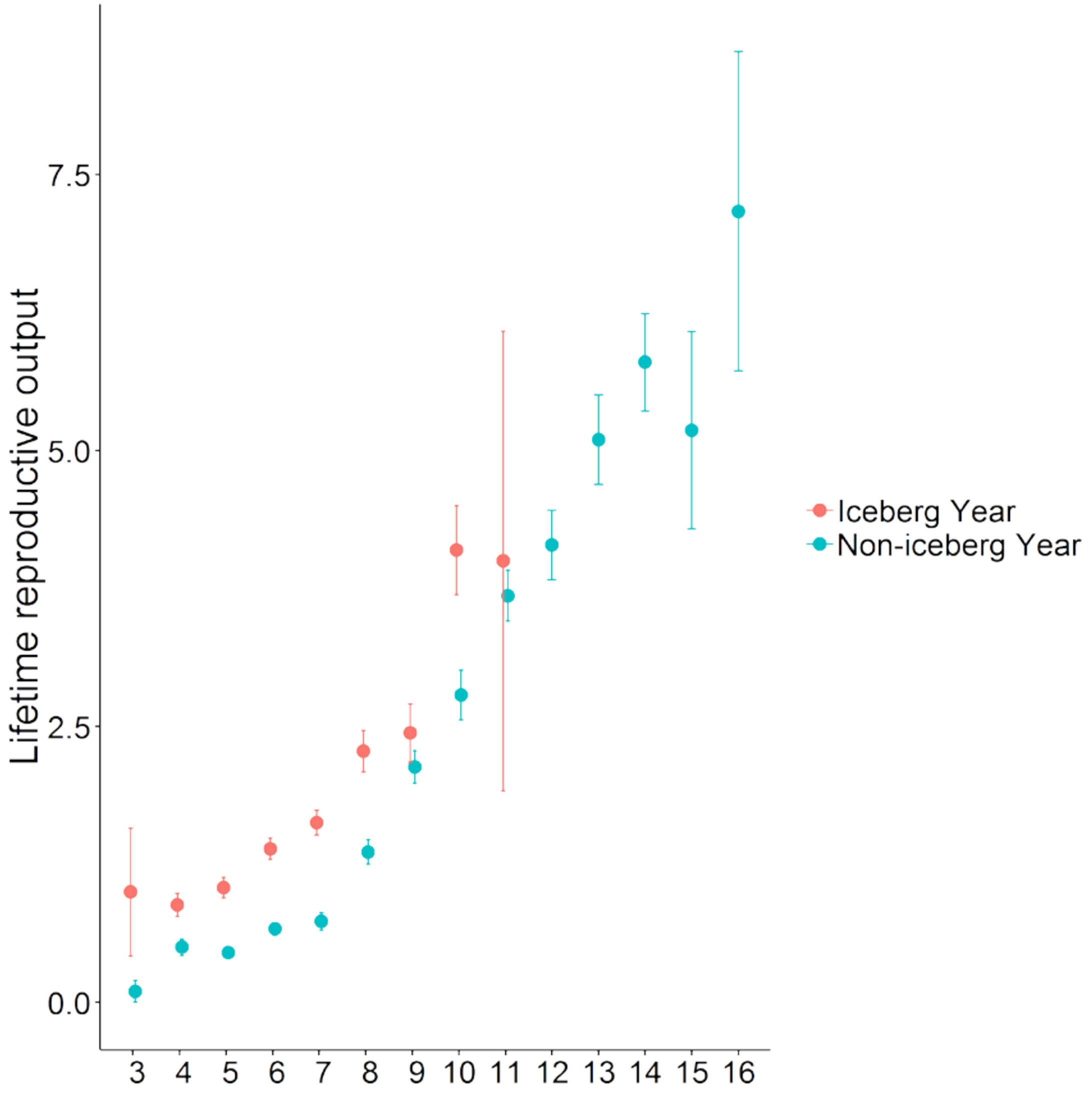


Figure 4.5. Relationship between longevity and lifetime reproductive output, of Adélie penguins in the iceberg-affected (pink circles) and non-iceberg-affected (blue triangles) cohorts breeding in the Ross Island, Antarctica meta-population. Lifetime reproductive output was measured as the total number chicks successful raised to enter a crèche over an individual’s lifetime. Data points are mean ± SE.

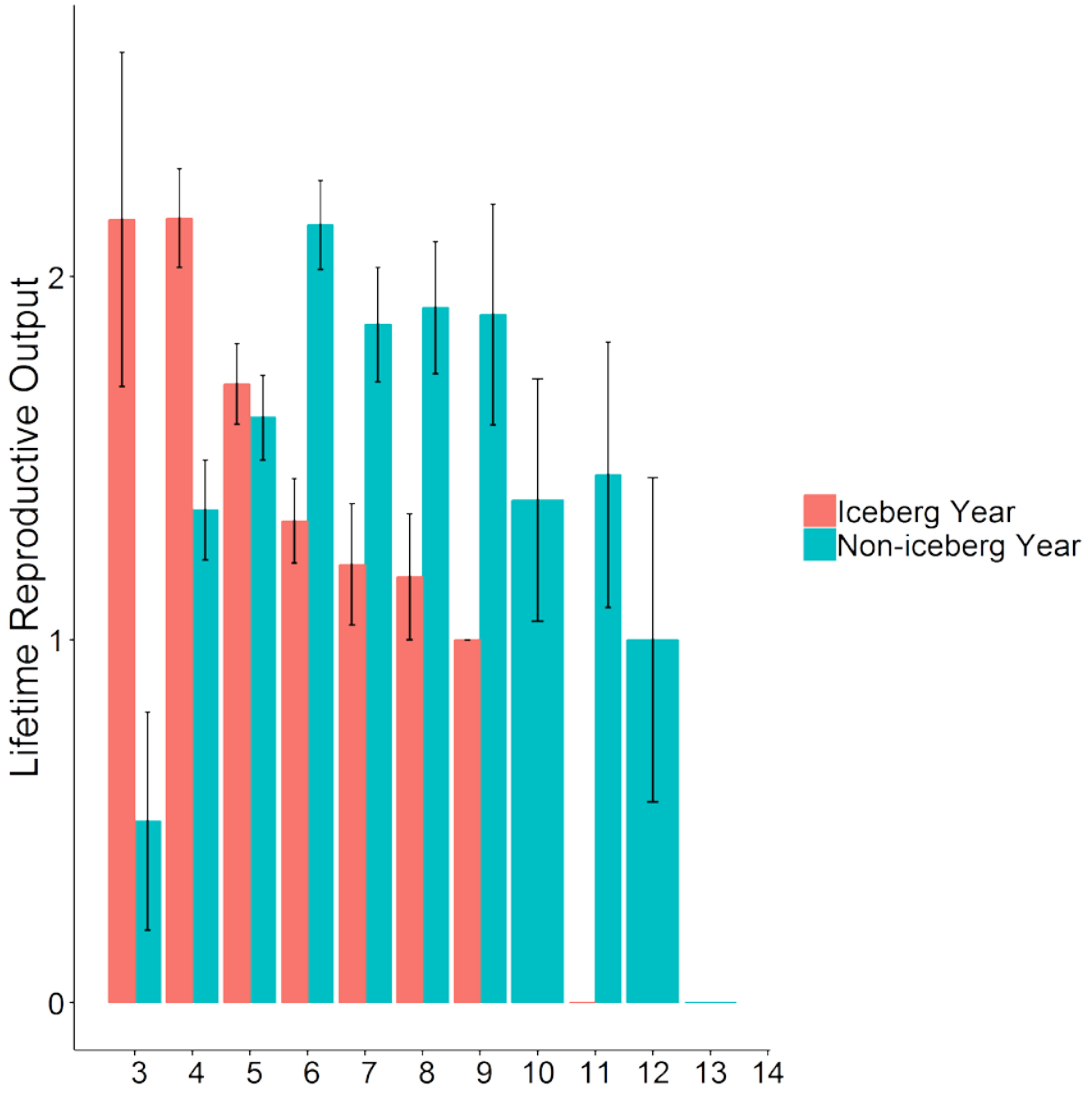


Figure 4.6. The mean lifetime reproductive success, measured as the total number chicks an individual raised that successfully entered a crèche, based on age at first reproduction of iceberg-affected and non-iceberg-affected cohorts. Data are means ± SE.

5 - CONCLUSION

In this dissertation I used a 19-year dataset of known-aged individual Adélie Penguins to investigate different aspects of reproductive performance.

In Chapter 2 I tested predictions from several hypothesis regarding early- and late-life reproductive performance to identify trade-offs associated alternative recruitment strategies (e.g., begin breeding early versus later in life) and compared results among three colonies differing in size by orders of magnitude. Overall patterns of age-related reproductive performance were similar at all three colonies. I found support for the constraint hypothesis and that pre-recruitment experience was an important factor for increasing breeding success of birds that delayed recruitment. Despite documenting different trade-offs between alternate recruitment strategies, such that individuals that initiated breeding at younger ages had shorter lifespans, the overall number of reproductive attempts and number of successful breeding attempts did not differ among recruitment strategies.

In Chapter 3 I used the same dataset to decompose population level averages in age-specific reproductive performance into the constituent processes of within-individual maturation, selective disappearance, and selective appearance and then compared those results between colonies. Despite similar patterns in mean age-specific reproductive performance at all three colonies decomposing these patterns in to the constituent processes revealed differences in the contributions the different processes among the colonies. At all three colonies selective appearance contributed negatively to estimates of age-specific reproduction, indicating that first time breeders had lower reproductive performance than similarly aged individuals but with more breeding experience. At the small and medium sized colonies improvements in age-related reproductive performance was driven by a combination of within-individual maturation (15% at both colonies) and selective disappearance (41% and 32%, respectively), but at the largest colony it was mostly driven by within-individual maturation (67%). I documented a drop in reproductive performance in late life stages at all three colonies but decomposition estimates, again revealed important differences. At the two smaller colonies, observed changes late in life were primarily driven by population level changes resulting from selective disappearance of individuals of lower phenotypic quality. However, at the largest colony, changes in performance were driven by a combination of within-individual maturation and the selective disappearance of individuals of higher phenotypic quality. These results may be due to a combination of potential trade-offs associated with alternative individual life history strategies and between different sized colonies.

In Chapter 4 I explored the role natal conditions have on age-related changes in life histories of Adélie penguins that experienced different early-life environmental conditions. Poor natal environmental conditions have long been thought to impose limitations on development resulting in poorly performing individuals. However, there is growing evidence that individuals can mitigate the effects of poor early-life conditions via adaptive behavioral, morphological or reproductive changes and the internal adaptive response (internal PAR) hypothesis predicts that individuals that are expected to experience reduced performance later in life, should act to mitigate that loss in performance by breeding earlier. I took advantage of a “natural experiment” provided by the arrival of two giant icebergs to investigate how the age-related life history decisions and lifetime reproductive performance of cohorts from the years the icebergs were present compared to cohorts that experienced more typical early life conditions. I documented significant differences in the sea ice conditions when the icebergs were present and when they were not. The icebergs acted as a physical barrier to penguins returning to their colonies to breed and accessing their foraging grounds during the breeding season. In addition, they substantially altered sea ice conditions throughout the entire southwestern Ross Sea for the duration of the 5 years they were present. I documented changes in the overall area of preferred wintering habitat between years the icebergs were present and years when they were absent, as well as the sea ice concentration on the winter grounds. I also found that fast ice extended further from the colonies when the icebergs were present and that sea ice concentration was higher. These metrics have been linked with reduced provisioning of chicks and fledging mass of chicks indicating that iceberg cohorts likely experienced stressful early-life conditions. In response, in accordance with predictions from the internal PAR hypothesis, these cohorts began breeding earlier, experienced higher breeding success, had shorter lifespan, but not overall reproductive lifespans as non-iceberg cohorts. Meanwhile non-iceberg cohorts, delayed breeding, never achieved levels of breeding success of iceberg cohorts, lived longer and have similar reproductive lifespans. Ultimately, they had slightly higher average lifetime reproductive success than iceberg cohorts, but iceberg cohorts were able to make life history decisions and reproductive adaptations that nearly entirely mitigated any early-life deficits and mitigated their potential fitness costs.

These results are highly interesting as they provide a possible explanation and mechanism for the Adélie penguin population dynamics that we have observed during the course of this study. After the icebergs became ungrounded and left the region, the Cape Bird and Cape Crozier colonies grew considerably, but Cape Royds did not. It’s possible that part of this growth is due to the alternate life history strategies employed by the iceberg cohorts that are seeking to mitigate the costs of poor early-life conditions and likely sub-optimal late life performance. More importantly, these results, provide evidence of phenotypic plasticity that may help long-lived k-selected species like the Adélie penguins adapt to and mitigate fitness costs associated with climate change. This process provides a direct likely between environmental factors and individual life histories for long-lived k-selected species and would have important ramifications for the population dynamics of these species and they experience climate change.

BIBLIOGRAPHY

Agresti, A. 2003. Categorical data analysis. John Wiley & Sons.

Ainley, D. G. 1980. Birds as marine organisms: a review. CalCOFI Rep **21**:48-52.

Ainley, D. G. 2002a. The Adélie Penguin: Bellwether of Climate Change. Columbia University Press, New York.

Ainley, D. G. 2002b. The Ross Sea, Antarctica, where all ecosystem processes still remain for study, but maybe not for long. Marine Ornithology **30**:55-62.

Ainley, D. G. 2010. A history of the exploitation of the Ross Sea, Antarctica. Polar Record **46**:233-243.

Ainley, D. G., G. Ballard, S. Ackley, L. K. Blight, J. T. Eastman, S. D. Emslie, A. Lescroel, S. Olmastron, S. E. Townsend, C. T. Tynan, P. Wilson, and E. Woehler. 2007. Paradigm lost, or is top-down forcing no longer significant in the Antarctic marine ecosystem? Antarctic Science **19**:283-290.

Ainley, D. G., G. Ballard, K. J. Barton, B. J. Karl, G. H. Rau, C. A. Ribic, and P. R. Wilson. 2003. Spatial and temporal variation of diet within a presumed metapopulation of Adelie Penguins. Condor **105**:95-106.

Ainley, D. G., G. Ballard, L. K. Blight, S. Ackley, S. D. Emslie, A. Lescroel, S. Olmastroni, S. E. Townsend, C. T. Tynan, P. Wilson, and E. Woehler. 2010a. Impacts of cetaceans on the structure of Southern Ocean food webs. Marine Mammal Science **26**:482-498.

Ainley, D. G., G. Ballard, and K. M. Dugger. 2006. Competition among penguins and cetaceans reveals trophic cascades in the western Ross Sea, Antarctica. Ecology **87**:2080-2093.

Ainley, D. G., G. Ballard, B. J. Karl, and K. M. Dugger. 2005a. Leopard seal predation rates at penguin colonies of different size. Antarctic Science **17**:335-340.

Ainley, D. G., E. D. Clarke, K. Arrigo, W. R. Fraser, A. Kato, K. J. Barton, and P. R. Wilson. 2005b. Decadal-scale changes in the climate and biota of the Pacific sector of the Southern Ocean, 1950s to the 1990s. Antarctic Science **17**:171-182.

Ainley, D. G., and D. P. Demaster. 1980. Survival and mortality in a population of Adélie Penguins. Ecology **61**:522-530.

Ainley, D. G., K. M. Dugger, M. La Mesa, G. Ballard, K. J. Barton, S. Jennings, B. J. Karl, A. Lescroel, P. O. Lyver, A. Schmidt, and P. Wilson. 2018. Post-fledging survival of Adelie penguins at multiple colonies: chicks raised on fish do well. Marine Ecology Progress Series **601**:239-251.

Ainley, D. G., and R. E. Leresche. 1973. The effects of weather and ice conditions on breeding in Adélie Penguins. Condor **75**:235-239.

Ainley, D. G., R. E. LeResche, and W. J. L. Sladen. 1983. Breeding biology of the Adélie Penguin. University of California Press, Berkeley.

Ainley, D. G., C. A. Ribic, G. Ballard, S. Heath, I. Gaffney, B. J. Karl, K. J. Barton, P. R. Wilson, and S. Webb. 2004. Geographic structure of Adélie Penguin populations: Overlap in colony-specific foraging areas. Ecological Monographs **74**:159-178.

Ainley, D. G., C. A. Ribic, and W. R. Fraser. 1994. Ecological structure among migrant and resident seabirds of the Scotia-Weddell Confluence Region. Journal of Animal Ecology **63**:347-364.

Ainley, D. G., J. Russell, S. Jenouvrier, E. Woehler, P. O. Lyver, W. R. Fraser, and G. L. Kooyman. 2010b. Antarctic penguin response to habitat change as Earth's troposphere reaches 2 degrees C above preindustrial levels. Ecological Monographs **80**:49-66.

Ainley, D. G., and R. P. Schlatte. 1972. Chick raising ability in Adélie Penguins. Auk **89**:559-566.

Ainley, D. G., P. R. Wilson, K. J. Barton, G. Ballard, N. Nur, and B. Karl. 1998. Diet and foraging effort of Adélie penguins in relation to pack-ice conditions in the southern Ross Sea. Polar Biology **20**:311-319.

Alatalo, R. V., and A. Lundberg. 1984. Denisty-dependence in breeding success of the Pied Flycathcer (*Ficedula hypoleuca*). Journal of Animal Ecology **53**:969-977.

Albon, S. D., T. H. Cluttonbrock, and F. E. Guinness. 1987. Early development and population-dynamics in red deer .2. Density-independent effects and cohort variation. Journal of Animal Ecology **56**:69-81.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management **74**:1175-1178.

Arrigo, K. R., and D. N. Thomas. 2004. Large scale importance of sea ice biology in the Southern Ocean. Antarctic Science **16**:471-486.

Arrigo, K. R., G. L. van Dijken, D. G. Ainley, M. A. Fahnestock, and T. Markus. 2002. Ecological impact of a large Antarctic iceberg. Geophysical Research Letters **29**.

Arrigo, K. R., D. Worthen, A. Schnell, and M. P. Lizotte. 1998. Primary production in Southern Ocean waters. Journal of Geophysical Research-Oceans **103**:15587-15600.

Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis **103**:458-473.

Aubry, L. M., D. N. Koons, J. Y. Monnat, and E. Cam. 2009. Consequences of recruitment decisions and heterogeneity on age-specific breeding success in a long-lived seabird. Ecology **90**:2491-2502.

Auer, S. K. 2010. Phenotypic plasticity in adult life-history strategies compensates for a poor start in life in Trinidadian guppies (*Poecilia reticulata*). American Naturalist **176**:818-829.

Balbontín, J., I. G. Hermosell, A. Marzal, M. Reviriego, F. De Lope, and A. P. Møller. 2007. Age-related change in breeding performance in early life is associated with an increase in competence in the migratory barn swallow *Hirundo rustica*. Journal of Animal Ecology **76**:915-925.

Ballance, L. T., D. G. Ainley, G. Ballard, and K. Barton. 2009. An energetic correlate between colony size and foraging effort in seabirds, an example of the Adélie penguin *Pygoscelis adeliae*. Journal of Avian Biology **40**:279-288.

Ballard, G., D. G. Ainley, C. A. Ribic, and K. R. Barton. 2001. Effect of instrument attachment and other factors on foraging trip duration and nesting success of Adélie Penguins. Condor **103**:481-490.

Ballard, G., K. M. Dugger, N. Nur, and D. G. Ainley. 2010a. Foraging strategies of Adélie penguins: Adjusting body condition to cope with environmental variability. Marine Ecology Progress Series **405**:287-302.

Ballard, G., D. Jongsomjit, S. D. Veloz, and D. G. Ainley. 2011. Coexistence of mesopredators in an intact polar ocean ecosystem: The basis for defining a Ross Sea marine protected area. Biological Conservation.

Ballard, G., D. Jongsomjit, S. D. Veloz, and D. G. Ainley. 2012. Coexistence of mesopredators in an intact polar ocean ecosystem: The basis for defining a Ross Sea marine protected area. Biological Conservation **156**:72-82.

Ballard, G., A. E. Schmidt, V. Toniolo, S. Veloz, D. Jongsomjit, K. R. Arrigo, and D. G. Ainley. 2019. Fine-scale oceanographic features characterizing successful Adélie penguin foraging in the SW Ross Sea. Marine Ecology Progress Series **608**:263-277.

Ballard, G., V. Toniolo, D. G. Ainley, C. L. Parkinson, K. R. Arrigo, and P. N. Trathan. 2010b. Responding to climate change: Adélie penguins confront astronomical and ocean boundaries. Ecology **91**:2056-2069.

Ballerini, T., G. Tavecchia, S. Olmastroni, F. Pezzo, and S. Focardi. 2009a. Nonlinear effects of winter sea ice on the survival probabilities of Adelie penguins. Oecologia **161**:253-265.

Ballerini, T., G. Tavecchia, S. Olmastroni, F. Pezzo, and S. Focardi. 2009b. Nonlinear effects of winter sea ice on the survival probabilities of Adélie penguins. Oecologia **161**:253-265.

Barbraud, C., and H. Weimerskirch. 2005. Environmental conditions and breeding experience affect costs of reproduction in blue petrels. Ecology **86**:682-692.

Bateson, P., D. Barker, T. Clutton-Brock, D. Deb, B. D'Udine, R. A. Foley, P. Gluckman, K. Godfrey, T. Kirkwood, M. M. Lahr, J. McNamara, N. B. Metcalfe, P. Monaghan, H. G. Spencer, and S. E. Sultan. 2004. Developmental plasticity and human health. Nature **430**:419-421.

Beckerman, A. P., T. G. Benton, E. Ranta, V. Kaitala, and P. Lundberg. 2002. Population dynamic consequences of delayed life-history effects. Trends in Ecology & Evolution **17**:263-269.

Birt, V., T. Birt, D. Goulet, D. Cairns, and W. Montevecchi. 1987. Ashmole's halo: direct evidence for prey depletion by a seabird. Marine Ecology Progress Series **40**:205-208.

Black, J. M., J. Prop, and K. Larsson. 2007. Wild goose dilemmas: population consequences of individual decisions in Barnacle Geese. Branta Press, Groningen, The Netherlands.

Blight, L. K., and D. G. Ainley. 2008. Southern Ocean not so pristine. Science **321**:1443.

Bolker, B. M. 2019. GLMM FAQ. https://bbolker.github.io/mixedmodels-misc/glmmFAQ.html#reml-for-glmms, https://bbolker.github.io/mixedmodels-misc/glmmFAQ.html#reml-for-glmms.

Bosman, D. S., H. J. P. Vercruijsse, E. W. M. Stienen, M. Vincx, and L. Lens. 2013. Age of first breeding interacts with pre- and post-recruitment experience in shaping breeding phenology in a long-lived gull. PLoS ONE **8**:12.

Both, C. 1998. Density dependence of clutch size: habitat heterogeneity or individual adjustment? Journal of Animal Ecology **67**:659-666.

Boulinier, T., and E. Danchin. 1997. The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. Evolutionary Ecology **11**:505-517.

Bouwhuis, S., A. Charmantier, S. Verhulst, and B. C. Sheldon. 2010. Individual variation in rates of senescence: natal origin effects and disposable soma in a wild bird population. Journal of Animal Ecology **79**:1251-1261.

Bouwhuis, S., B. C. Sheldon, S. Verhulst, and A. Charmantier. 2009. Great tits growing old: selective disappearance and the partitioning of senescence to stages within the breeding cycle. Proceedings Of The Royal Society B-Biological Sciences **276**:2769-2777.

Bradley, J. S., R. D. Wooller, and I. J. Skira. 2000. Intermittent breeding in the short-tailed shearwater *Puffinus tenuirostris*. Journal of Animal Ecology **69**:639-650.

Bregnballe, T. 2006. Age-related fledgling production in great cormorants *Phalacrocorax carbo*: influence of individual competence and disappearance of phenotypes. Journal of Avian Biology **37**:149-157.

Breuner, C. 2008. Maternal stress, glucocorticoids, and the maternal/fetal match hypothesis. Hormones and Behavior **54**:485-487.

Brommer, J. E., J. Merila, and H. Kokko. 2002. Reproductive timing and individual fitness. Ecology Letters **5**:802-810.

Brommer, J. E., H. Pietiäinen, and H. Kolunen. 1998. The effect of age at first breeding on Ural owl lifetime reproductive success and fitness under cyclic food conditions. Journal of Animal Ecology **67**:359-369.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Selection: A Practical Information Theoretic Approach. Springer Verlag.

Cam, E. 2009. Contribution of capture-mark-recapture modeling to studies of evolution by natural selection. Pages 83-129 *in* D. L. Thompson, E. G. Cooch, and M. J. Conroy, editors. Modeling demographic processes in marked populations. Springer Verlag, New York, USA.

Cam, E., W. A. Link, E. G. Cooch, J. Y. Monnat, and E. Danchin. 2002. Individual covariation in life-history traits: Seeing the trees despite the forest. American Naturalist **159**:96-105.

Cam, E., and J. Y. Monnat. 2000a. Apparent inferiority of first-time breeders in the kittiwake: the role of heterogeneity among age classes. Journal of Animal Ecology **69**:380-394.

Cam, E., and J. Y. Monnat. 2000b. Stratification based on reproductive state reveals contrasting patterns of age-related variation in demographic parameters in the kittiwake. Oikos **90**:560-574.

Caswell, H. 2001. Matrix Population Models. 2 edition. Sinauer Associates, Sunderland, MA.

Chatterjee, S., and A. S. Hadi. 2015. Regression analysis by example. John Wiley & Sons.

Clutton-Brock, T. H. 1984. Reproductive effort and terminal investment in iteroparous animals. American Naturalist **123**:212-229.

Clutton-Brock, T. H. 1988. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press.

Comiso, J. C., R. Kwok, S. Martin, and A. L. Gordon. 2011. Variability and trends in sea ice extent and ice production in the Ross Sea. Journal of Geophysical Research-Oceans **116**:C4.

Conroy, M. J. 2009. Application of capture-recapture to addressing questions in evolutionary ecology. Pages 131-156 *in* B. C. Thompson, E. G. Cooch, and M. J. Conroy, editors. Modeling demographic processes in marked populations (Environmental and Ecological Statistics). Springer Verla.

Coulson, T., and S. Tuljapurkar. 2008. The dynamics of a quantitative trait in an age-structured population living in a variable environment. American Naturalist **172**:599-612.

Croxall, J. P., P. N. Trathan, and E. J. Murphy. 2002. Environmental change and Antarctic seabird populations. Science **297**:1510-1514.

Curio, E. 1983. Why do young birds reproduce less well? Ibis **125**:400-404.

Danchin, E., T. Boulinier, and M. Massot. 1998. Conspecific reproductive success and breeding habitat selection: Implications for the study of coloniality. Ecology **79**:2415-2428.

Danchin, E., and R. H. Wagner. 1997. The evolution of coloniality: the emergence of new perspectives. Trends in Ecology & Evolution **12**:342-347.

Dantzer, B., A. E. M. Newman, R. Boonstra, R. Palme, S. Boutin, M. M. Humphries, and A. G. McAdam. 2013. Density triggers maternal hormones that increase adaptive offspring growth in a wild mammal. Science **340**:1215-1217.

Daunt, F., S. Wanless, M. P. Harris, L. Money, and P. Monaghan. 2007. Older and wiser: improvements in breeding success are linked to better foraging performance in European shags. Functional Ecology **21**:561-567.

Davis, L. S. 1982. Créching behaviour of Adélie penguin chicks (*Pygoscelis adeliae*). New Zealand Journal of Zoology **9**:279-286.

Davis, L. S., P. D. Boersma, and G. S. Court. 1996. Satellite telemetry of the winter migration of Adélie penguins (*Pygoscelis adeliae*). Polar Biology **16**:221-225.

Davis, L. S., R. G. Harcourt, and C. J. A. Bradshaw. 2001. The winter migration of Adélie penguins breeding in the Ross Sea sector of Antarctica. Polar Biology **24**:593-597.

Davis, L. S., and F. T. McCaffrey. 1986. Survival analysis of eggs and chicks of Adélie penguins (*Pygoscelis adeliae*). Auk **103**:379-388.

Descamps, S., S. Boutin, D. Berteaux, and J. M. Gaillard. 2006. Best squirrels trade a long life for an early reproduction. Proceedings Of The Royal Society B-Biological Sciences **273**:2369-2374.

Descamps, S., S. Boutin, D. Berteaux, and J. M. Gaillard. 2007. Female red squirrels fit Williams' hypothesis of increasing reproductive effort with increasing age. Journal of Animal Ecology **76**:1192-1201.

Descamps, S., S. Boutin, D. Berteaux, A. G. McAdam, and J. M. Gaillard. 2008. Cohort effects in red squirrels: the influence of density, food abundance and temperature on future survival and reproductive success. Journal of Animal Ecology **77**:305-314.

Douhard, M., J. M. Gaillard, D. Delorme, G. Capron, P. Duncan, F. Klein, and C. Bonenfant. 2013. Variation in adult body mass of roe deer: early environmental conditions influence early and late body growth of females. Ecology **94**:1805-1814.

Douhard, M., L. E. Loe, A. Stien, C. Bonenfant, R. J. Irvine, V. Veiberg, E. Ropstad, and S. Albon. 2016. The influence of weather conditions during gestation on life histories in a wild Arctic ungulate. Proceedings Of The Royal Society B-Biological Sciences **283**:8.

Douhard, M., F. Plard, J. M. Gaillard, G. Capron, D. Delorme, F. Klein, P. Duncan, L. E. Loe, and C. Bonenfant. 2014. Fitness consequences of environmental conditions at different life stages in a long-lived vertebrate. Proceedings Of The Royal Society B-Biological Sciences **281**:8.

Dugger, K. M., D. G. Ainley, P. O. Lyver, K. Barton, and G. Ballard. 2010. Survival differences and the effect of environmental instability on breeding dispersal in an Adélie penguin meta-population. Proceedings of the National Academy of Sciences of the United States of America **107**:12375-12380.

Dugger, K. M., G. Ballard, D. G. Ainley, and K. J. Barton. 2006. Effects of flipper bands on foraging behavior and survival of Adélie penguins (*Pygoscelis adeliae*). Auk **123**:858-869.

Dugger, K. M., G. Ballard, D. G. Ainley, P. O. B. Lyver, and C. Schine. 2014. Adélie penguins coping with environmental change: results from a natural experiment at the edge of their breeding range. Frontiers in Ecology and Evolution **2**:68.

Dugger, K. M., E. D. Forsman, A. B. Franklin, R. J. Davis, G. C. White, C. J. Schwarz, K. P. Burnham, J. D. Nichols, J. E. Hines, C. B. Yackulic, P. F. Doherty, L. Bailey, D. A. Clark, S. H. Ackers, L. S. Andrews, B. Augustine, B. L. Biswell, J. Blakesley, P. C. Carlson, M. J. Clement, L. V. Diller, E. M. Glenn, A. Green, S. A. Gremel, D. R. Herter, J. M. Higley, J. Hobson, R. B. Horn, K. P. Huyvaert, C. McCafferty, T. McDonald, K. McDonnell, G. S. Olson, J. A. Reid, J. Rockweit, V. Ruiz, J. Saenz, and S. G. Sovern. 2016. The effects of habitat, climate, and Barred Owls on long-term demography of Northern Spotted Owls. Condor **118**:57-116.

Elliott, K. H., K. J. Woo, A. J. Gaston, S. Benvenuti, L. Dall'Antonia, and G. K. Davoren. 2009. Central-place foraging in an arctic seabird provides evidence for Storer-Ashmole's halo. Auk **126**:613-625.

Emmerson, L., and C. Southwell. 2008. Sea ice cover and its influence on Adélie Penguin reproductive performance. Ecology **89**:2096-2102.

Emmerson, L., and C. Southwell. 2011. Adélie penguin survival: age structure, temporal variability and environmental influences. Oecologia **167**:951-965.

Endler, J. A. 1986. Natural selection in the wild. Princeton University Press, Princeton, New Jersey.

Ezard, T. H. G., P. H. Becker, and T. Coulson. 2007. Correlations between age, phenotype, and individual contribution to population growth in common terns. Ecology **88**:2496-2504.

Forcada, J., and P. N. Trathan. 2009. Penguin responses to climate change in the Southern Ocean. Global Change Biology **15**:1618-1630.

Forchhammer, M. C., T. H. Clutton-Brock, J. Lindstrom, and S. D. Albon. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. Journal of Animal Ecology **70**:721-729.

Ford, R. G., D. G. Ainley, A. Lescroël, P. O. Lyver, V. Toniolo, and G. Ballard. 2015. Testing assumptions of central place foraging theory: a study of Adelie penguins Pygoscelis adeliae in the Ross Sea. Journal of Avian Biology **46**:193-205.

Forslund, P., and T. Pärt. 1995. Age and reproduction in birds - hypotheses and tests. Trends in Ecology & Evolution **10**:374-378.

Fox, G. A., B. E. Kendall, J. W. Fitzpatrick, and G. E. Woolfenden. 2006. Consequences of heterogeneity in survival probability in a population of Florida scrub-jays. Journal of Animal Ecology **75**:921-927.

Fraser, A. D., R. A. Massom, and K. J. Michael. 2010. Generation of high-resolution East Antarctic landfast sea-ice maps from cloud-free MODIS satellite composite imagery. Remote Sensing of Environment **114**:2888-2896.

Fraser, A. D., R. A. Massom, K. J. Michael, B. K. Galton-Fenzi, and J. L. Lieser. 2012. East Antarctic landfast sea ice distribution and variability, 2000-08. Journal Of Climate **25**:1137-1156.

Fraser, W. R., W. Z. Trivelpiece, D. G. Ainley, and S. G. Trivelpiece. 1992. Increases in Antarctic penguin populations - Reduced competition with whales or a loss of sea ice due to environmental warming. Polar Biology **11**:525-531.

Froy, H., S. Lewis, D. H. Nussey, A. G. Wood, and R. A. Phillips. 2017. Contrasting drivers of reproductive ageing in albatrosses. Journal of Animal Ecology **86**:1022-1032.

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. Ecology Letters **16**:642-649.

Gaillard, J. M., J. M. Boutin, D. Delorme, G. VanLaere, P. Duncan, and J. D. Lebreton. 1997. Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. Oecologia **112**:502-513.

Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics **31**:367-393.

Gaillard, J. M., A. Loison, C. Toigo, D. Delorme, and G. Van Laere. 2003. Cohort effects and deer population dynamics. Ecoscience **10**:412-420.

Gluckman, P. D., M. A. Hanson, and H. G. Spencer. 2005. Predictive adaptive responses and human evolution. Trends in Ecology & Evolution **20**:527-533.

Grafen, A. 1988. On the uses of data on lifetime reproductive success. Pages 454-471 *in* T. H. Clutton-Brock, editor. Reproductive Success. Studies of Individual Variation in Contrasting Breeding Systems. University of Chicago Press, Chicago, IL.

Gustafsson, L., and T. Part. 1990. Acceleration of senescence in the collared flycatcher (*Ficedula albicollis*) by reproductive costs. Nature **347**:279-281.

Gustafsson, L., and W. J. Sutherland. 1988. The costs of reproduction in the collared flycatcher (*Ficedula albicollis*). Nature **335**:813-815.

Halpern, B. S., S. Walbridge, K. A. Selkoe, C. V. Kappel, F. Micheli, C. D'Agrosa, J. F. Bruno, K. S. Casey, C. Ebert, H. E. Fox, R. Fujita, D. Heinemann, H. S. Lenihan, E. M. P. Madin, M. T. Perry, E. R. Selig, M. Spalding, R. Steneck, and R. Watson. 2008. A global map of human impact on marine ecosystems. Science **319**:948-952.

Hamilton, W. D. 1966. The moulding of senescence by natural selection. Journal of Theoretical Biology **12**:12-45.

Hammers, M., D. S. Richardson, T. Burke, and J. Komdeur. 2013. The impact of reproductive investment and early-life environmental conditions on senescence: support for the disposable soma hypothesis. Journal of Evolutionary Biology **26**:1999-2007.

Hanssen, S. A., I. Folstad, and K. E. Erikstad. 2003. Reduced immunocompetence and cost of reproduction in common eiders. Oecologia **136**:457-464.

Harshman, L. G., and A. J. Zera. 2007. The cost of reproduction: the devil in the details. Trends in Ecology & Evolution **22**:80-86.

Hastings, K. K., L. A. Jemison, T. S. Gelatt, J. L. Laake, G. W. Pendleton, J. C. King, A. W. Trites, and K. W. Pitcher. 2011. Cohort effects and spatial variation in age-specific survival of Steller sea lions from southeastern Alaska. Ecosphere **2**:21.

Hayward, A. D., A. J. Wilson, J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, and L. E. B. Kruuk. 2013. Reproductive senescence in female Soay sheep: variation across traits and contributions of individual ageing and selective disappearance. Functional Ecology **27**:184-195.

Hilborn, R., and M. Mangel. 1997. The ecological detective: confronting models with data. Princeton University Press.

Hinke, J. T., S. G. Trivelpiece, and W. Z. Trivelpiece. 2014. Adelie penguin (Pygoscelis adeliae) survival rates and their relationship to environmental indices in the South Shetland Islands, Antarctica. Polar Biology **37**:1797-1809.

Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? Trends in Ecology & Evolution **15**:56-61.

Hunt, G. L., Z. A. Eppley, and D. C. Schneider. 1986. Reproductive-performance of seabirds - the importance of population and colony size. Auk **103**:306-317.

IPCC. 2007. Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II, and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

Irvine, L. G., J. R. Clarke, and K. R. Kerry. 2000. Low breeding success of the Adélie penguin at Béchervaise Island in the 1998/99 season. Ccamlr Science **7**:151-167.

Jankowiak, L., D. Zyskowski, and D. Wysocki. 2018. Age-specific reproduction and disposable soma in an urban population of Common Blackbirds *Turdus merula*. Ibis **160**:130-144.

Jennings, S. 2015. Provisioning, growth and survival of Adélie Penguin chicks at Cape Crozier, Ross Island, Antarctica. Oregon State University, Corvallis, OR.

Jennings, S., A. Varsani, K. M. Dugger, G. Ballard, and D. G. Ainley. 2016. Sex-based differences in Adelie Penguin (*Pygoscelis adeliae*) chick growth rates and diet. PLoS ONE **11**:13.

Jenouvrier, S. 2013. Impacts of climate change on avian populations. Global Change Biology **19**:2036-2057.

Jensen, H., T. Svorkmo-Lundberg, T. H. Ringsby, and B. E. Saether. 2006. Environmental influence and cohort effects in a sexual ornament in the house sparrow, Passer domesticus. Oikos **114**:212-224.

Kim, S. Y., A. Velando, R. Torres, and H. Drummond. 2011. Effects of recruiting age on senescence, lifespan and lifetime reproductive success in a long-lived seabird. Oecologia:1-12.

Kirkwood, T. B. 1977. Evolution of ageing. Nature **270**:301.

Kuzawa, C. W. 2005. Fetal origins of developmental plasticity: Are fetal cues reliable predictors of future nutritional environments? American Journal of Human Biology **17**:5-21.

LaRue, M. A., D. G. Ainley, M. Swanson, K. M. Dugger, P. O. Lyver, K. Barton, and G. Ballard. 2013. Climate change winners: Receding ice fields facilitate colony expansion and altered dynamics in an Adélie Penguin metapopulation. PLoS ONE **8**.

Lea, A. J., J. Altmann, S. C. Alberts, and J. Tung. 2015. Developmental Constraints in a Wild Primate. American Naturalist **185**:809-821.

Lemaître, J. F., V. Berger, C. Bonenfant, M. Douhard, M. Gamelon, F. Plard, and J. M. Gaillard. 2015. Early-late life trade-offs and the evolution of ageing in the wild. Proceedings Of The Royal Society B-Biological Sciences **282**:10.

Lescroël, A., G. Ballard, D. Grémillet, M. Authier, and D. G. Ainley. 2014. Antarctic climate change: extreme events disrupt plastic phenotypic response in Adélie penguins. PLoS ONE **9**:e85291.

Lescroël, A., G. Ballard, V. Toniolo, K. J. Barton, P. R. Wilson, P. O. Lyver, and D. G. Ainley. 2010. Working less to gain more: when breeding quality relates to foraging efficiency. Ecology **91**:2044-2055.

Lescroël, A., K. M. Dugger, G. Ballard, and D. G. Ainley. 2009. Effects of individual quality, reproductive success and environmental variability on survival of a long-lived seabird. Journal of Animal Ecology **78**:798-806.

Limmer, B., and P. H. Becker. 2007. The relative role of age and experience in determining variation in body mass during the early breeding career of the Common Tern (Sterna hirundo). Behavioral Ecology and Sociobiology **61**:1885-1896.

Limmer, B., and P. H. Becker. 2009. Improvement in chick provisioning with parental experience in a seabird. Animal Behaviour **77**:1095-1101.

Limmer, B., and P. H. Becker. 2010. Improvement of reproductive performance with age and breeding experience depends on recruitment age in a long-lived seabird. Oikos **119**:500-507.

Lindström, J. 1999. Early development and fitness in birds and mammals. Trends in Ecology & Evolution **14**:343-348.

Lindström, J., and H. Kokko. 2002. Cohort effects and population dynamics. Ecology Letters **5**:338-344.

Lynch, H. J., W. F. Fagan, R. Naveen, S. G. Trivelpiece, and W. Z. Trivelpiece. 2012. Differential advancement of breeding phenology in response to climate may alter staggered breeding among sympatric pygoscelid penguins. Marine Ecology-Progress Series **454**:135-+.

Lynch, H. J., and M. A. Larue. 2014. First global census of the Adelie Penguin. Auk **131**:457-466.

Lyver, P. O., M. Barron, K. J. Barton, D. G. Ainley, A. Pollard, S. Gordon, S. McNeill, G. Ballard, and P. R. Wilson. 2014. Trends in the breeding population of Adélie Penguins in the Ross Sea, 1981-2012: a coincidence of climate and resource extraction effects. PLoS ONE **9**:10.

Lyver, P. O., C. J. MacLeod, G. Ballard, B. J. Karl, K. J. Barton, J. Adams, D. G. Ainley, and P. R. Wilson. 2011. Intra-seasonal variation in foraging behavior among Adélie penguins (*Pygocelis adeliae*) breeding at Cape Hallett, Ross Sea, Antarctica. Polar Biology **34**:49-67.

Madsen, T., and R. Shine. 2000. Silver spoons and snake body sizes: prey availability early in life influences long-term growth rates of free-ranging pythons. Journal of Animal Ecology **69**:952-958.

Massom, R. A., and S. E. Stammerjohn. 2010. Antarctic sea ice change and variability - Physical and ecological implications. Polar Science **4**:149-186.

McCleery, R. H., C. M. Perrins, B. C. Sheldon, and A. Charmantier. 2008. Age-specific reproduction in a long-lived species: the combined effects of senescence and individual quality. Proceedings Of The Royal Society B-Biological Sciences **275**:963-970.

McElligott, A. G., R. Altwegg, and T. J. Hayden. 2002. Age-specific survival and reproductive probabilities: evidence for senescence in male fallow deer (Dama dama). Proceedings Of The Royal Society B-Biological Sciences **269**:1129-1137.

Metcalfe, N. B., and P. Monaghan. 2001. Compensation for a bad start: grow now, pay later? Trends in Ecology & Evolution **16**:254-260.

Millon, A., S. J. Petty, and X. Lambin. 2010. Pulsed resources affect the timing of first breeding and lifetime reproductive success of tawny owls. Journal of Animal Ecology **79**:426-435.

Millon, A., S. J. Petty, B. Little, and X. Lambin. 2011. Natal conditions alter age-specific reproduction but not survival or senescence in a long-lived bird of prey. Journal of Animal Ecology **80**:968-975.

Monaghan, P. 2008. Early growth conditions, phenotypic development and environmental change. Philosophical Transactions of the Royal Society B-Biological Sciences **363**:1635-1645.

Monaghan, P., A. Charmantier, D. H. Nussey, and R. E. Ricklefs. 2008. The evolutionary ecology of senescence. Functional Ecology **22**:371-378.

Moyes, K., B. J. T. Morgan, A. Morris, S. J. Morris, T. H. Clutton-Brock, and T. Coulson. 2009. Exploring individual quality in a wild population of red deer. Journal of Animal Ecology **78**:406-413.

Nettle, D., W. E. Frankenhuis, and I. J. Rickard. 2013. The evolution of predictive adaptive responses in human life history. Proceedings Of The Royal Society B-Biological Sciences **280**:9.

Nevoux, M., H. Weimerskirch, and C. Barbraud. 2007. Environmental variation and experience-related differences in the demography of the long-lived black-browed albatross. Journal of Animal Ecology **76**:159-167.

Newton, I. 1989. Lifetime Reproduction in Birds. Academic Press, San Diego, California.

Newton, I., and P. Rothery. 1997. Senescence and reproductive value in Sparrowhawks. Ecology **78**:1000-1008.

Nol, E., and J. N. M. Smith. 1987. Effects of age and breeding experience on seasonal reproductive success in the song sparrow. Journal of Animal Ecology **56**:301-313.

Nur, N. 1984a. The consequences of brood size for breeding Blue Tits. I. Adult survival, weight change and the cost of reproduction. Journal of Animal Ecology **53**:479-496.

Nur, N. 1984b. Increased reproductive success with age in the California gull: due to increased effort or improvement in skill? Oikos **43**:407-408.

Nur, N. 1988. The consequences of brood size for breeding Blue Tit. III. Measuring the cost of reproduction: survival, future fecundity, and differential dispersal. Evolution **42**:351-362.

Nussey, D. H., T. Coulson, M. Festa-Bianchet, and J. M. Gaillard. 2008. Measuring senescence in wild animal populations: towards a longitudinal approach. Functional Ecology **22**:393-406.

Nussey, D. H., H. Froy, J. F. Lemaitre, J. M. Gaillard, and S. N. Austad. 2013. Senescence in natural populations of animals: Widespread evidence and its implications for bio-gerontology. Ageing Research Reviews **12**:214-225.

Nussey, D. H., L. E. B. Kruuk, A. Donald, M. Fowlie, and T. H. Clutton-Brock. 2006. The rate of senescence in maternal performance increases with early-life fecundity in red deer. Ecology Letters **9**:1342-1350.

Nussey, D. H., L. E. B. Kruuk, A. Morris, and T. H. Clutton-Brock. 2007. Environmental conditions in early life influence ageing rates in a wild population of red deer. Current Biology **17**:R1000-R1001.

Ollason, J. S., and G. M. Dunnet. 1988. Variation in breeding success in Fulmars. Pages 263-278 *in* T. H. Clutton-Brock, editor. Reproductive Success. Studies of Individual Variation in Contrasting Breeding Systems. Univ. of Chicago Press, Chicago, IL.

Olmastroni, S., F. Pezzo, V. Volpi, and S. Focardi. 2004. Effects of weather and sea-ice on the reproductive performance of the Adélie penguin at Edmonson Point, Ross Sea. Ccamlr Science **11**:99-109.

Oppel, S., A. Beard, D. Fox, E. Mackley, E. Leat, L. Henry, E. Clingham, N. Fowler, J. Sim, J. Sommerfeld, N. Weber, S. Weber, and M. Bolton. 2015. Foraging distribution of a tropical seabird supports Ashmole's hypothesis of population regulation. Behavioral Ecology and Sociobiology **69**:915-926.

Orell, M., and E. J. Belda. 2002. Delayed cost of reproduction and senescence in the willow tit Parus montanus. Journal of Animal Ecology **71**:55-64.

Panagakis, A., S. Hamel, and S. D. Cote. 2017. Influence of early reproductive success on longevity and late reproductive success in an alpine ungulate. American Naturalist **189**:667-683.

Pardo, D., C. Barbraud, M. Authier, and H. Weimerskirch. 2013. Evidence for an age-dependent influence of environmental variations on a long-lived seabird's life-history traits. Ecology **94**:208-220.

Parkinson, C. L. 2002. Trends in the length of the Southern Ocean sea-ice season, 1979-99. Pages 435-440 *in* J. G. Winther and R. Solberg, editors. Annals of Glaciology, Vol 34, 2002. Int Glaciological Soc, Cambridge.

Pärt, T., L. Gustafsson, and J. Moreno. 1992. Terminal investment and a sexual conflict in the collard flycatcher (*Ficedula albicollis*). American Naturalist **140**:868-882.

Partridge, L., and P. H. Harvey. 1988. The ecological context of life-history evolution. Science **241**:1449-1455.

Penney, R. L., and G. Lowry. 1967. Leopard seal predation on Adélie penguins. Ecology **48**:878-&.

Perdeck, A. C., and A. J. Cavé. 1992. Laying date in the Coot: Effects of age and mate choice. Journal of Animal Ecology **61**:13-19.

Polito, M. J., A. K. Miller, S. G. Trivelpiece, and W. Z. Trivelpiece. 2010. Maturation increases early reproductive investment in Adélie Penguins *Pygoscelis adeliae*. Ibis **152**:38-47.

Price, G. R. 1970. Selection and covariance. Nature **227**:520-&.

Rattiste, K. 2004. Reproductive success in presenescent common gulls (*Larus canus*): the importance of the last year of life. Proceedings of the Royal Society of London Series B-Biological Sciences **271**:2059-2064.

Rebke, M., T. Coulson, P. H. Becker, and J. W. Vaupel. 2010. Reproductive improvement and senescence in a long-lived bird. Proceedings of the National Academy of Sciences of the United States of America **107**:7841-7846.

Reed, J. M., and A. P. Dobson. 1993. Behavioral constraints and conservation biology - conspecific attraction and recruitment. Trends in Ecology & Evolution **8**:253-256.

Reed, T. E., L. E. B. Kruuk, S. Wanless, M. Frederiksen, E. J. A. Cunningham, and M. P. Harris. 2008. Reproductive senescence in a long-lived seabird: Rates of decline in late-life performance are associated with varying costs of early reproduction. American Naturalist **171**:E89-E101.

Reid, J. M., E. M. Bignal, S. Bignal, D. I. McCracken, and P. Monaghan. 2003. Age-specific reproductive performance in red-billed choughs *Pyrrhocorax pyrrhocorax*: patterns and processes in a natural population. Journal of Animal Ecology **72**:765-776.

Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos **44**:257-267.

Ribic, C., and D. Ainley. 1988/1989. Constancy of seabird species assemblages: an exploratory look. Biological oceanography **6**:175-202.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution **43**:223-225.

Robinson, N. J., and M. J. M. Williams. 2012. Iceberg-induced changes to polynya operation and regional oceanography in the southern Ross Sea, Antarctica, from in situ observations. Antarctic Science **24**:514-526.

Rödel, H. G., A. Bora, J. Kaiser, P. Kaetzke, M. Khaschei, and D. von Holst. 2004. Density-dependent reproduction in the European rabbit: a consequence of individual response and age-dependent reproductive performance. Oikos **104**:529-539.

Rose, K. E., T. H. Clutton-Brock, and F. E. Guinness. 1998. Cohort variation in male survival and lifetime breeding success in red deer. Journal of Animal Ecology **67**:979-986.

Sæther, B. 1990. Age-specific variation in reproductive performance of birds. Pages 251-283 *in* D. M. Power, editor. Current Ornithology. Plenum Publishing Corporation, New York.

Sæther, B. E. 1997. Environmental stochasticity and population dynamics of large herbivores: A search for mechanisms. Trends in Ecology & Evolution **12**:143-149.

Sloboda, D. M., G. J. Howie, A. Pleasants, P. D. Gluckman, and M. H. Vickers. 2009. Pre- and postnatal nutritional histories influence reproductive maturation and ovarian function in the rat. PLoS ONE **4**:8.

Smith, R. C., D. Ainley, K. Baker, E. Domack, S. Emslie, B. Fraser, J. Kennett, A. Leventer, E. Mosley-Thompson, S. Stammerjohn, and M. Vernet. 1999. Marine ecosystem sensitivity to climate change. Bioscience **49**:393-404.

Smith, W. O., D. G. Ainley, and R. Cattaneo-Vietti. 2007. Trophic interactions within the Ross Sea continental shelf ecosystem. Philosophical Transactions of the Royal Society B-Biological Sciences **362**:95-111.

Smith, W. O., and L. I. Gordon. 1997. Hyperproductivity of the Ross Sea (Antarctica) polynya during austral spring. Geophysical Research Letters **24**:233-236.

Smith, W. O., P. N. Sedwick, K. R. Arrigo, D. G. Ainley, and A. H. Orsi. 2012. The Ross Sea in a sea of change. Oceanography **25**:90-103.

Spurr, E. 1975. Breeding of the Adélie penguin *Pygoscelis adeliae* at Cape Bird. Ibis **117**:324-338.

Stammerjohn, S., R. Massom, D. Rind, and D. Martinson. 2012. Regions of rapid sea ice change: An inter-hemispheric seasonal comparison. Geophysical Research Letters **39**.

Stammerjohn, S. E., D. G. Martinson, R. C. Smith, and R. A. Iannuzzi. 2008a. Sea ice in the western Antarctic Peninsula region: Spatio-temporal variability from ecological and climate change perspectives. Deep-Sea Research Part Ii-Topical Studies in Oceanography **55**:2041-2058.

Stammerjohn, S. E., D. G. Martinson, R. C. Smith, X. Yuan, and D. Rind. 2008b. Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño-Southern Oscillation and Southern Annular Mode variability. Journal of Geophysical Research-Oceans **113**:C03S90, doi: 10.1029/2007JC004269.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.

Suryan, R. M., and D. B. Irons. 2001. Colony and population dynamics of black-legged kittiwakes in a heterogeneous environment. Auk **118**:636-649.

Sydeman, W. J., J. F. Penniman, T. M. Penniman, P. Pyle, and D. G. Ainley. 1991. Breeding performance in the Western Gull: effects of parental age, timing of breeding and year in relation to food availability. Journal of Animal Ecology **60**:135-149.

Taylor, R. H. 1962. The Adélie penguin *Pygoscelis adeliae* at Cape Royds. Ibis **104**:176-204.

Team, R. C. 2018. *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria.

Thomas, C., and J. Coulson. 1988. Reproductive success of kittiwake gulls, Rissa tridactyla. Pages 251-262 *in* T. H. Clutton-Brock, editor. Reproductive Success. Studies of Individual Variation in Contrasting Breeding Systems. Univ. of Chicago Press, Chicago, IL.

Tynan, C. T., D. G. Ainley, and I. Stirling. 2010. Sea ice: a critical habitat for polar marine mammals and birds. Pages 395-424 *in* D. N. Thomas and G. S. Dieckmann, editors. Sea ice. Wiley-Blackwell, Oxford, UK.

Van de Pol, M., L. W. Bruinzeel, D. Heg, H. P. Van der Jeugd, and S. Verhulst. 2006. A silver spoon for a golden future: long-term effects of natal origin on fitness prospects of oystercatchers (Haematopus ostralegus). Journal of Animal Ecology **75**:616-626.

van de Pol, M., and S. Verhulst. 2006. Age-dependent traits: A new statistical model to separate within- and between-individual effects. American Naturalist **167**:766-773.

Vaupel, J. W., and V. C. Romo. 2002. Decomposing demographic change into direct vs. compositional components. Demographic Research **7**:1-14.

Vaupel, J. W., and A. I. Yashin. 1985. Heterogeneity ruses - some surprising effects of selection on population-dynamics. American Statistician **39**:176-185.

Watanuki, Y., A. Kato, K. Sato, Y. Niizuma, C. A. Bost, Y. Le Maho, and Y. Naito. 2002. Parental mass change and food provisioning in Adelie penguins rearing chicks in colonies with contrasting sea-ice conditions. Polar Biology **25**:672-681.

Weimerskirch, H. 1990. The influence of age and experience on breeding performance of the Antarctic fulmar *Fulmarus glacialoides*. Journal of Animal Ecology **59**:867-875.

Weladji, R. B., A. Loison, J. M. Gaillard, O. Holand, A. Mysterud, N. G. Yoccoz, M. Nieminen, and N. C. Stenseth. 2008. Heterogeneity in individual quality overrides costs of reproduction in female reindeer. Oecologia **156**:237-247.

Wells, J. C. K. 2006. Is early development in humans a predictive adaptive response anticipating the adult environment? Trends in Ecology & Evolution **21**:424-425.

Whitehead, A. L., P. O. Lyver, G. Ballard, K. Barton, B. J. Karl, K. M. Dugger, S. Jennings, A. Lescroël, P. R. Wilson, and D. G. Ainley. 2015. Factors driving Adelie penguin chick size, mass and condition at colonies of different sizes in the Southern Ross Sea. Marine Ecology Progress Series **523**:199-213.

Williams, G. C. 1957. Pleiotropy, natural selection, and the evolution of senescence. Evolution **11**:398-411.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. The American Naturalist **100**:687-690.

Wilson, P. R., D. G. Ainley, N. Nur, S. S. Jacobs, K. J. Barton, G. Ballard, and J. C. Comiso. 2001. Adélie penguin population change in the pacific sector of

Antarctica: relation to sea-ice extent and the Antarctic Circumpolar Current. Marine Ecology-Progress Series **213**:301-309.

Wooller, R. D., J. S. Bradley, and J. P. Croxall. 1992. Long-term population studies of seabirds. Trends in Ecology & Evolution **7**:111-114.

Wooller, R. D., J. S. Bradley, I. J. Skira, and D. L. Serventy. 1990. Reproductive success of short-tailed shearwaters *Puffinus tenuirostris* in relation to their age and breeding experience. Journal of Animal Ecology **59**:161-170.

Yeates, G. 1968. Studies on the Adélie penguin at Cape Royds 1964–65 and 1965–66. New Zealand Journal of Marine and Freshwater Research **2**:472-496.

APPENDICES

APPENDIX A – Chapter 2 supplementary materials

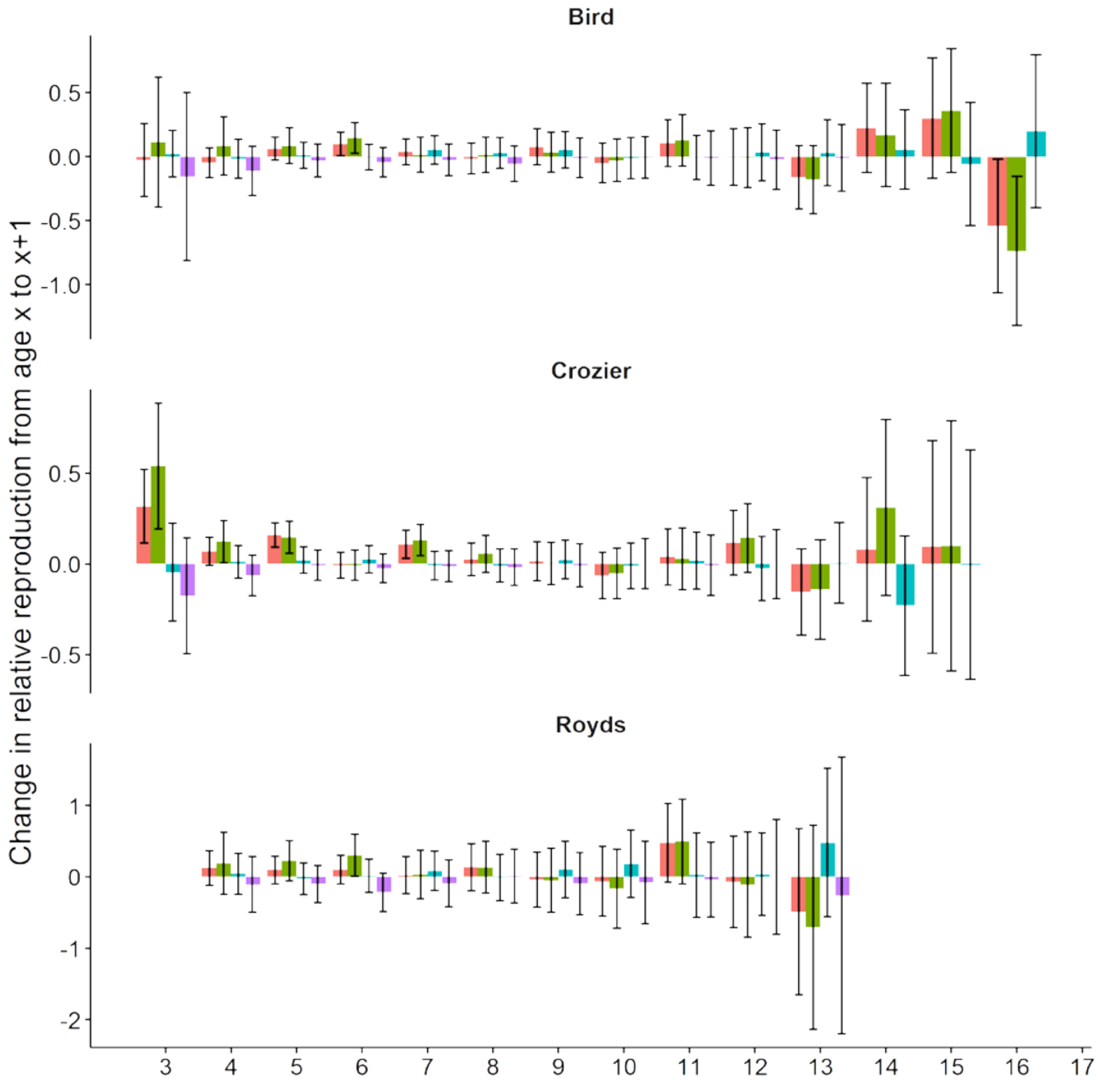


Figure A1. The change in population level relative reproduction from age *x* to *x* + 1 (pink bars); green, light blue, and purple bars represent the amount of change attributable to processes of within-individual maturation, selective disappearance, and selective appearances, respectively. The error bars represent 95% confidence intervals.

APPENDIX B – Chapter 4 supplemental materials

Table B1. Summary of the number of known-aged banded Adélie penguins breeding at capes Bird, Royds, and Crozier that had a break in their resighting history after recruiting to the breeding population.

Seasons not observed	Count	Percent
0	1942	94.6%
1	74	3.6%
2	22	1.1%
3	7	0.3%
4	4	0.2%
5	3	0.1%

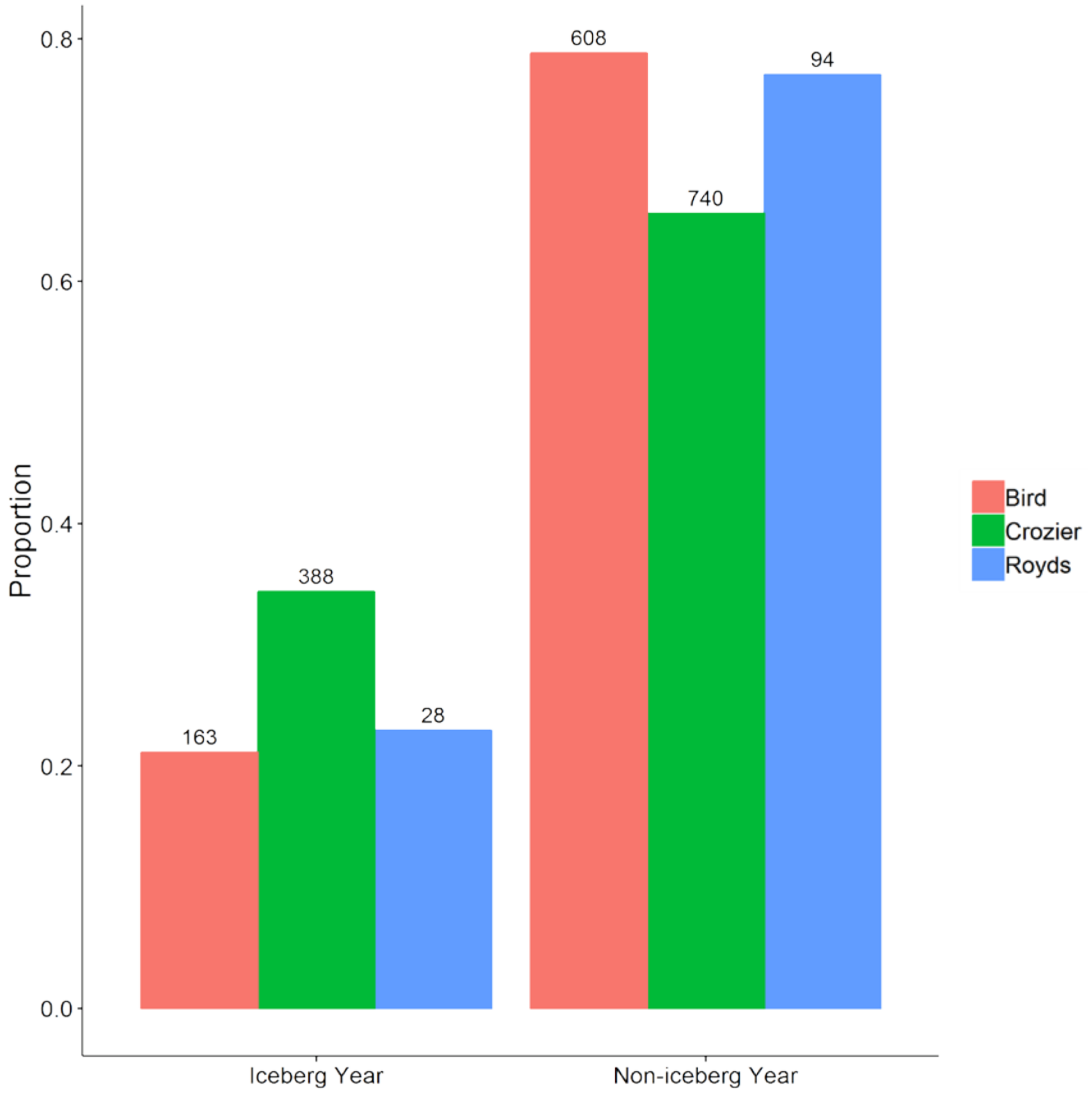
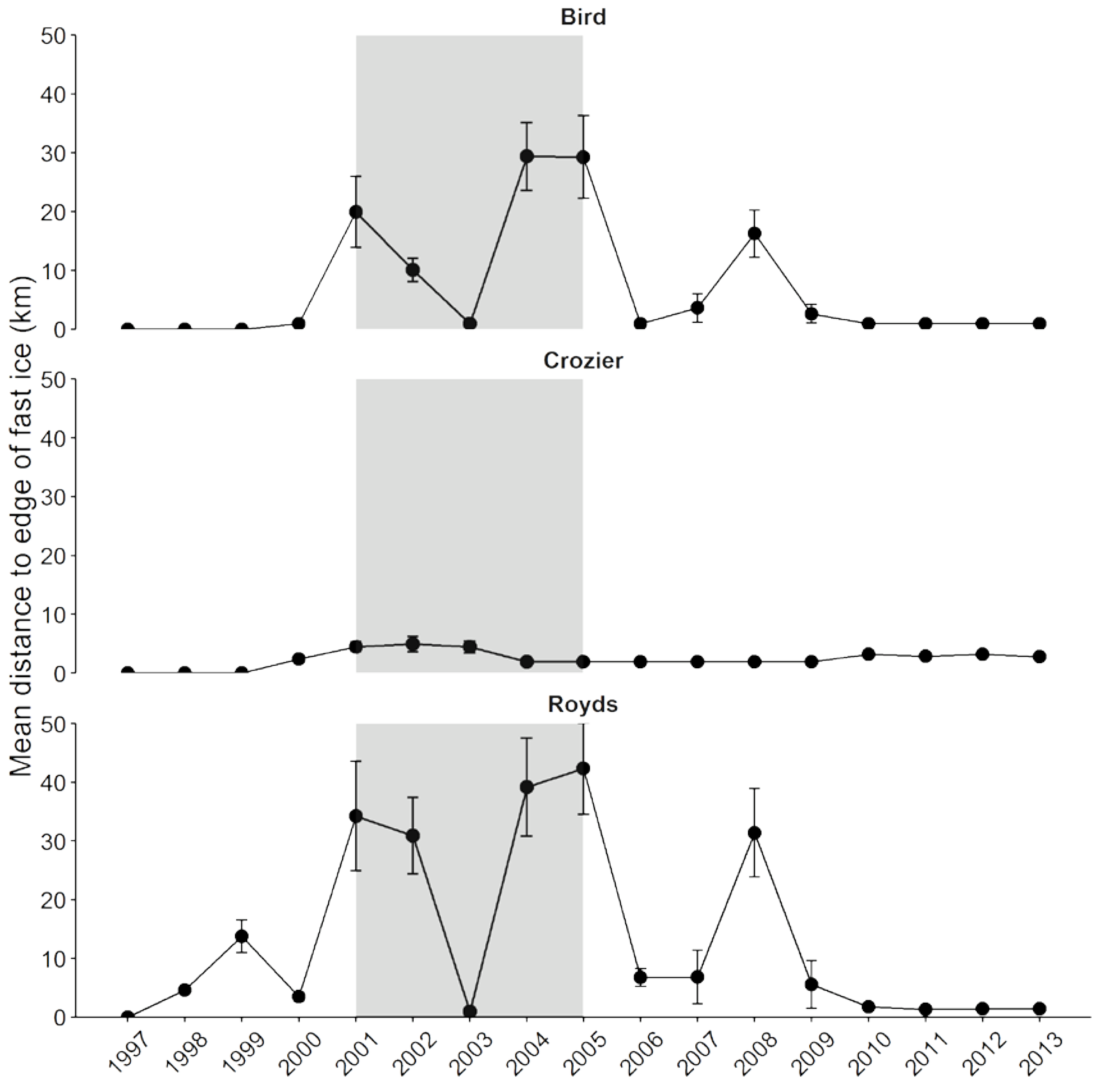


Figure B1. Proportion of known-aged Adélie penguins from iceberg (2001 – 2005) and non-iceberg (1994 – 2000; 2006-2013) cohorts that recruited to the breeding populations at Capes Bird (pink), Crozier (green), and Royds (blue), Ross Island Antarctica. Numbers above bars represent the number of individuals.

A)


Bird
Crozier
Royds
Mean distance to edge of fast ice (km)
0
10
20
30
40
50
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013

B)

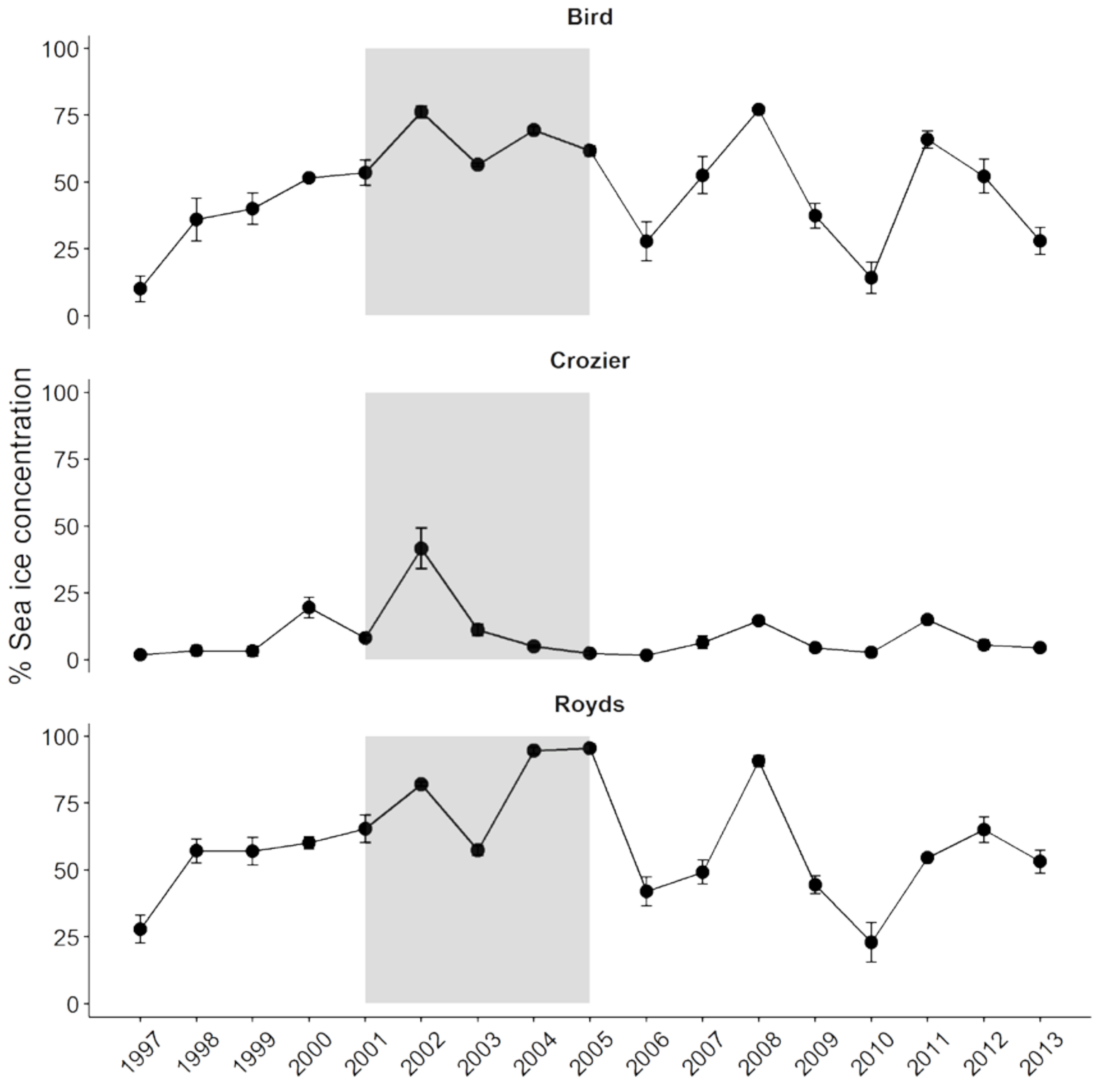


Figure B2. Median (± SE) annual trends in (A) fast ice extent, and (B) sea ice concentration on the foraging grounds of Capes Bird, Crozier, and Royds during the breeding season. The presence of giant icebergs is indicated by shading. More information on each metric can be found in Table 4.2.

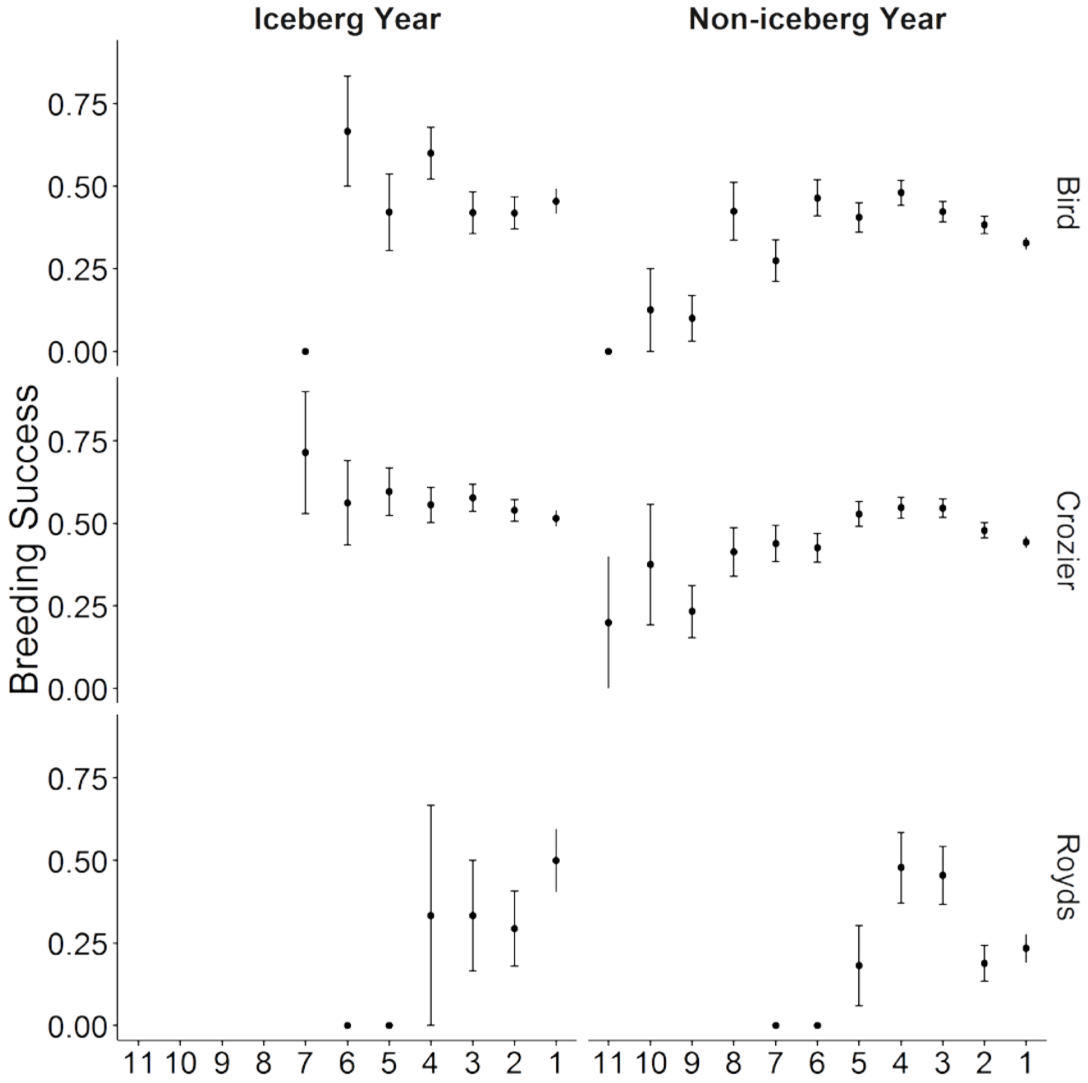


Figure B3. The relationship between years before death (1 being equal to the last year of life) and the proportion of successful breeding attempts (measured as the number of occasions at least 1 chick was successfully raised to enter a crèche) for cohorts born during iceberg-affected and non-iceberg-affected years at Capes Bird, Crozier, and Royds. Data points are the mean ± SE; *n* = 2052 individuals.

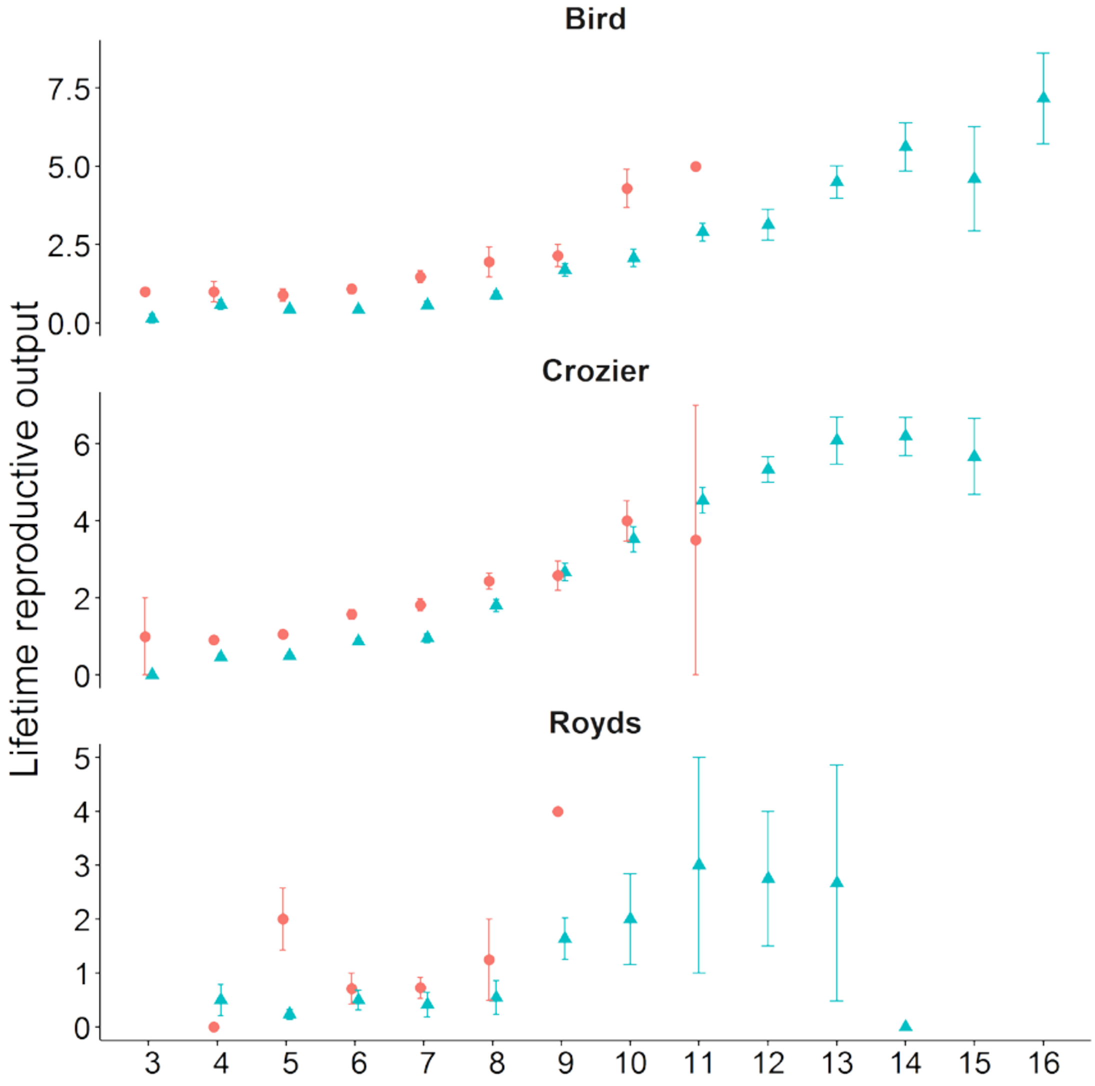


Figure B4. Relationship between longevity and lifetime reproductive output, of Adélie penguins in the iceberg-affected (pink circles) and non-iceberg-affected (blue triangles) cohorts breeding at Capes Bird, Crozier, and Royds in the Ross Island, Antarctica meta-population. Lifetime reproductive output was measured as the total number chicks successful raised to enter a crèche over an individual's lifetime. Data points are mean ± SE.

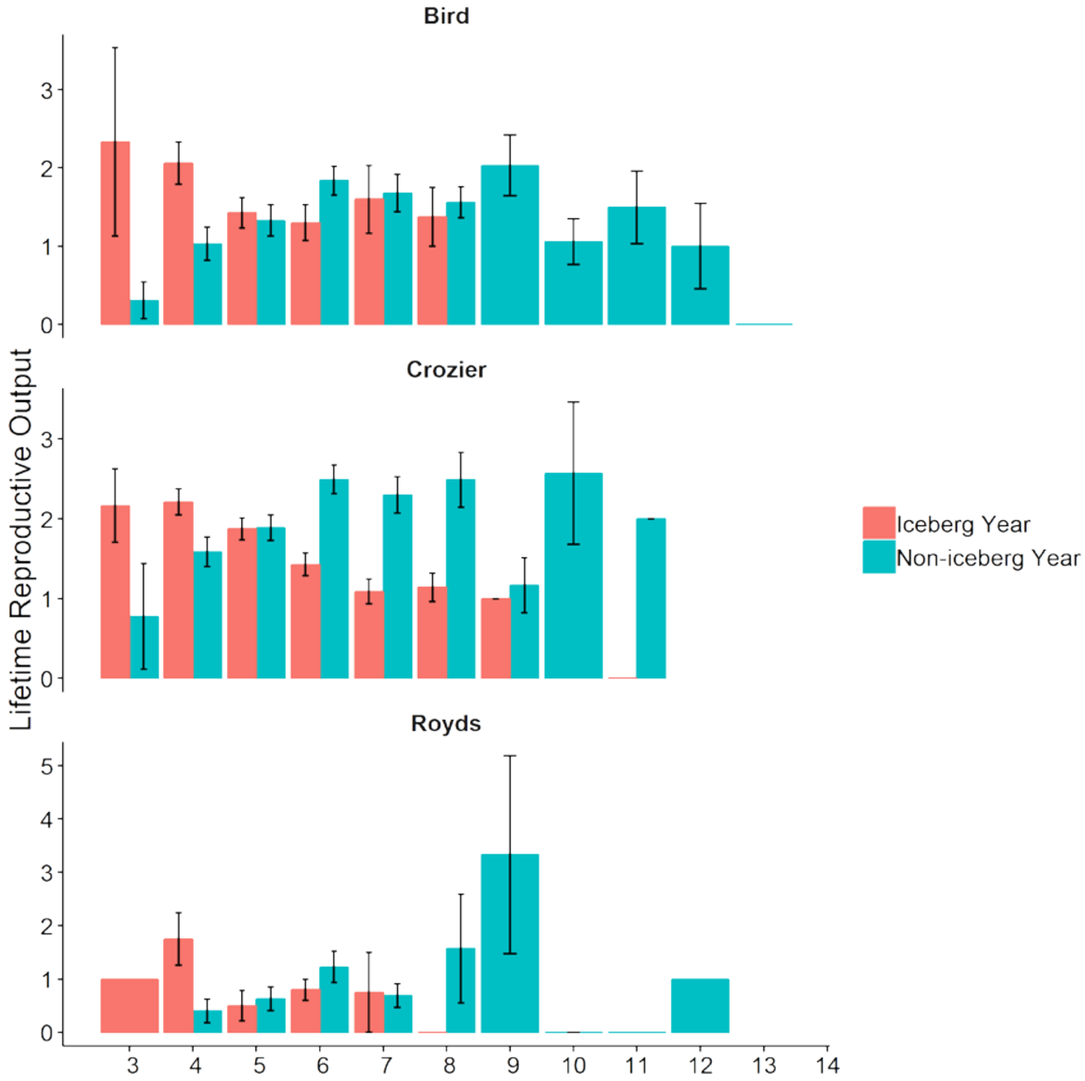


Figure B5. The mean lifetime reproductive success, measured as the total number chicks an individual raised that successfully entered a crèche, based on age at first reproduction of iceberg-affected and non-iceberg-affected cohorts at Capes Bird, Crozier, and Royds, Ross Island, Antarctica. Data are means ± SE.