

The breeding ecology and behavioural adaptations of African Black Oystercatchers in light of climate change



Bukola Debola Aderewa Azaki (Nee Braimoh)

BSc. Zoology, MSc. Conservation Biology University of Jos, Nigeria



Thesis presented for the degree of Doctor of Philosophy

Biological Sciences Department, Faculty of Science, University of Cape Town

January 2021

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

Supervisors:

Professor Les Underhill

Dr Susan Cunningham

Copyright

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

Declaration

I declare that all the work presented in this thesis is my own except where otherwise acknowledged in the text. This thesis has not been submitted in whole or in part for a degree at any other university.

Signed:

Signed by candidate

Date: 31 January 2021

General abstract

This thesis examined how weather conditions and other environmental factors influence the vulnerability of nesting African Black Oystercatchers *Haematopus moquini* (oystercatchers) to climate and habitat change. I explore, for the first time, the behavioural adaptations used by the species to cope with breeding in a limited strip of beach, between high tides and terrestrial predators, and with little nesting shelter, and their breeding decisions to maximise breeding outcomes. Behavioural and breeding data were collected over three breeding seasons (2016—2018) on Robben Island, South Africa (a site with about 5% of the global population of the species) using time-lapse digital cameras and direct observations. Climate and environmental variables were obtained either through on-site iButton data loggers or from the relevant South African meteorological agencies. The results show that oystercatchers are vulnerable to increasing heat loads as temperature increases. However, oystercatchers used a suite of thermoregulatory behaviours to cope with a wide range of environmental temperatures and decreased the length of their incubation bouts as temperature increased. The proximity of the oystercatchers' breeding site to the ocean appears to contribute significantly to their capacity to cope with increasing heat loads. But such sites potentially expose the oystercatchers to the risk of nest losses to storm surges. Oystercatchers reduced this risk by using habitat selection to optimise the placement of their nests close to the midpoint of the beach, but some were constrained by the narrowness of their territories. Oystercatchers also used the biweekly semilunar spring tide cycle to synchronise the incubation start date of their clutches probably to minimise the number of spring tides that they experience during incubation. Predation was the main cause of oystercatcher nest failure. Surprisingly, Mole Snakes *Pseudaspis cana* were responsible in all cases where the predator identity was known rather than Kelp Gulls which have historically been suggested to be the main agent. Nest predation probability was influenced by temperature and distance to predator-concealing vegetation and increased as more nests became available, causing a seasonal decline of nest survival. Hence, oystercatcher pairs laying large clutches early in the season were more likely to produce one juvenile in a season. The average number of fledgelings per pair per season was 0.38 and close to that (0.35) required to maintain a stable population. These findings improve our understanding of the breeding ecology and behavioural adaptations of the oystercatchers which might help them to cope with climate change as well as provide new insights on which management decisions and further studies can be based.

Dedication

This, too, is for you, Adaniwayetodamiwaye! Thank you for being there every step of the way. To my mum, Mrs Roseline Binola Braimoh, for all the sacrifices she made to ensure that my siblings and I got educated.

To the loving memory of my dad, Pa Sam Oke Braimoh, who passed on August 6, 2020, just a few months to the completion of this thesis. I wish you were here to see that your girl overcame all the odds to get this done! The values of hard work, sense of responsibility, honesty, faith, determination, and love that you instilled in us remain and will continue with us. I will forever cherish you in my heart, dad.

To Professor Will Cresswell for his commitment to excellence, research integrity, and for inspiring and mentoring many early-career individuals in the natural sciences, particularly in Africa (one of whom I am).

Acknowledgements

The success of this PhD journey is tied to the contributions and support of many people for whom I am forever grateful. Mr Tasso Leventis: thanks for covering the project costs and all other expenses relating to my studies at the University of Cape Town through the A.P. Leventis Ornithological Research Institute (APLORI) Foundation. Mr Phillip Hall: thanks for always checking on my progress and ensuring that funds get to my account in a timeous manner every quarter.

Professor Will Cresswell: when I attended your R class for the first time in 2013, I had no idea what a significant role you were going to play in my journey to getting a PhD. Without a doubt, I would not have been able to complete this thesis without the huge contributions you made into my thesis. Your sense of responsibility towards your students, mutual respect, prompt responses and the effectiveness with which you get the best out of all your students, irrespective of background or race, is highly commendable. Your award of ‘Teaching Excellence from St Andrews University, Scotland’ is well deserved. Thank you for believing in me and for providing an excellent professional example to emulate. Thanks for the equipment that you provided and for feedbacks that improved my proposal. Thanks for your thorough and constructive feedback on all my chapters: they always improved my work and got me closer to my goals because they got me to think deeply about what I am researching, search for more knowledge and learn a lot in the process. Thank you for choosing to invest substantially into my thesis without expecting anything in return and for being there at the very low moment of my PhD journey — it was priceless to know there was someone who could see through what was happening. In talking about you, my brother, Juwon Braimoh, said, “every once in a while, God gives the gift of men to aid our journey. I think that is what the UK Academic is”. I am blessed and grateful for your help and the role you played in the pursuit and realisation of my dreams. May God bless you and all yours and reward you tremendously in a manner that only He can. Dr Susan Cunningham: thank you so much for agreeing to take on the task of co-supervising me at a crucial point in this journey. Thank you for the support and help you provided that made it possible for me to complete this thesis. Thanks for the many administrative interventions you had to make and for your constructive feedback on all my chapters — they were very helpful. Thank you for introducing me to the wonderful members of your lab and for being a caring and amazing soul. Kia Ora!

Professor Les Underhill, thank you for the PhD experience; at the end of it all, I am stronger. I thank Professor Sue Harrison, Professor Maano Ramutsindela, Professor Jeff Murugan, Associate Professor David Gammon and Professor Muasya Muthama for the role they played at different points to ensure that this thesis got completed and submitted for examination. I am grateful to Dr Robert Thompson for his support and assistance during the difficult time of getting this thesis written.

I am grateful to all the academics who taught me, cheered me on at one stage or another in my academic journey: Professor Ulf Ottosson, Dr Soladoye Iwajomo, Dr Mark Wilson, Dr Martijn Hammers, Dr Shiiwua Manu, Dr Adams Chaskda, Dr Anthony Dawet, Dr Matthew Grainger and Dr Mary Molokwu-Odozi. I thank Dr Yahkat Barshep for her guidance at the start of my study at the University of Cape Town.

Immense thanks to Mr Sabelo Madlala, Phakamile Zungu, Inga Sipuka, Salinda Xasa, Andile Mdluli and all the members of the Environmental Unit of Robben Island Museum for all the logistical support and access to the island during the data collection phase of this study. Thanks to Mr Christopher Wilke of the Department of Agriculture, Forestry and Fisheries, South Africa and Mr Sabelo Madlala for always being ready to answer my questions about the wildlife on Robben Island and the historical culling activities which had occurred on the island.

I am grateful to all who came to the field with me at one point or another during data collection: Laurie Johnson, Amour McCarthy, Dr Elsa Bussiere, Andreas Ioannides, María López Gómez, Caitlin Smith, Sanjo Rose, Toluwanimi Simeon Adesola, Gloria Aaron, Nailantei Kamotho, Idoia Fuertes, Peta Brom, Emmanuel Oluwadunsin Adekola, Huw Irlam, Olivia Venter, Leigh Kelly, Zakhele Ramadikela, Andile Mdluli and Unai Apodaka. I thank Sue Kuyper for helping process tickets for everyone. I am grateful to Dane Paijmans for his support during the early days of this study.

I thank Joel Avni of Ecotone Africa and Professor Will Cresswell for the discussions around the choice of appropriate digital cameras. I acknowledge the weather data provided by the South African Weather Services and appreciate Elsa DeJager, Lucky Dlamini, and Musa Mkhwanazi for helping me to gain access to the data. I am grateful to the Hydrographer, South African Navy, Ruth Farre, for releasing tide data for the Cape Town harbour area.

I thank the organisers of the Student Conference on Conservation Science in Cambridge for the opportunity to attend the conference and a one-month internship program at Professor

Will Cresswell's lab at the University of St Andrews, Scotland, the UK in 2017. The experience at the conference and the internship contributed enormously to helping me get started with my PhD and to broadening my network. I thank the International Wader Study Group for their support towards my attendance at the 2018 IWSG conference in Workum, Netherlands and Dr Ens Bruno for assistance during and after the conference. I am thankful to Dr Alan Lee and the Editors of the Ostrich Journal of African Ornithology for the award of the Best Ostrich Student Paper 2018. The award came at a very crucial time in my career journey. It reaffirmed and boosted my resolve to continue to pursue my dreams and to forge ahead to complete this thesis.

Dr Dayo Osinubi, Dr Zingfa Wala, Dr Chima Nwaogwu, Emmanuel Adekola, Kwanje Bitrus, Sarah, Femi, Chris, and Daniel: Thank you for friendship, and the times we shared laughter and food. The warmth was always refreshing. Thanks to Colin and Roni Jackson as well as Nosipho Mali for friendship and introducing me to the Jubilee Community Church on my arrival to Cape Town. Thanks to Gill and Ken Bowley for all the gifts, walks and meals, during the course of this PhD, you are truly amazing. Thanks to friends from TCC, Muizenberg and Diep River connect groups: Luke Giles, Denzil and Debbie Abrahams, Michael and Rene Watson, Graham and Nina van Veen as well as Joy and Bill Phelps for their friendship and prayers during the writing phase of this thesis. I thank Professor Ishmael and Professor Tolu Ogboru, Justice Obayomi and family, the Dahilos, the Azakis and my lovely mother-in-law Mrs Mary Azaki for all their care, support and prayers for the successful completion of this thesis.

I am grateful to my late dad Pa Samuel Oke Braimoh, mum Mrs Roseline Binola Braimoh, sisters (Mrs Biodun Omotayo Akobe, Miss Deborah Omoyeni Braimoh and Barrister Bosede Otoayo Braimoh), and brother (Engineer Juwon Boluwaji Davids Braimoh) for the love, support, prayers, and everything that they have been to me all my life and especially through the long journey of getting this project completed. Thanks to Jason & Isaac Akobe and Mr Bola Akobe for coming along so nicely with lots of encouragement. My ever-loving, caring, and supportive husband, Joshua Azaki, I lack words to thank you enough for the many sacrifices you made to ensure that this thesis got completed. Thank you for the many days in the field, the encouragement, and the many times I requested, "please, honey, read this section, do you understand what I am trying to say?". I love you dearly. Finally, I thank God the Father of light in whom there is no variableness for giving me this wonderful support system, for all He has endowed me with and for carrying me through this journey, despite all the odds. To Him be glory, honour, power, and praise forever!

Table of Content

Copyright.....	iii
Declaration.....	iv
General abstract.....	v
Dedication.....	vi
Acknowledgements.....	vii
Table of Content	x
Chapter One: General Introduction	1
1.11 Biological diversity and the concept of fitness	1
1.12 Life-history traits.....	2
1.13 Environmental conditions lead to adaptive traits	3
1.14 Seasonal optimisation.....	6
1.15 Global changes.....	7
1.16 Flexibility and evidence of adaptation to climate change	8
1.2 Study system	10
1.21 Shorebirds	10
1.22 Justification of the study.....	11
1.23 Aim and objectives of the study	11
1.24 General methods	15
1.241 Study species: African Black Oystercatchers	15
1.242 Study site: Robben Island, Western Cape, South Africa	17
1.243 Trapping and sexing adult African Black Oystercatchers.....	19
1.244 Camera set-up around the nest.....	20
1.3 Ethics clearance and funding	21
1.4 Thesis structure/data source and contributions.....	21
Chapter Two: Cues for nest-site timing and selection by African Black Oystercatchers: Effects of semilunar spring tide periodicity and breeding habitat width	24
Abstract.....	25
2.1 Introduction	27
2.2 Methods.....	30
2.21 Nest search and estimation of the incubation start date of nests	30
2.22 The probability of nest losses to storm surges	31
2.23 Moon phase data and daily maximum tide hight on a given moon day	31
2.24 Habitat measurements	32
2.25 Data analysis	33

2.3 Results	35
2.31 Incubation start dates of oystercatchers' nests in relation to spring tide cycles	35
2.32 How does the breeding habitat width and the timing of the start of incubation relative to the spring tide cycle influence nest-site selection of oystercatchers?	37
2.4 Discussion.....	38
2.41 The onset of incubation by oystercatchers relative to the semilunar spring tide cycle.....	39
2.42 The impact of breeding habitat width on nest-site selection by oystercatchers	41
2.43 The impact of the spring tide cycle on nest-site selection by oystercatchers.....	42
2.44 Oystercatchers' nest placement relative to the middle of the breeding habitat affects the risk of nest losses to storm surges.....	42
2.5 Conclusion	43
Appendix	44
Chapter Three: On-bout thermoregulation behaviours used by African Black Oystercatchers to cope with varying temperatures during incubation	45
Abstract.....	46
3.1 Introduction	48
3.2 Methods.....	52
3.21 Footage analysis and scoring thermoregulatory behaviours.....	52
3.22 Temperature data collection	53
3.23 Data analysis	54
3.3 Results.....	56
3.31 Thermoregulatory behaviours used by oystercatchers as air temperature changes.....	56
3.32 Thermoregulatory behaviours used by oystercatchers across different hours of the day	59
3.33 Temperature variation within oystercatchers' breeding season.....	60
3.34 Comparisons among air, nest, and operative temperatures.....	61
3.4 Discussion.....	63
3.41 Heat dissipating behaviours used by oystercatchers under elevated evaporative cooling demand	63
3.42 Heat conservation behaviours: backrest posture	68
3.43 Were the oystercatchers able to modulate the temperature of their nest?	69
3.44 Implications of the increasing number of days with high air temperatures within the breeding season	70
3.5 Conclusions	72
Appendix	73
Chapter Four: Incubation scheduling by African Black Oystercatchers: Effects of weather, tide phase, and time of day	75
Abstract.....	76

4.1 Introduction	78
4.2 Methods.....	83
4.21 Video data extraction.....	83
4.22 Weather data and tide data.....	84
4.23 Data analysis	85
4.3 Results.....	87
4.31 Bout interruptions, nest exposure and associated changes in nest temperature	87
4.32 Overall nest attentiveness and sex contributions	88
4.33 Environmental factors influencing oystercatchers' incubation bout lengths.....	89
4.4 Discussion.....	94
4.41 Factors influencing oystercatchers' incubation bout lengths:.....	94
4.42 Thermoregulation importance of the proximity to the ocean for the oystercatchers and its potential to minimise the risk of nest abandonment under high heat loads.....	99
4.43 Bout interruptions, nest exposure and the associated changes in nest temperature	100
4.44 Overall nest attentiveness and sex contributions	102
4.5 Conclusion.....	103
Appendix	104
Chapter Five: The relative importance of different nest predators and predictors of nest predation in African Black Oystercatchers	105
Abstract.....	106
5.1 Introduction	108
5.2 Methods.....	111
5.21 Nest searching and monitoring.....	111
5.22 Habitat measurements as predictors of nest predation.....	114
5.23 Video placement and video-monitoring of nests	116
5.231 The potential effect of video deployment and other research activities on nest predation probability.....	117
5.24 Data analysis	117
5.3 Results.....	120
5.31 The predictors of nest predation	120
5.32 Camera monitored nests	124
5.33 Predator identity and the proportion of nests predated by each predator type.....	125
5.4 Discussion.....	126
5.41 Predictors of nest predation of oystercatchers	126
5.42 Predator identity, the relative importance of each predator.....	134
5.43 The impact of research activities on the fate of oystercatchers' nests.....	139

5.5 Conclusions and management implications	140
Appendix	142
Chapter Six: Population size, breeding parameters and predictors of breeding success of African Black Oystercatchers on Robben Island	147
Abstract	148
6.1 Introduction	149
6.2 Methods	153
6.21 Human disturbance	153
6.22 Estimating the numbers of adult oystercatchers and breeding pairs	154
6.23 Finding nests, ageing, and monitoring them to failure or success	155
6.24 Monitoring chicks to fledging	156
6.25 Data collection (predictors of nest survival and overall breeding success)	157
6.25 Data analysis	157
6.3 Results	160
6.31 The numbers of adult oystercatchers and breeding pairs	160
6.32 How many nests were found, what were their fate and how many produced at least a chick?	160
6.33 Predictors of daily nest survival	162
6.34 Overall breeding success	164
6.4 Discussion	167
6.41 Overall population, breeding population and number of nests found	167
6.42 Predictors of daily nest survival	168
6.43 The number of fledgelings per pair per year	173
6.5 Conclusion	176
Appendix	177
Chapter Seven: General discussion	180
7.1 Introduction	180
7.2 Evidence of adaptation to environmental variations	180
7.3 Potential impacts of future climate change	198
7.4 Prospectus	203
7.41 Management recommendations for African Black Oystercatchers	203
7.42 Future research	204
References	207

Chapter One: General Introduction

1.11 Biological diversity and the concept of fitness

Biological diversity (biodiversity) occurs at three distinct levels: species diversity (involving the many species of living organisms on earth), genetic diversity (the different genetic components within species), and ecosystem diversity (encompassing different biological communities and their associations with the environment) (Dalziel et al. 2009; Primack 2010). The continued persistence of all three forms of biodiversity in the face of increasing anthropogenic disruptions, is the goal of conservation biology (DeClerck et al. 2010; Primack 2010; Tscharncke & Tylianakis 2010). For biological diversity to persist (not go extinct), individuals within a species need to thrive enough to survive, grow and reproduce successfully to pass on their genetic components to subsequent generations and the populations within communities need to be maintained in sizes sufficient to retain genetic diversity, increase resilience to environmental change and minimize the risk of extinction (Ricklefs & Travis 1980; Reed & Frankham 2003; Reed 2005; Orr 2009; Markert et al. 2010).

Fitness, a concept that is central to evolutionary and behavioural ecological thinking, is used to describe how well the natural properties of an organism allows it to fit into its environment to enable growth, survival (survival fitness), attain sexual maturity and successfully reproduce itself (reproductive fitness) relative to others in a population (Kimbrough 1980; Ariew & Lewontin 2004; Krimbas 2004). Reproductive fitness is the probabilistic propensity to produce offspring and quantified as the number of fertile offspring contributed by an organism in its lifetime, relative to others, in a given generation into the population (gene pool) of future generations (Mills & Beatty 1979; Tetsuji 1996; Stadler & Stephens 2003; Pence & Ramsey 2013). One of the basic indices of fitness is the reproductive success of individuals, making the breeding stage of avian life cycles an important component of fitness and necessary for the continued persistence of species (Manier 1969; Urfi 2003; Pincheira-Donoso & Hunt 2017). Fitness has also been viewed as reproductive power, i.e., the rate of conversion of acquired energy into offspring by an organism (Brown et al. 1993). However, ultimately reproductive success is measured by the number of offspring that reach reproductive maturity (Snapp 1976).

1.12 Life-history traits

In between the time of birth and death of living organisms are key events and patterns that define their life-history – the patterns of how organisms develop, reproduce, and die (Nylin & Gotthard 1998). Life history traits describe the quantitative and demographic properties of the life cycle of organisms such as growth rate, age at sexual maturity, timing and schedule of breeding, pattern of parental care, number, and size of young, reproductive lifespan, patterns of ageing and death (Stearns 1977). Life-history traits are significantly linked to fitness through their close association with survival and reproduction and thus influences population growth rates (Sæther & Bakke 2000; Flatt & Heyland 2011).

Life-history traits are subject to environmental constraints (Price & Schluter 1991). Since environmental conditions vary widely geographically and temporally, the patterns of life-history traits vary widely among species and populations (Berven & Gill 1983; Carnicer et al. 2012). For example, species occurring in southern latitudes characterised by high predation rates usually lay fewer eggs per clutch compared with those in northern latitudes characterised by lower predation rates (Martin 1996). Other environmental conditions such as climate and patterns of food availability may also explain the differences in the life-history traits between high and low latitude species (Ricklefs 1980; Koenig 1984; Hussell 1985). Also, while some species may be long-lived (long life span), exhibit extensive parental care, and breed once a year, others may be short-lived (short life span), show minimal or no parental care and breed multiple times a year (Ricklefs 1990; Badyaev & Ghalambor 2001; Allen et al. 2017).

Several life history theories have been developed to facilitate the understanding of the numerous variations in the patterns of life-history traits among living organisms and the mechanisms driving such variations (Huey & Slatkin 1976; Stearns 1977; Nylin & Gotthard 1998; Martin 2002). Central to life-history theories is the idea that organisms have limited resources (e.g., time, food, habitat) and an investment of these resources in one fitness activity could result in a deficit in another (van Noordwijk & de Jong 1986; Varpe et al. 2009; Brosset et al. 2016). Hence the need for trade-offs that balance the investment of resources into competing fitness activities in a manner that maximises overall lifetime fitness (Badyaev & Ghalambor 2001; Ghalambor & Martin 2001). For example, life history theory expects long-lived species to invest more resources in body maintenance activities thereby

maximising survival over current reproduction while short-lived species should maximize current reproduction over body maintenance activities (Williams 1966). This is because by maximising survival over current reproduction under constraining environmental conditions long-lived species could increase their chance of staying alive to maximise future breeding opportunities potentially maximising overall lifetime reproductive output (Williams 1966; Ricklefs 2000). Examples of traits that could vary between long-lived and short-lived species include the number or size of offspring and the number of successful broods per breeding season with short-lived species more likely to attempt multiple broods per breeding season than long-lived species (Nagy & Holmes 2005; Brosset et al. 2016).

1.13 Environmental conditions lead to adaptive traits

There are several environmental conditions (biotic and abiotic) that could act as constraints to the successful growth, survival, and reproduction of organisms (the overall fitness of individuals) (Table 1.1). Individuals with genetic and behavioural traits that are well adapted into their environments usually experience higher fitness (higher survival rates and reproductive success) thereby leaving more offspring compared with individuals with poorer adaptation (Rosenberg 1983; Ariew & Lewontin 2004). Any trait that an organism possesses which helps it overcome the environmental constraints within its locality of occurrence in a manner that gives it a fitness advantage over other individuals in that population is an adaptive trait (Tetsuji 1996; Kingsolver & Huey 2003). The adaptive strategies used by the same species under two different environmental conditions could differ (Koenig 1984). Even the same individual may vary its adaptive strategy if placed under different environments (Both et al. 2019). The ability of a single genotype to produce different phenotypes under different environmental conditions is known as the reaction norm (Stearns & Koella 1986; Flatt & Heyland 2011). Studying the breeding ecology of organisms entails exploring these reaction norms: how weather conditions and other environmental constraints (biotic and abiotic) determine the life history traits of organisms, and influence individual breeding decisions, parameters, and outcomes (Ollason & Dunnet 1978; Mares et al. 2017; Millones & Frere 2017; Carlzon et al. 2018).

Table 1.1: Some examples of environmental conditions that could act as constraints and the corresponding adaptive traits used by species to cope.

Environmental condition	Adaptive /life history strategy	Example reference
Territory quality: usually vary in the amount of food available and/or protection from predators	The ability of individuals to vary clutch size to match territory quality (smaller clutches in poor territories and larger clutches in high-quality territories)	Hogstedt 1980; Tinbergen & Daan 1990
	The ability of individuals to secure and defend better-quality territory	Burger 1984; Ens et al. 1992
Adult predation pressure: the risk of being preyed upon could vary geographically and temporally and increase during reproduction	Preference for large group sizes which potentially increases survival probability through increased vigilance of the many eyes of group members to enhance prompt escape from predators, thereby minimising mortality risk.	Lima & Dill 1990; Etienne 2006; Thünken et al. 2014
	The ability to select nest-sites that conceal the breeding individuals and their nest but increases the early detection of potential predators	Amat & Masero 2004a; Anteau et al. 2012; Devries et al. 2018
Nest predation pressure: one of the major sources of breeding failure; varies by locality, type of nest, and predator type	Nest-site selection to minimise the risk of nest predation by making it hard for predators to detect the nest either by using camouflage or placement of nests in a concealed area	Hockey 1982; Lee et al. 2010; Troscianko et al. 2016; Gómez et al. 2018; Grant et al. 2019; Laidlaw et al. 2020
	Reduced parental activity rates around the nest to minimise the chance of revealing nests to nest predators	Martin et al. 2000; Ghalambor & Martin 2002; Matysioková & Remeš 2018
	The propensity of individuals to synchronise the timing of some stages of the reproductive cycle to coincide with those of other individuals in the population could reduce nest predation and increase productivity either by increasing predator deterrence, collective nest defence or predator swamping	Snapp 1976; Ims 1990; Moreiras et al. 2012; De Marchi et al. 2017

Daily and annual variation in photoperiod: Increased day length may correlate with the timing of other favourable conditions for successful breeding and may also increase foraging time for diurnally active species	The ability to use photoperiodic cues to trigger an internal process to ensure that critical fitness events occur at the most suitable time of the year	Dixit & Singh 2011; Kumar 1997; Kumar et al. 2010
Food abundance: temporal variation in abundant food availability	Timing the peak demand for food to coincide with the period of high food abundance or store up during abundance for use during scarcity	Olsson 1996; Varpe et al. 2009
Temperature: an important variable that can have positive fitness impacts when at moderate degrees, but which can negatively affect the energetics of adults and/or compromise the viability of eggs or dependent young at extremely low or high degrees during the breeding stage	The ability to use different thermoregulatory behaviours to manage the thermal challenges posed by varying degrees of temperature to adults, eggs, or dependent young.	Bartholomew & Dawson 1979; Smit et al. 2013; Clauser & McRae 2017
	The ability to time thermally demanding breeding activities to coincide with favourable temperatures.	Barrientos et al. 2007; Visser et al. 2009; Dolenec & Dolenec 2011; Watts et al. 2019
	The ability to select habitats in thermally buffered areas and/or build nests with thermoregulatory capacity.	Amat & Masero 2004b; de Zwaan & Martin 2018; Kubelka et al. 2019
	The ability to vary incubation attentiveness in response to environmental temperature	Prescott 1964; Conway & Martin 2000; Delia et al. 2013; Hoppe et al. 2019
Extreme weather events, e.g., storm surges/tidal flooding: Constrains coastal breeding birds by washing nests away	Timing the most vulnerable stages of breeding away from the most threatening storm surges The use of nest-site selection away from the reach of storm surges	Shriver et al. 2007; Benvenuti et al. 2018; Bailey et al. 2019

1.14 Seasonal optimisation

The timing of breeding is an important factor that influences several traits such as clutch size, fledging success and juvenile survival (Kaliński et al. 2019). Temporally, certain periods of the year are more favourable for successful reproduction than others in terms of both adult and offspring survival (Ims 1990; Svensson 1995). Organisms rely on their internal biological clocks and seasonal environmental cues e.g., rainfall, temperature, and photoperiod to determine when to or not to breed (Svensson 1995; Hahn & MacDougall-Shackleton 2008). They breed when conditions are most favourable to successfully produce viable offspring (Cockrem 1995; Le Corre 2001; Moreau 2008). Favourable conditions for successful reproduction are characterised by the availability of critical resources (e.g. food and breeding habitat) and prevalence of an optimal micro-climate (Martin 1987; Barrientos et al. 2007; Sinclair 2008; Brightsmith et al. 2018).

Aside from the annual seasonality of favourable conditions for breeding, there exists a within-season variability that makes certain periods within the breeding season more supportive of successful breeding than others (Verhulst & Nilsson 2008). For example, food availability, nest predator abundance/activity and temperature may vary within the season in a way that makes the nests initiated at the start or the middle of the breeding season more likely to succeed than those initiated later (Dawson 2008; Smith & Wilson 2010). This within breeding season variability and decline in favourable conditions as the season advances suggests that individuals should align their breeding dates to the most favourable conditions to maximise their chance of producing more offspring (Daan et al. 1990; Tinbergen & Daan 1990; Kaliński et al. 2019). However, the ability of individuals to breed at the best time depends on the individual quality (body condition, age, experience, and general state) (Christians et al. 2001; van De Pol & Verhulst 2006). Eventually, breeding dates and performance are likely to reflect a trade-off between individual quality and environmental conditions (Drent & Daan 1980): with high-quality individuals more likely to align high reproductive investment (e.g., large clutch size) to the best dates thereby producing more offspring than low quality individuals (Crick et al. 1993; Christians et al. 2001).

1.15 Global changes

The ongoing global climate change caused by increased emission of greenhouse gases from human activities such as energy use, agriculture and deforestation is affecting environmental conditions making them more variable in pattern, frequency and magnitude than they were historically (Dunn & Winkler 1999, 2010; IPCC 2007a; Gardali et al. 2012; Stern 2013; Turner et al. 2020). These changes have profound impacts on the fitness of organisms because traits that were previously adaptive under previous climate patterns may be maladaptive under current climate conditions (Reynolds et al. 2015; Lany et al. 2016).

The most pronounced aspect of climate change acting on living organisms has been the effect of rising temperatures (Thomas et al. 2004; Barbraud et al. 2012; Sippel et al. 2020). The earth has been warming at an unprecedented rate causing increased frequency and intensity of daily temperature extremes thereby exposing wildlife to new survival challenges to deal with the physiological consequences of increased heat loads (Stott 2016; Galgano 2019). Temperature increases also indirectly influence the breeding ecology of organisms through their effects on food availability patterns, suitable habitat, and optimal breeding micro-climates (Wen et al. 2014).

Another aspect of climate change which mostly affects coastal dwelling or breeding organisms is sea-level rise (van de Pol et al. 2010; Ma et al. 2019). Increasing global temperatures lead to increases in sea-level due to the thermal expansion of oceanic water and the melting of glaciers and ice sheets (Galbraith et al. 2002; IPCC 2007b; Kirshen et al. 2008). The global average sea-level rose by an estimated 1.8 ± 0.3 mm per year between 1950 and 2000 (Church et al. 2004) and increased rapidly thereafter (IPCC 2007b). Sea-levels, coastal flooding frequency and magnitude are still on the rise and projected to continue (Woth et al. 2006; Ezcurra & Rivera-Collazo 2018; Von Holle et al. 2019; Muis et al. 2020). The current and projected increases in sea-levels, coastal flooding frequency and magnitude could adversely affect coastal organisms in two ways – the destruction of habitat (feeding and breeding habitats) and an increased risk of washing nests away (Reynolds et al. 2015; Bailey et al. 2019; Vitale et al. 2020).

The impacts of climate change on habitat, breeding ecology and other biological events (e.g. migration and moult) together with other anthropogenic disturbances constitute a

significant selective pressure on bird species globally (Walther et al. 2002; Ramírez et al. 2018). Some species are unable to cope with increased heat loads during incubation and thus abandon their nests leaving their eggs exposed to threatening temperatures that could make the eggs unable to hatch resulting in poor breeding success (Sharpe et al. 2019; Bourne 2020). Following a series of seasons of poor breeding productivity, the population sizes of some species can decline to levels that threaten their ability to remain viable (van de Pol et al. 2010).

Increases in temperature, sea-level rise or a combination of both may also indirectly influence avian breeding outcomes through their impact on other ecological agents such as nest predators (Kubelka et al. 2018). For example, nest predation by snakes and avian predators are known to increase with temperature (Cox et al. 2013), suggesting that more nests might be lost to predation by snakes and avian predators under future climate change (Oswald et al. 2020). As sea-level continues to rise and the mean water levels move towards the vegetated area of the shore, coastal breeding birds may move away from the ocean to minimise the risk of nest losses to storm surges and flooding (Benvenuti et al. 2018). This movement away from the ocean would make their nests closer or higher up into predator concealing vegetation and may increase nest predation (Ma 2019).

1.16 Flexibility and evidence of adaptation to climate change

Behavioural adaptation has been highlighted as one of the mechanisms through which birds may adjust to reduce the negative impacts of climate change (Cunningham et al. 2015; Smit et al. 2016; Durant et al. 2019). Birds could exhibit plasticity that enables them to change their behaviour (modify body posture, alter activity patterns or move away from a threatening area to safer ones) in response to the prevailing conditions in their surroundings in a manner that maximises their fitness (Beever et al. 2017; Durant et al. 2019). For example, some species have exhibited significant variation in their breeding phenology and expanded or contracted their geographical breeding ranges in response to climate change (Crick & Sparks 1999; Chambers et al. 2013; Wen et al. 2014; Hällfors et al. 2020). Others may vary their incubation patterns or use heat-dissipating behaviours such as panting and gular fluttering to cope with increased heat stress induced by increases in temperature (AlRashidi 2016; Cook et al. 2020). The use of these behaviours, however, comes at certain costs and while some may be very beneficial (Both et al. 2019; van de Ven et al. 2019), some

may result in phenological and ecological mismatches resulting in poor fitness outcomes (Reynolds et al. 2015; Both et al. 2019; van de Ven et al. 2019; Visser & Gienapp 2019).

The availability of favourable micro-habitats and breeding habitat in general which breeding birds could utilize to buffer the negative impacts of climate change has also been highlighted as being crucial to their ability to cope with climate change (Bailey et al. 2019; Massimino et al. 2020). This is because some species have been observed to use habitat selection to reduce the negative impacts of climate change (Hannah et al. 2014; Suggitt et al. 2018). For example, Eurasian Oystercatchers *Haematopus ostralegus* used habitat selection to reduce the risk of nest losses to flooding caused by extreme climatic events (Bailey et al. 2019). However, when optimal breeding habitat is not available in sufficient amounts or deteriorates because of anthropogenic activities, the ability of species to cope using habitat selection is weakened (Bailey et al. 2017; Southwell & Emmerson 2020; Vitale et al. 2020). It is vital to understand the breeding habitat needs of species and the extent of the availability of such habitats. This knowledge of habitat needs and availability could inform management interventions to enhance the resilience of species to climate change where necessary (Campobello et al. 2017).

A species by species assessment is required to understand the magnitude of impact that climate change would have on species and the likely conservation management intervention that may be needed (Visser & Both 2005; Both et al. 2009; Gardali et al. 2012). This is because the exposure, vulnerability and response to climate change may vary extensively between species, populations, communities, and ecosystems. (Sparks & Carey 1995; Both et al. 2009; Bailey et al. 2017; Irons et al. 2017). Here I study the vulnerability of a ground-nesting shorebird, the African Black Oystercatcher *Haematopus moquini*, to climate and habitat change, and the behavioural adaptations that may allow it to compensate.

1.2 Study system

1.21 Shorebirds

Shorebirds, also known as waders or wetland birds, are members of the avian order Charadriiformes (Evans 1976; Livezey 2010). They are widespread and most are strongly associated with coastal wetlands with their bills showing diverse adaptations for extracting prey from shallow waters, intertidal mudflats, sandy shores, and intertidal rocks (Spearpoint et al. 1988; Ntiamoa-Baidu et al. 1998; Castro et al. 2009; Booty et al. 2020). They are important in moderating the population of their invertebrate prey organisms in the intertidal zone thereby providing important ecosystem functions and services (Kushlan 1981; Booty et al. 2020). They show a wide range of diversity in morphology, behaviour, breeding systems, migration, moult patterns and other life-history characteristics (Battley et al. 2003; Livezey 2010).

Many shorebirds are monogamous with both parents providing parental care (Lislevand & Thomas 2006). They are mostly long-lived, and show high mate and site fidelity (Méndez et al. 2018). Most shorebirds are ground-nesters making simple scrapes on the ground which they sometimes line using materials found around the nest (Tjørve 2006; McKinnon & Bêty 2009). Being ground-nesters exposes them to high predation rates, resulting in their exhibiting diverse antipredation adaptations including using camouflage and nest-site selection to make their eggs less conspicuous to predators as well as displaying various antipredator nest defence strategies (Hockey 1982; Larsen et al. 1996; Macdonald & Bolton 2008; Laidlaw et al. 2015, 2019).

Globally, many shorebird populations are declining and threatened with extinction due to the loss of suitable breeding and foraging habitats following the degradation and disappearance of wetland habitats because of climate change or intense anthropogenic activities such as coastal development, agriculture, aquaculture, and/or tourism (Galbraith et al. 2002; Ehmke et al. 2016; Melville et al. 2016; Studds et al. 2017; Monk et al. 2020). Since shorebirds forage on some prey items that serve as food sources for humans e.g., oysters, mussels, crabs, overharvesting of these resources by humans also leads to food shortages for shorebirds, especially during the breeding season (Ehmke et al. 2016). Many shorebird species migrate long distances annually between their breeding and wintering

habitats thereby needing to deal with the challenges of climate change from two distinct environments (Smith et al. 2010; Carneiro et al. 2020).

1.22 Justification of the study

The African Black Oystercatcher *Haematopus moquini* (described below in Section 1.241) is vulnerable to climate change-related increases in heat loads, nest predation by snakes and birds, nest losses to storm surges, as well as to other sources of disturbances, because of the nature of its breeding habitat (Tjørve 2006; Loewenthal et al. 2016). However, the extent of its vulnerability to the potential impacts of projected climate change and the adaptations by which the species could cope has not been explored. Also, the African Black Oystercatcher population on Robben Island, South Africa has experienced habitat change in predator composition (Spiby 2012; Whittington et al. 2016) and habitat extent which could further exacerbate the effects of climate change.

But the impact of these changes on overall breeding productivity is currently unknown. This thesis focuses on addressing some of these issues by using direct observation, iButton data loggers and digital time-lapse cameras to collect breeding, behavioural, weather, and environmental data on Robben Island over three African Black Oystercatcher breeding seasons to increase knowledge on the breeding ecology, vulnerability, and adaptations of the species to climate change, to provide the tools to guide management decisions and future research.

1.23 Aim and objectives of the study

This thesis aims to determine how weather conditions and other environmental factors associated with the limited availability of their beach habitat influence the vulnerability of the African Black Oystercatchers to climate and habitat change during the breeding season as well as the behavioural adaptations used by the species to cope, guide breeding decisions, and maximise breeding outcomes.

The specific objectives include:

1. To determine how African Black Oystercatchers use nest-site selection and timing to minimise the risk of losing nests to storm surges:

Like other shore-breeding birds, African Black Oystercatchers, are potentially vulnerable to the climate change associated sea-level rise, and increased frequency and magnitude of storm surges which may lead to nest losses, especially during the semilunar spring high tides (Tjørve 2006; Ma et al. 2019). Nest-site selection and synchronisation of nest initiation with the semilunar cycle have been observed to be two adaptive strategies used by birds (e.g., the European Oystercatchers *Haematopus ostralegus* and Saltmarsh Sparrow *Ammospiza caudacuta*) to cope with the risk of nest losses to storm surges (Shriver et al. 2007; Bailey et al. 2019). However, the extent and ways in which African Black Oystercatchers might use nest-site selection and/or timing of onset of nests with the semilunar cycle to manage the risk of nest losses to storm surges are yet to be explored in detail. Yet, it is important to understand the current strategies used by the species to help evaluate the species' vulnerability to future climate change, seeing that the frequency and magnitude of storms are projected to increase under future climate change. This aspect of the thesis was designed to answer the question: how do African Black Oystercatchers use nest-site selection and the timing of the start of incubation relative to the semilunar cycle to minimise their risk of nest losses to storm surges? I hypothesised that African Black Oystercatchers would use the breeding habitat width to inform nest-site selection and synchronise onset of clutch incubation with the semilunar cycle to minimise the risk of nest losses to storm surges.

2. To determine the on-bout thermoregulation behaviours used by African Black Oystercatchers to cope with heat stress during incubation:

Because African Black Oystercatchers, like many shorebirds, breed on the ground in habitats exposed to direct solar radiation during the day, temperatures normally reach levels that are considered potentially stressful for the incubating adults and their eggs (Amat & Masero 2004b; AlRashidi 2016). Hall (1959) observed that during the heat of the afternoon, incubating African Black Oystercatchers held their bills open most of the time and occasionally turned their bill into the back feathers. These observations suggest that African

Black Oystercatchers may employ some thermoregulation behaviours to cope with increased heat loads. However, the variety of thermoregulation behaviours that they employ while on their nests and the extent of use of these behaviours have not been quantified, nor have these behaviours been carefully linked to temperature quantitatively to determine important temperature thresholds at which these behaviours are used. The knowledge of how species use thermoregulation behaviours to deal with increased heat loads during their energetically demanding reproductive phase is increasingly important as the temperature continues to rise under current climate change. Under this section of the thesis, I asked what array of on-bout thermoregulation behaviours do African Black Oystercatchers use to cope with the air temperatures they experience in the wild during incubation? I hypothesised that African Black Oystercatchers would use a variety of thermoregulation behaviours as air temperature changes in a manner that potentially help them to cope with thermal loads and moderate the nest temperature experienced by their eggs.

3. To determine how African Black Oystercatchers vary incubation schedules with the time of day, weather, and other environmental variables:

Incubation patterns of African Black Oystercatchers and how the species varies incubation scheduling with environmental factors to balance its energy needs with the thermal needs of its eggs remain poorly known. Hall (1959) first noted that both parents incubate but that the way they relieved each other was not studied. The next study to understand the incubation behaviour of African Black Oystercatchers and the implication of human disturbance for the temperature of oystercatchers' eggs was by Adams et al. (1999). They observed that human disturbance may not negatively affect the viability of African Black Oystercatchers eggs because egg temperature remained within optimum ranges during their observation periods. They also suggested that African Black Oystercatchers abandon their nests at night, a behaviour which is contrary to that of the American Black Oystercatchers *Haematopus bachmani*, which incubate both day and night and even have longer incubation bouts at night (Spiegel et al. 2012). Adams et al. (1999) recommended that the night-time behaviour of incubating oystercatchers be explored further. Examining the patterns of incubation bouts and the flexibility of incubating oystercatchers in responding to varying environmental conditions could enhance our knowledge on the

incubation behaviour of the species and how changes in environmental conditions due to climate change might affect the species and their breeding outcomes in future. In this aspect of the thesis, I asked how do African Black Oystercatchers schedule incubation bout in response to dynamic environmental conditions? I hypothesised that African Black Oystercatchers would vary their incubation bouts with the time of day (day versus night), air temperature, windspeed and tide height in ways that potentially help them to balance their energy and thermoregulatory needs with that of their thermally dependent eggs.

4. To determine the predator identity as well as the temporal, weather, and environmental predictors of nest predation of African Black Oystercatchers on Robben Island:

One of the challenges faced by species under global climate and habitat change is dealing with the biotic components of the environment e.g., vegetation and predators which might themselves be affected by changes in the environment (Munro 2017; Flemming et al. 2019). African Black Oystercatchers, like other ground-nesting birds, are exposed to high predation rates from a range of predator species that could potentially be influenced by climate change (Tjørve 2006; Cox et al. 2013). Exploring how the biotic and abiotic components of the environment may interact to determine nest predation rate under current climate conditions might be useful to predict how these ecological factors could affect nest predation patterns under future climate change. Here, I asked what is the identity of the main nest predator of African Black Oystercatchers on Robben Island and what biological and ecological factors makes a nest more vulnerable to predation? I hypothesised that an array of weather, environmental and temporal factors would influence the nest predation risk of the African Black Oystercatchers.

5. To determine how weather and other environmental factors influence the overall breeding output of African Black Oystercatchers:

Ultimately, how biotic, and abiotic components of the environment together with human disturbance affect life-history traits and overall breeding output under current climate conditions will provide useful insight into the extent of species vulnerability and guide management decisions under future climatic conditions. Here, I asked what the current breeding population size of African Black Oystercatchers was on Robben Island, as well as

what factors influence the hatching (probability that a nest would produce at least one chick) and overall breeding success (the probability that a pair would fledge at least one juvenile) of the species on the island? I hypothesised that anthropogenic disturbances, temporal, spatial, environmental, and weather variables would affect the hatching and overall breeding success of African Black Oystercatchers.

1.24 General methods

1.241 Study species: African Black Oystercatchers

The African Black Oystercatcher is a member of the avian order Charadriiformes, suborder Charadrii and family Haematopodidae (Ens & Underhill 2014). The family Haematopodidae consists of the twelve species of oystercatchers distributed along most of the coastlines in North and South America, Europe, Asia and Australasia but absent from arctic coastlines, tropical Africa and southern Asia (Hockey 1983a; Ens & Underhill 2014). The African Black Oystercatcher is one of the most range-restricted of the oystercatcher species and is endemic to the coastline of southern Africa (Hockey 1983a; Brown et al. 2019). It is the only extant species of oystercatcher breeding in Africa (Summers & Cooper 1977; Ens & Underhill 2014). The Canary Island Oystercatcher *Haematopus meadewaldoi* would have been the second, but it went extinct before 1940 due to anthropogenic activities and disturbances (Hockey 1997; Senfeld et al. 2020).

African Black Oystercatchers, like the rest of the oystercatcher species, are stocky (about 42–45 cm long with an average adult mass of 665 g (male) and 730 g (female)), with thick long bills that are adapted to forage on hard-shelled prey items extracted from rocks and mud in the intertidal zone (Leseberg 2001; Hockey et al. 2005). They feed at low tides on mussels, limpets and other invertebrates which are considered to be available in the intertidal zone in large proportions year-round especially along the west coast of their geographical range in southern Africa (Hockey & Underhill 1984; Schurink & Griffiths 1991; Kohler et al. 2011). The successful invasion of South African coastlines by the Mediterranean Mussel *Mytilus galloprovincialis* since the 1970s has brought about the availability of an abundance of food which is believed to have contributed significantly to recent increases in the population size of African Black Oystercatchers (Kohler et al. 2011; Assis et al. 2015; Loewenthal et al. 2015). African Black Oystercatchers were classified as near threatened for the first time locally and internationally in 1988 due to their small population size, small

breeding range extent, and low productivity (Kemper et al. 2007; Ens & Underhill 2014). After 30 years they were recategorized in 2018 as Least Concern on the IUCN red-list (Birdlife International 2019) because of the population increase observed across most of its range (Loewenthal et al. 2015; Brown et al. 2019). This increase in the population size of the African Black Oystercatcher is also believed to be linked to the improved protection of the species breeding habitats e.g. the banning of vehicles along the mainland beaches where the species breed (Williams et al. 2004; Tjørve & Underhill 2006; Loewenthal et al. 2015).

The African Black Oystercatcher exhibits strong breeding seasonality, breeding at the time of year (October of a year to March/April of the subsequent year) that is warm, dry and with the smallest wave heights (Summers & Cooper 1977; Hockey et al. 2005; Tjørve 2006). Unlike the European Oystercatcher which has colonised several habitats including roof-tops and farmlands, African Black Oystercatchers are obligate coastal breeders preferring to locate their nests within 50 meters of the ocean (Hockey 1982, 1983b; Watson et al. 1997; Tjørve 2006). They are monogamous, territorial and exhibit high site and mate fidelity (Summers & Cooper 1977; Hockey 1983a). They have a modal clutch size of two eggs but one-egg and three-egg clutches also occur in lower frequencies (Paijmans et al. 2015). Their chicks are semi-precocial and can move away from the nest within 24 hours of hatching (Tjørve 2006). However, they cannot handle hard-shelled prey items and therefore rely on their parents for feeding for an extended period even after fledging (Hockey 1997; Parsons 2006). The substantial dependence of the chicks on the parents for foraging and the tidally entrained foraging regime of the oystercatchers makes it difficult for parents to successfully raise more than one young per season while meeting their own energy needs (Hockey 1983b; Leseberg et al. 2000). Hence most oystercatcher pairs raise only one fledgling per season but some make second and even third attempts if the first attempt fails to produce a young (Tjørve 2006).

Like other oystercatchers and shorebirds in general, oystercatchers exhibit high survival rates and are a long-lived species (Leseberg 2001; Méndez et al. 2018). However, unlike other species of oystercatchers, African Black Oystercatchers are non-migratory and remain on their territories year-round (Hockey 1983a). The juveniles disperse away from their natal grounds to nurseries where they remain until they attain breeding ages (usually three years for females and four for males) and move back to their natal grounds to seek breeding

territories on which to settle (Leseberg 2001; Hockey 2003; Loewenthal 2007; Rao et al. 2014).

1.242 Study site: Robben Island, Western Cape, South Africa

Robben Island, Western Cape, South Africa (33° 48'S, 18° 22'E), located 7km away from the nearest mainland at Bloubergstrand, is the biggest offshore island in South Africa with an area of 507 ha and a shoreline of about 10km (Crawford & Dyer 2000; Underhill et al. 2001; Figure 1.1). It was designated a marine protected area by the South African Government in 2019 to conserve and protect the biodiversity and ecological processes associated with the island (Marine Conservation Institute 2020). The warmest and driest time of year on Robben Island is summer (October–March), while winter (April–September) is mostly cold and wet (Sherley 2010). It is an important breeding site for several sea- and shore- birds (Sherley et al. 2011). It is renowned for its cultural and historical heritage and was declared a World Heritage Site in 1999 (UNESCO World Heritage Committee 2003) and receives several thousand tourists annually (Robben Island Museum 2017).

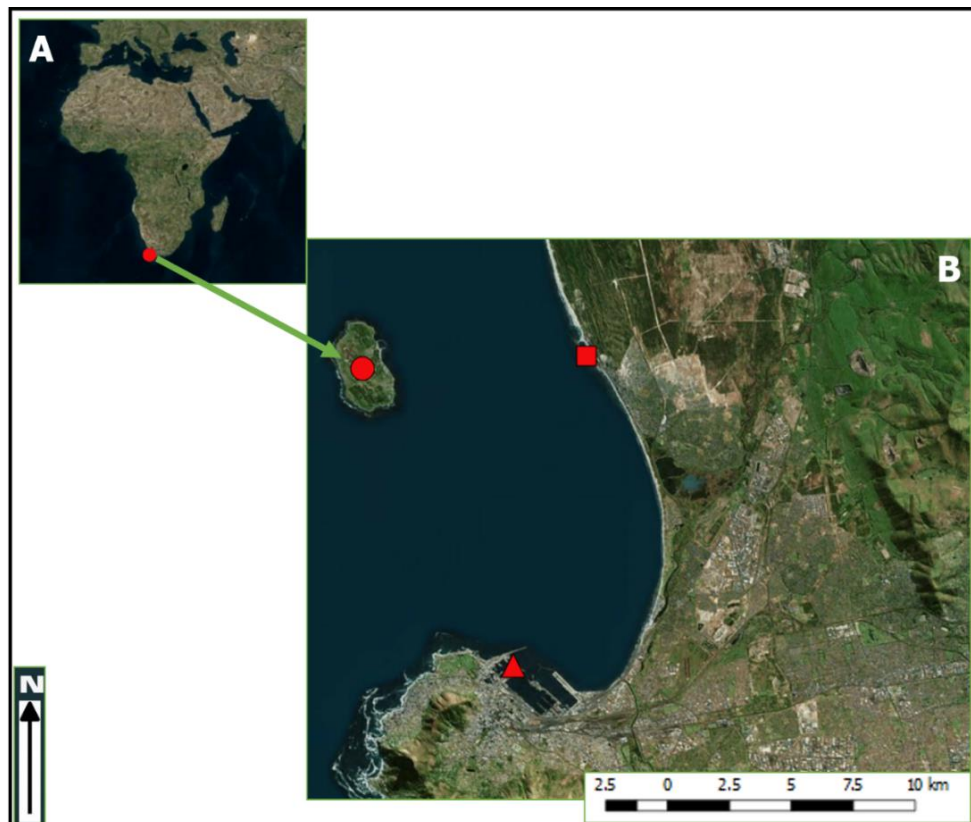


Figure 1.1: The location of Robben Island on the African continent (red circle in A). Robben Island location (red circle in B) relative to the nearest mainland point at Bloubergstrand, Cape Town (red square in B) and the Cape Town Harbour (red triangle in B).

Robben Island supports more than 5% of the global population of African Black Oystercatchers (Tjørve 2006; Braby & Underhill 2007). Adult oystercatchers are common residents on Robben Island and breed on the coastline of the island where they place their nests in simple scrapes in the area above the mean high watermark and below the vegetation (Tjørve 2006; Sherley et al. 2011; Figure 1.2). Important sources of breeding failure for African Black Oystercatcher on the island have been predation and nest losses to storm surges (Tjørve 2006). The Kelp Gull *Larus dominicanus* (one of the suspected predators of the nests of oystercatchers on the island) population has increased from a historically small size to thousands of breeding pairs (Calf et al. 2003; Whittington et al. 2016). The increased breeding population of Kelp Gulls was suspected to be the main current threat to breeding oystercatchers on the island (Underhill 2014).

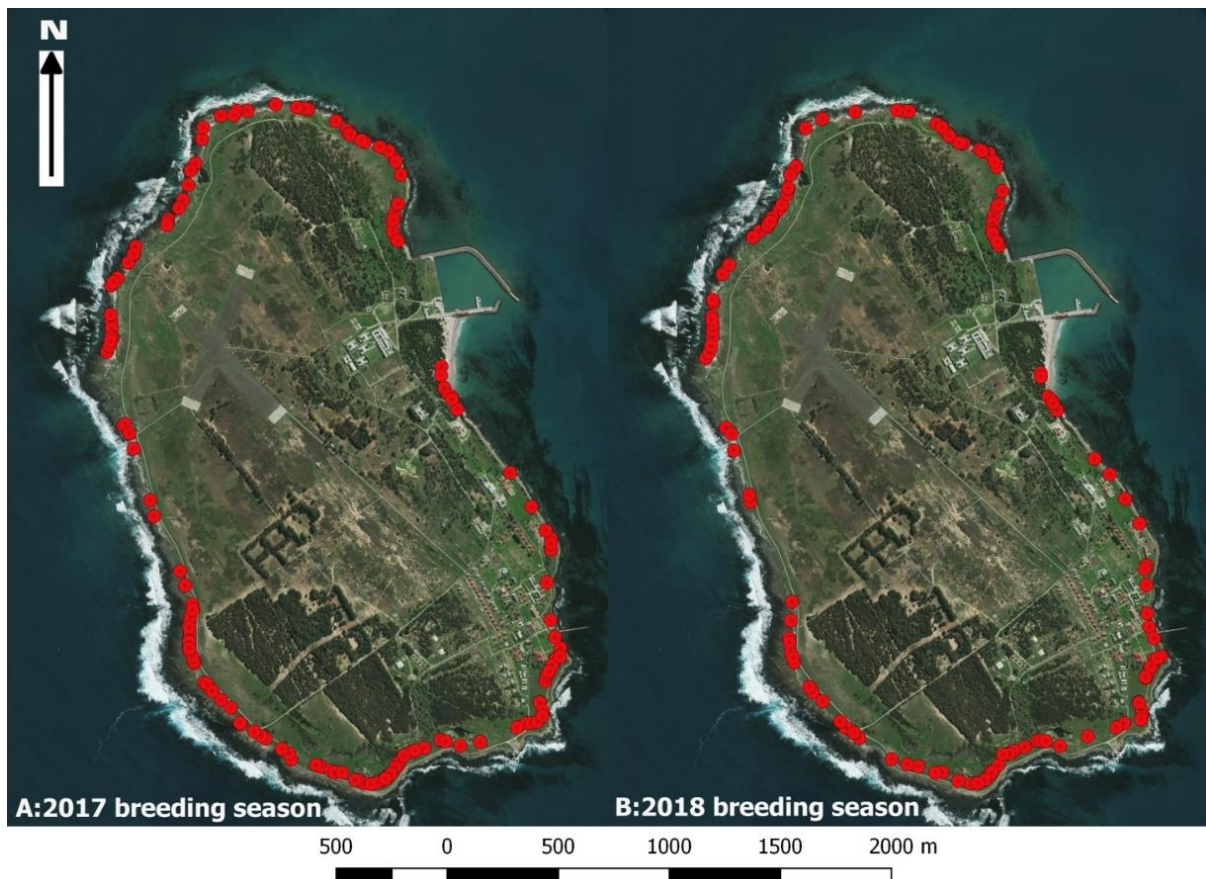


Figure 1.2: Oystercatchers' nest locations on Robben Island in 2017 (the red circles in the map on the left) and 2018 (the red circles in the map on the right) breeding seasons. The 2016 location data is unavailable. The GPS used for location data collection in 2017/2018 only became available (bought) from 2017

1.243 Trapping and sexing adult African Black Oystercatchers

To control for sex-related effects in the data analysis of the objectives on the incubation scheduling (Chapter Four) and on-bout thermoregulation behaviours (Chapter Three) of African Black Oystercatchers, I needed to trap, sex, and individually mark the adults. Adult African Black Oystercatchers were trapped on their nests using a walk-in trap from a minimum of 7-10 days post clutch completion (Hockey 1981). The trapping of incubating adults was restricted to cooler times of day to avoid exposing the eggs to high air temperatures. The trapped oystercatchers were given a unique plastic colour ring and a numbered SAFRING metal ring. Standard morphometrics including bill, tarsus, total head length and wing length were measured to the nearest 0.1 mm, using a 150mm dial calliper and 300mm wing rule. Oystercatchers were weighed to the nearest 10 g, using a Pesola spring balance of 1000 g /10 g accuracy. Sex was determined by a combination of morphometrics and examination of eye flecks. Adult female oystercatchers are generally larger than males (Hockey 1981) and have very dark eye flecks, while adult males either typically lack eye flecks completely or have them in small amounts (Figure 1.3), as a light patch (Kohler et al. 2009).

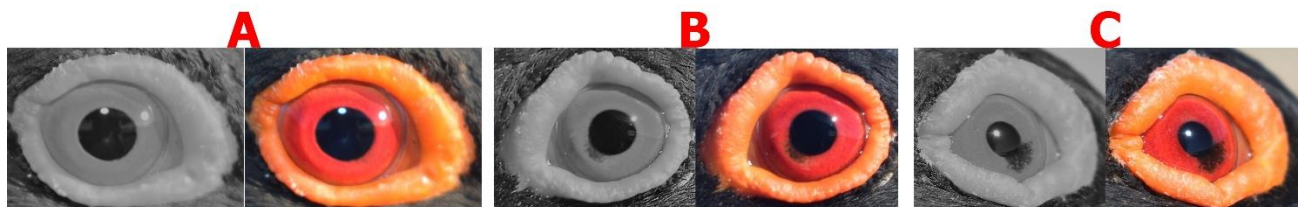


Figure 1.3: Eye flecks absent (A), present in a small proportion (B) or present in a large proportion (C) in the eyes of African Black Oystercatchers trapped on Robben Island. The black-white images in A, B, C are the same as the coloured ones.

Within pair comparisons of biometrics and eye-flecks may enhance the probability of reliably discriminating between male and female oystercatchers (Kohler et al. 2009; van de Pol et al. 2009). Hence an attempt was made to trap both individuals of a pair where possible. To aid the identification of incubating male and female oystercatchers on video footage taken at night (Section 1.244) when the reading of actual numbers and colours of the rings are impossible because they appear in black and white, the leg on which the ring is placed for individuals that were trapped were varied. For nests where only one member of the pair was trapped, the rings were always on the right leg. For nests where both parents

were trapped, the first member of the pair to be trapped gets ringed on the right leg, while the second to be trapped gets the ring on the left leg. Biometric details as well as the nest identity, number on the metal ring, colour of the plastic ring, and the leg on which the ring is worn were recorded for each trapped individual. In total, 73 adults from 53 nests were trapped and individually marked. Twenty of the 53 nests had both individuals trapped and individually marked. Seventy-three adults and 53 nests (unique breeding pairs) constitute 15 % and 36 % of the average adult population size and the average number of breeding pairs on the island (Chapter Six).

1.244 Camera set-up around the nest

Only the nests from which at least one individual had been trapped and marked were video monitored and included in the data analysis used to address objectives 2 (Chapter Three) and 3 (Chapter Four). This means that none of the cameras was placed before seven days post clutch completion. Incubating African Black Oystercatchers were video monitored between November 2017–February 2018 and November 2018–February 2019. The plan was to increase the sample size as the number of different nests rather than lots of days from the same nest, so I could model many individual short duration (± 24 hours) samples to get an idea of the pattern robustly. Time-lapse digital cameras with infrared lights (Acorn 6510MC/6310MC) were set up 1-3 meters beside the nest to take 1-minute of footage followed by a break of 30 seconds. This distance between the nest and the camera permitted the identification of each incubating adult during footage analysis and is within the range used in similar literature (e.g. AlRashidi et al. (2010); Gill et al. (2016); Ribeiro-Silva et al. (2018); Sládeček et al. (2019)). Cameras were retrieved following battery failure or after the loss of the eggs to natural or anthropogenic (only one case) causes. During footage analyses, the colour rings and/or the leg on which the ring is worn were used to identify previously sexed individuals (Section 1.243). It was possible to camera monitor two different nests from the same pair (replacement nests) within the same season, but to avoid pseudo-replication in the dataset extracted from the video footage, only one nest per pair per season was camera monitored. Also, efforts were made to not camera monitor the nest of the same pairs in subsequent seasons. However, two pairs had their nests monitored both in the 2017 and 2018 breeding seasons because they met the criteria of at least one member of the pair being marked and their eggs being incubated for at least seven days or

more post clutch completion, early in the 2018 breeding season when others had not yet met the criteria. Samples highlighting some of the observations from the footage have been saved on Google drive. The links to those observations are shared at the relevant points within the text of the data chapters.

1.3 Ethics clearance and funding

Approval was given by the Science Faculty Animal Ethics Committee (SFAEC) University of Cape Town for the implementation of the protocols of this project (approval number 2018/v5/LU). The South African marine research permit was issued by the Department of Agriculture Forestry and Fisheries (DAFF) and Department of Environmental Affairs (DEA) with reference numbers RES2017/48 and RES2018/48. The South African Ringing Scheme (SAFRING) issued a single species permit to ring the African Black Oystercatchers (Ringer number: 15347). Funding was provided by the Leventis Foundation through the A. P. Leventis Ornithological Research Institute, Jos Nigeria.

1.4 Thesis structure/data source and contributions

Chapter One: This chapter introduced the thesis and general methods. To avoid repetition, the study site, and species as well as some methods that remain the same across chapters have been presented under this chapter and will not be repeated under the data chapters, except when necessary (e.g., camera settings for Chapter Five were slightly different to those of Chapters Three and Four. The general camera setting for Chapters Three and Four have been presented under Chapter One and will not be repeated in those chapters. But a camera setting section is presented in Chapter Five to capture its own small peculiarities). The data chapters are presented as independent articles for eventual publications in journals and have an abstract, introduction, methods (including data analysis), results, discussions, and appendix sections. A single overall reference section is provided at the end of the last chapter.

Chapter Two contains the detailed exploration of objective one under the title - Cues for nest-site timing and selection by African Black Oystercatchers: Effects of semilunar spring tide periodicity and breeding habitat width.

Chapter Three contains a detailed exploration of objective two under the title - On-bout thermoregulation behaviours used by African Black Oystercatchers to cope with varying temperatures during incubation.

Chapter Four addressed objective three under the title - Incubation scheduling by African Black Oystercatchers: Effects of weather, tide phase, and time of day.

Chapter Five addressed objective four under the title - The relative importance of different nest predators and predictors of nest predation in African Black Oystercatchers.

Chapter Six explored objective five under the heading - Population size, breeding parameters and predictors of breeding success of African Black Oystercatchers on Robben Island.

Chapter Seven: This chapter synthesised and discussed the main findings from the data chapters and made recommendations for management and future research.

Field work and data collection in the 2016 breeding season was more restricted compared with the 2017 and 2018 breeding seasons. Some chapters, therefore, used data from two seasons (2017 and 2018), while others used three seasons (2016, 2017 and 2018). More details are contained in Table 1.2.

Table 1.2: Summary of the data used in the main analyses of each data chapter and the seasons in which they were collected

Data type	Season collected	Chapters where the data was used
Habitat data (distances to vegetation, mean high watermark and habitat width)	2017 and 2018	Chapters Two, Five and Six
iButton temperature data for a subset of nests (only video-monitored nests)	2017 and 2018	Chapters Three and Four
On-bout thermoregulation behaviour data extracted from camera monitored nests	2017 and 2018	Chapter Three
Incubation scheduling data extracted from camera monitored nests	2017 and 2018	Chapter Four
Air temperature data taken at five minutes interval on Robben Island collected by the South African weather Services	2017 and 2018	Chapters Three, Four, Five and Six
Daily maximum air temperature data on Robben Island collected by the South African weather Services	2001-2019	Chapter Three
Nest predation data from digital cameras	2017 and 2018	Chapter Five
Egg mass and size measurements for ageing nests	2016, 2017 and 2018	Chapters Two, Five and Six

Complete nest fate monitoring	2017 and 2018	Chapters Two, Five and Six
Windspeed data on Robben Island collected by the South African weather Services	2017 and 2018	Chapter Four
Predicted hourly tide height data for Cape Town Harbour collected by the South African Navy	2017 and 2018	Chapter Four

I collected all the breeding, behavioural and habitat data analysed in this thesis. I collected on-site nest and around nest temperatures using iButton data loggers. Air temperature and windspeed data for Robben Island were supplied to me by the South African Weather Services. Predicted hourly tide data for Cape Town Harbour (Figure 1.1), the nearest location to Robben Island for which tide data exist, were supplied to me by the Hydrographer, South African Navy. I carried out all the data preparation, analysis, and write-up of each of the chapters of this thesis. Professor Will Cresswell commented and made inputs into my proposal draft, data analyses, and on all the initial drafts and revised versions of all seven chapters. Dr Susan Cunningham commented on my data analyses and on all seven chapters of this thesis. Professor Les Underhill introduced me to Mr Sabelo Madlala of the Environmental Unit of Robben Island Museum. Mr Sabelo Madlala facilitated my access to Robben Island.



**Chapter Two: Cues for nest-site timing and selection by African Black Oystercatchers:
Effects of semilunar spring tide periodicity and breeding habitat width**



Abstract

The selection of an optimal nest site within a breeding territory is an important decision made by birds in order to maximise the chance of nest survival. An important threat to the nest survival of coastal breeding birds (in addition to predation) is the risk of losing nests to storm surges, especially during a spring tide. Consequently, the timing and extent to which the waves of a spring tide reach up the beach and correspondingly, the width of the beach may be important considerations for beach breeding birds when selecting an optimal nest-site. This study examined how African Black Oystercatchers *Haematopus moquini* (oystercatchers), an obligate coastal breeding shorebird, trades-off nest predation risk (distance away from the top of the beach because the vegetation at the top of the beach could potentially conceal nest predators) against nest losses to storm surges (distance away from the bottom of the beach). Specifically, how they might use the periodic spring tides occurring around the new/full moon dates (spring tide dates) to time the onset of clutch incubation to minimise exposure to storm surges, and whether oystercatchers maximise distance from storm surges or distance from potential predation risk when constrained by nesting on narrow beaches. I hypothesised that oystercatchers would synchronise the start of clutch incubation around spring tide dates to reduce the number of exposures to potentially threatening spring tides and select safe nest-sites. However, the chance of choosing a safe nest-site away from the ocean without increasing vulnerability to nest predation may depend on breeding habitat (i.e., beach) width, as individuals in wider beaches may have the opportunity to choose optimal nest-sites (sufficiently away from the top and bottom of the beach) while those in narrow habitats may be constrained. These ideas were explored using breeding data (2016—2018 breeding seasons) and habitat data (2017—2018 breeding seasons) collected on Robben Island, South Africa. New/full moon dates for Robben Island were extracted from the Times and Dates.com website. The maximum and the total number of nests for which incubation started on a given day increased from two days after a spring tide date, peaked between days 5—9 and subsequently declined. The probability of a nest occurring in the upper half of the beach declined as the width of the habitat increased. These results show that oystercatchers time the onset of clutch incubation in a manner that reduces the number of spring tide cycles they experience during incubation and maximise distance from the top of the beach in wide beaches but select sites closer to the top of the beach in narrow beaches, suggesting that

individuals constrained by narrow habitats prioritise safety from storm surges over predation risk. These results contribute to our knowledge of how oystercatchers may use the semilunar spring tide cycle and nest-site selection to manage the risk of nest loss.



2.1 Introduction

The selection of an optimal site within more extensive breeding habitat in which to locate a nest is one of many important decisions made by birds before the start of nest building, egg-laying and incubation to maximise nest survival (Patrick & Colwell 2014). Nest locations are very crucial because they need to remain safe for the incubating adults and their eggs throughout incubation (Anteau et al. 2012). To select secure nest positions, individuals need to assess biotic and abiotic environmental factors such as food availability, breeding success of conspecifics, protection from predators, human disturbances and harsh weather conditions (Pärt & Doligez 2003; Tieleman et al. 2008; Webber et al. 2013; Coates et al. 2019).

An important threat to the nest survival of coastal breeding birds is the risk of losing nests to wave-motivated storm surges, especially during extreme high tides (Shriver et al. 2007; van de Pol et al. 2010). This threat can vary daily and along the semilunar cycle (Takemura et al. 2010). For every 24 hours, there are two high tides and low tides (Bulla et al. 2017). The extent to which the storm surges from a given high tide pushes into the beach is dependent on beach topography as well as dynamic factors such as windspeed and air pressure (Idier et al. 2019). Strong winds and low air pressure produce strong storm surges that may go beyond the typical mean high watermark, potentially increasing the risk of washing nests away (Li et al. 2020). Contrary to the unpredictability of winds and atmospheric pressure, the position of the moon in relation to the earth and the sun changes constantly in a predictable way that varies the gravitational pull on the earth (Grant et al. 2009; Chakraborty 2018). The maximum gravitational pull on the earth occurs twice per month at full and new moons giving rise to the spring tides (Chakraborty 2018). In contrast, the pull is minimal around the first and third quarter moons producing the neap tides (Bhatnagar et al. 2016; Bulla et al. 2017). The daily high tides associated with spring tides are generally higher than those associated with neap tides (Bulla et al. 2017) making the surge from the former more dangerous to the nests of beach breeding birds especially when in association with strong winds (Gjerdrum et al. 2005; Shriver et al. 2007). These potentially dangerous storm surges from spring high tides to beach nesting birds occur approximately every 15 days at new or full moon dates. However, the daily high tides occurring about two to three days pre

and post a new or full moon date (spring tide date) are usually similar in height (Gjerdrum et al. 2005).

Some coastal breeding birds are known to synchronise clutch initiation with the semilunar spring tide periodicity as an adaptation to reduce the risk of losing nests to storm surges (Gjerdrum et al. 2005; Plaschke et al. 2019). There are two main explanations in the literature for why synchronising nest initiation with the semilunar spring tide periodicity might be beneficial to coastal breeding birds. First, by starting a nest few days after a spring tide date birds may avoid the subsequent sets of spring tides or at least minimise the number of spring tides they experience during incubation, depending on the length of incubation (Shriver et al. 2007). Second, because the storm surges of spring high tides are higher than at other times, birds could track the actual spring high tide water levels to inform the selection of nest positions that are safe from the reach of subsequent spring tides (Plaschke et al. 2019). While the placement of nests away from the ocean may reduce the risk of nest losses to storm surges, being further up the beach and closer to the vegetation could increase the risk of nest predation (Ma et al. 2019; Chapter Five). Hence, coastal breeding birds need to balance nest placement in a way that reduces the risk of nest flooding without becoming too vulnerable to predation (Benvenuti et al. 2018).

However, the extent to which coastal breeding birds can use the cues from the highest spring tides to inform nest placement without increasing vulnerability to nest predation may depend on the width of the available breeding habitat. Individuals in wider habitats may have opportunity to minimise predation risk, and nest losses to storm surges by placing nests sufficiently away from both the top and bottom of the habitat (Chapters Five & Six). Predators may find it harder and less profitable to search for nests in wider areas of the shore, so leading to lower nest predation rates (Muir & Colwell 2010; Chapter Five). Wider areas of shore may also be less steep compared with narrower ones such that nests in wider areas are less vulnerable to the risk of getting washed away (Benvenuti et al. 2018). In contrast to birds in wider habitats, individuals in narrow habitats may be constrained and able to minimise only one of the two threats by placing their nests away from the threat they perceive to be greater (Ma et al. 2019).

African Black Oystercatchers *Haematopus moquini* (oystercatchers) place their nests in the area of shore just above the mean high watermark and forage in the adjacent intertidal

zone at low tide (Hockey 1982; Tjørve 2006; Kemper et al. 2007). They generally position their nests less than 50 m from the high watermark (Hockey 1983a; Watson et al. 1997). Oystercatchers have a minimum and average incubation period of 27 and 30 days, respectively, suggesting that they would experience two sets of spring tides during incubation (Hockey et al. 2005; Tjørve 2006). Hall (1959) noted that oystercatchers exhibit a 'scrape ceremony' where they make several scrapes within their territory and eventually choose the one that presumably minimises the risk of nest losses to predators and storm surges during spring tides. The nest scrape ceremony described by Hall (1959) is commonly observed in some territories of the population of oystercatchers breeding on Robben Island. However, how oystercatchers use the semilunar spring tide periodicity and habitat width to inform nest-site selection and timing of the onset of incubation is yet to be examined. This is important in the light of the increasing sea-level rise and frequency and magnitude of storms, both affected by climate change (van de Pol et al. 2010; Vitale et al. 2020). Understanding how oystercatchers use lunar periodicity and habitat width to inform nest-site selection could provide information which may be useful if habitat management for the species becomes necessary.

In this chapter, I asked: how do oystercatchers time the incubation start dates of their nests in relation to the spring tide cycle? How is oystercatchers' nest placement relative to the midpoint of the breeding habitat influenced by habitat width and the time during the spring tide cycle that clutch incubation started? Also, how is the risk of nest losses to storm surges influenced by the placement of nests relative to the middle of the breeding habitat (middle of the beach)? I hypothesised that oystercatchers would synchronise the start of clutch incubation in a manner that reduces the set of spring tides they experience during incubation (Shriver 2010). I hypothesised that oystercatchers in wider habitats would have more opportunities to optimise the placement of their nests to trade-off predation and nest flooding risks than those constrained by narrow habitats (Muir & Colwell 2010; Ehmke et al. 2016). Because the storm surges associated with spring tides usually extend further into the beach than at other times, the individuals initiating incubation around (or a few days after) a spring tide date may be able to use the information of spring tide surge levels to inform nest-site placement which are higher in the beach than those starting later (Plaschke et al. 2019). Finally, I hypothesised that the placement of nests relative to the midpoint of the

breeding habitat would be adaptive such that nests located below the midpoint should be more at risk of getting washed away by storm surges than those above it (Benvenuti et al. 2018). Since the risk of nest losses to storm surges could vary between breeding seasons due to between-season stochasticity (Plaschke et al. 2019), breeding season was controlled for in the analysis.

2.2 Methods

2.2.1 Nest search and estimation of the incubation start date of nests

Intensive nest searches and monitoring was conducted between October of a year until the end of April the following year, starting from the October of 2016 to April of 2019 (i.e., three breeding seasons comprising 2016, 2017 and 2018). Each new nest found was given a unique identity. The eggs were marked as I, II or III depending on the clutch size and weighed (mass was taken to the nearest 0.1 g, using an electronic balance (American Weigh Scale AC-650 with a capacity of 650g and 0.1g resolution)). The length (L) and two breadth measurements (b1 and b2 taken at right angles to each other over the broadest part of the egg) were measured to the nearest 0.1 mm using a 150 mm dial calliper (Tjørve 2006). Dates and times when measurements were taken were recorded (Tjørve 2006).

The extent to which the eggs in a nest had been incubated before they were found was calculated by fitting the egg measurements into the equation specified in Underhill & Calf (2005) for the oystercatcher population on Robben Island. The equation specified in Underhill & Calf (2005) relates the size of an egg to its mass based on the principle that avian eggs lose about 16 % of their mass during incubation. The extent to which the oldest egg in a nest had been incubated before the nest was found was used to determine the clutch incubation start date by counting days backwards, starting from the date the nest was first found (Underhill & Calf 2005; Parsons 2006). Oystercatchers have a modal clutch size of 2 eggs with one- and three- egg clutches occurring less frequently (Paijmans et al. 2015). Oystercatchers take two or four days to complete a clutch with 2 or 3 eggs, respectively (Hockey 1983b; Tjørve 2006). Although they tend their nests partially after laying the first egg, full incubation usually commences after clutch completion (Hockey et al. 2005; Parsons 2006). Hence, the calculated dates of the onset of clutch incubation would correspond to at least one to four days after the nests were built and initiated.

2.22 The probability of nest losses to storm surges

A detailed description of the fate of all the nests monitored is captured in Chapter Six. For this section, the focus is on the risk of nest losses to storm surges. Nests were scored as washed away by a storm surge (if nest-sites were covered with freshly washed-up kelp or if eggs were seen displaced from the nests and covered with fresh kelp), predated (if eggs vanished days before the expected hatch date, a direct predation event was observed, a broken egg was seen) or hatched (if chicks or eggshells from hatched chicks were found around the nest, and/or if parents showed aggressive chick guarding behaviour) (Allan & Hockey 1984; Tjørve & Tjørve 2016).

2.23 Moon phase data and daily maximum tide height on a given moon day

Full moon and new moon dates for Robben Island were extracted from the Times and Dates.com website at <https://www.timeanddate.com/moon/phases/@3362356>.

The pattern of daily maximum tide heights in Cape Town Harbour (the closest point to Robben Island for which tide data exist, Figure 1.1) is shown in Figure 2.1 to provide context for the study site.

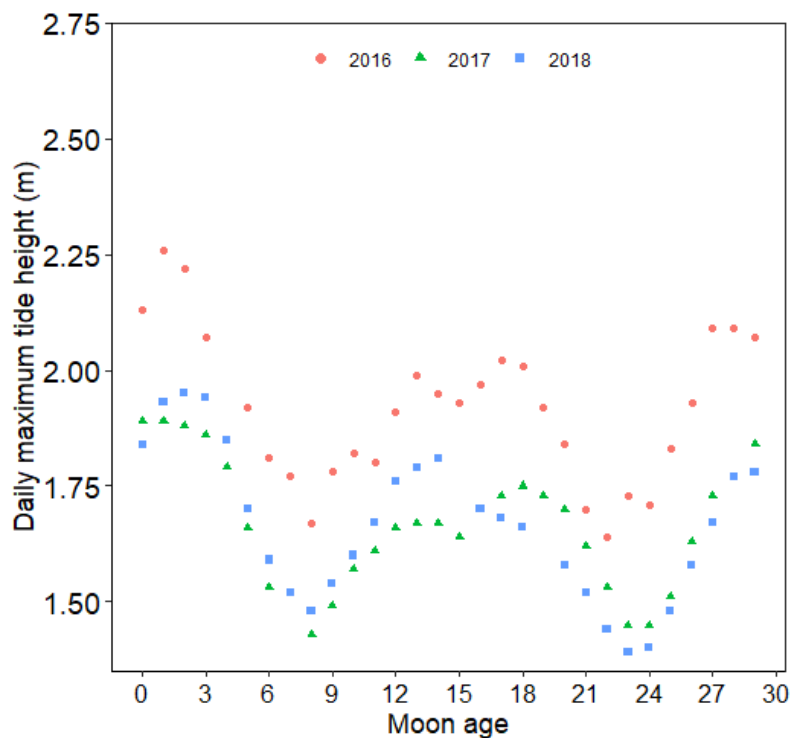


Figure 2.1: Data points showing the patterns of predicted daily maximum tide heights across the 29.5 days lunar cycle at Cape Town Harbour during the summers of 2016, 2017 and 2018. Moon age was counted as the number of days since the new moon (New moon day = 0, Full moon = 15, last day of the moon cycle = 30)—source: South African Navy.

2.24 Habitat measurements

One measurement of habitat width was taken per territory, using the nest as a reference point. First, the distance of each nest to the mean high watermark and the vegetation above it (Figure 2.2) were taken in meters using a laser range finder or a 10 m rule in the 2017 and 2018 breeding seasons. The width of the breeding habitat of a pair was then estimated by summing the distances of a nest to the vegetation and the mean high watermark over the area where the nest is located. No habitat data were collected in 2016.

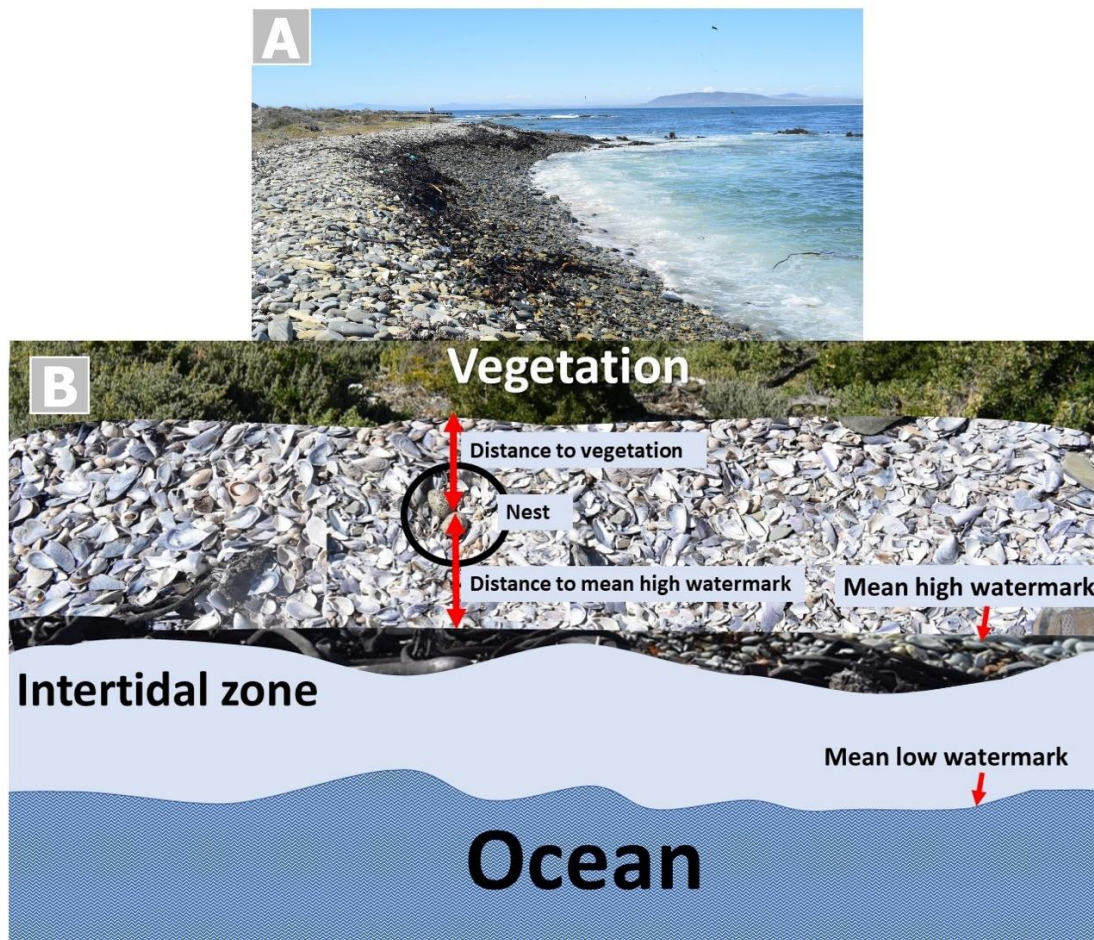


Figure 2.2: Illustration of the breeding habitat of the oystercatchers. Figure 2.2A represents an actual image of a typical oystercatcher breeding habitat on Robben Island: more images of this are presented in Appendix 2.1. The mean line where the water reaches during high tide on Robben Island is generally characterised by piles of debris and kelp: this line of debris and kelp was used as a reference for the mean high watermark. Figure 2.2B is not drawn to scale and is only for illustrative purposes to show how the distances to vegetation and the mean high water were taken.

2.25 Data analysis

Spring tides occur around the timing of the new and full moon dates (as explained in Section 2.1 above). To examine whether oystercatchers synchronise the start of clutch incubation with the timing of spring tides (i.e., whether incubation is started for more nests around the timing of spring tides than at other times), each day of the breeding season was assigned a spring tide day as the number of days from a new or full moon date. The spring tide days span 1–14, 15 or 16, depending on the length of the semilunar cycle because it could vary between 14–16 days long. There were as many spring tide day 1s in a breeding season as there were new and full moon dates (usually between 8 and 9) per breeding season. The number of nests for which incubation started on a given spring tide day (nest frequency) was visualised by spreading out all the data from the start to the end of the breeding season. There were many days with zero nests across all spring tide days. To get rid of the zeros without losing any of the nest data, the maximum number of nests (highest count of nests) for which incubation started on a given spring tide day of a breeding season was determined for each of the three breeding seasons monitored using the 'group-by' and 'summarise' functions of the Tidyverse R package version 1.2.1 (Hadley 2017). Because using the maximum number of nests for a given spring tide day would still leave out some nests (i.e., those less than the maximum number but greater than zero), the total number of nests (the sum of all the nests for which incubation started on a given spring tide day of a breeding season) was calculated using the 'group-by' and 'summarise' functions of the Tidyverse R package version 1.2.1 (Hadley 2017). The total number of nests was used instead of the mean number of nests because the mean value would still be influenced by the many days with zero nests across all the spring tide days.

The maximum number, and the total number of nests for which incubation started on a given spring tide day were modelled as a function of the number of days from a new or full moon date (i.e., spring tide day) using a general linear model. A quadratic of spring tide day was included in the model to identify whether the number of nests for which incubation started showed a curvilinear pattern with spring tide days.

Tide heights on about two to three days before and after a new or full moon date are similar and usually higher than at other times of the semilunar cycle (Gjerdrum et al. 2005; Bulla et al. 2017). Since the spring tide day of the semilunar cycle with very high tide heights is not

restricted to only the date of a new or full moon but can include about two to three days pre- and post- the date of a new or full moon and the fact that the number of days from a new or full moon date (spring tide day) is a circular measure, the only biologically meaningful start date of the spring tide cycle would be that from the oystercatchers' point of view. Hence a start date which fitted the oystercatcher data best (produced the clearest optima) was selected. This was done by varying the start day of the spring tide cycle as day 1, 2 or 3 after a new or full moon date and using those to fit three different models using the maximum number of nests for which incubation started on a given spring tide day as the response variable. The AIC of the three models were examined. The model with the scale which started at days 1 and 2 after a new or full moon date had similar AIC values (160.13 and 160.05 respectively), while day 3 had the greatest (163.99). The scale starting at day 2 post a new or full moon date was selected, hence the reason why the scale of the results presented starts at 2 days post a new or full moon date.

The structure of the model tested was: the maximum number of nests for which incubation started $\sim$ spring tide day + spring tide day² + breeding season (Three-level factor: 2016, 2017 and 2018). The same model was fitted for the total number of nests for which incubation started on a given spring tide day. 'Breeding season' made the models worse (larger AICs) and thus was removed from both models. The diagnostic residual versus fitted and the quantile-quantile plots showed no violation of model assumptions.

To examine the impact of the breeding habitat width and spring tide cycle on the nest-site selection of oystercatchers, habitat width was divided into two halves (to arrive at the midpoint i.e., 50% of the breeding habitat). The distance of nests to the mean high watermark (DMHWM) was used to classify the nests into those which were located above (DMHWM > 50% of habitat width) or below (DMHWM < 50% of habitat width) the midpoint of the breeding habitat. The nests were also grouped based on their incubation start date relative to a new or full moon date. Since tide heights are similar from a few days before and after a new or full moon date, nests for which incubation started 2 days before to 2 days after a new or full moon date were grouped as 'Around'. The nests for which incubation started between days 3 –9 post a new or full moon date were grouped as 'Between' while those initiated between days 10–13 post a new or full moon date were

grouped as 'Far'. This grouping of nests by their incubation start date relative to a new or full moon date is termed 'spring tide group' hereafter.

A generalised linear model with a binomial error distribution was then used to test whether the oystercatchers' nest location above the midpoint of the habitat width was determined by the width of the breeding habitat and by spring tide group. The model structure was: Nest position relative to the midpoint of breeding habitat (above the midpoint=1, below=0) ~ breeding habitat width + spring tide group + breeding season.

Finally, to examine the probability of nest losses to storm surges based on their position relative to the midpoint of the habitat, all nests with fate as predated or hatched were scored as 0, while those which were washed away by storm surges were scored as 1 (Benvenuti et al. 2018). A generalised linear model with a binomial error distribution was used to fit a model with structure: Nest fate (washed=1, predated or hatched=0) ~ position of nest relative to the midpoint of habitat (two-level factor: above or below) + breeding season.

2.3 Results

Four hundred and eighty-eight nests were observed in all three breeding seasons (2016–2018). Nests were located on average 9.30 ± 0.50 (0–58.5) m from the mean high watermark and 8.04 ± 0.64 (0–84) m from the vegetation. The average width of the breeding habitat where oystercatchers' nests were placed was 17.34 ± 0.80 (1–89) m (based on 288 habitat measurements from 2017 and 2018 breeding seasons).

2.31 Incubation start dates of oystercatchers' nests in relation to spring tide cycles

The maximum and the total number of nests for which incubation started on a given spring tide day increased from two days after a new or full moon date, peaked between days 5–9 followed by a decline (Table 2.1; Figure 2.3, Panels A & B).

Table 2.1: Models examining the relationship between the maximum and the total number of oystercatchers' nests for which incubation started on a given spring tide day on Robben Island over three breeding seasons (2016–2018).

	Estimate	SE	t value	p
A: Maximum number of nests $F_{2,44} = 6.22$, $p = 0.0042$, $R^2 = 0.19$				
Intercept	1.91	0.79	2.41	0.020
Spring tide day	0.55	0.19	2.84	0.0068
spring tide day ²	-0.032	0.010	-3.22	0.0024
B: Total number of nests $F_{2,44} = 8.71$, $p < 0.001$, $R^2 = 0.25$				
Intercept	3.37	2.44	1.38	0.17
Spring tide day	2.14	0.59	3.63	<0.001
spring tide day ²	-0.12	0.031	-3.98	<0.001

Significant p-values are in bold

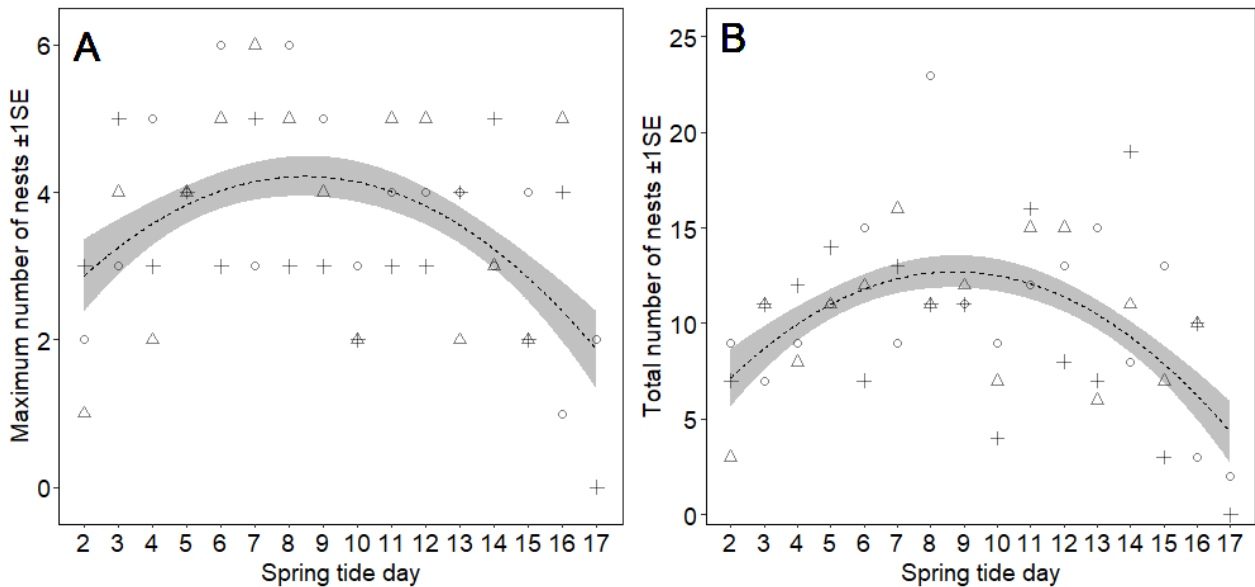


Figure 2.3: The predicted relationship between the maximum (panel A) and total (B) number of oystercatchers' nests for which incubation started on a given day, and the number of days from a new or full moon date (spring tide day) on Robben Island over three breeding seasons. The predicted values in panels A & B are from the models in Table 2.1 A & B, respectively. The points represent the raw datapoints for 2016 (circles), 2017 (triangles) and 2018 (plus signs).

2.32 How does the breeding habitat width and the timing of the start of incubation relative to the spring tide cycle influence nest-site selection of oystercatchers?

The probability of a nest occurring above the midpoint of the breeding habitat declined as the width of the breeding habitat (beach) increased in the two seasons examined (Table 2.2A; Figure 2.4, Panel A). The nests for which incubation started within -2 to +2 days of a new or full moon date (i.e., 'Around') and those initiated between 3—9 days post a new or full moon date (i.e., 'Between') had a slightly higher chance of occurring above the midpoint of the breeding habitat than those initiated 10—13 days post a new or full moon date (i.e., 'Far') (Figure 2.4 Panel B), but this was not statistically significant (Table 2.2A). The nests located below the midpoint of the breeding habitat were more likely to get washed away by storm surges compared with those above it (Table 2.2B, Figure 2.4, Panel C).

Table 2.2: Generalised linear models exploring: the probability of oystercatchers' nests occurring above the midpoint of the breeding habitat relative to beach width and the spring tide period when incubation started for the nests (Section A); probability of a nest getting washed away with respect to its position below or above the midpoint of the breeding habitat (Section B) on Robben Island in 2017 & 2018 breeding seasons

	Estimate	SE	t value	p
A: Probability of occurring above the midpoint of breeding habitat Sample size = 288				
Intercept	1.77	0.37	4.83	<0.001
Habitat width	-0.037	0.011	-3.48	<0.001
Spring tide group: Between	-0.011	0.31	-0.037	0.97
Spring tide group: Far	-0.63	0.36	-1.74	0.081
Season: 2018	-1.02	0.27	-3.78	<0.001
B: Probability of losing nests to storm surges varies with nest location Sample size = 277				
Intercept	-4.31	0.65	-6.66	<0.001
Season: 2018	1.08	0.53	2.05	0.042
Below habitat midpoint	2.25	0.60	3.77	<0.001

Significant p-values are in bold. In Section A, spring tide group: Around and 2017 breeding season take the value of the intercept. In Section B, above habitat midpoint and 2017 season are represented by the value of the intercept. Significant p-values are in bold

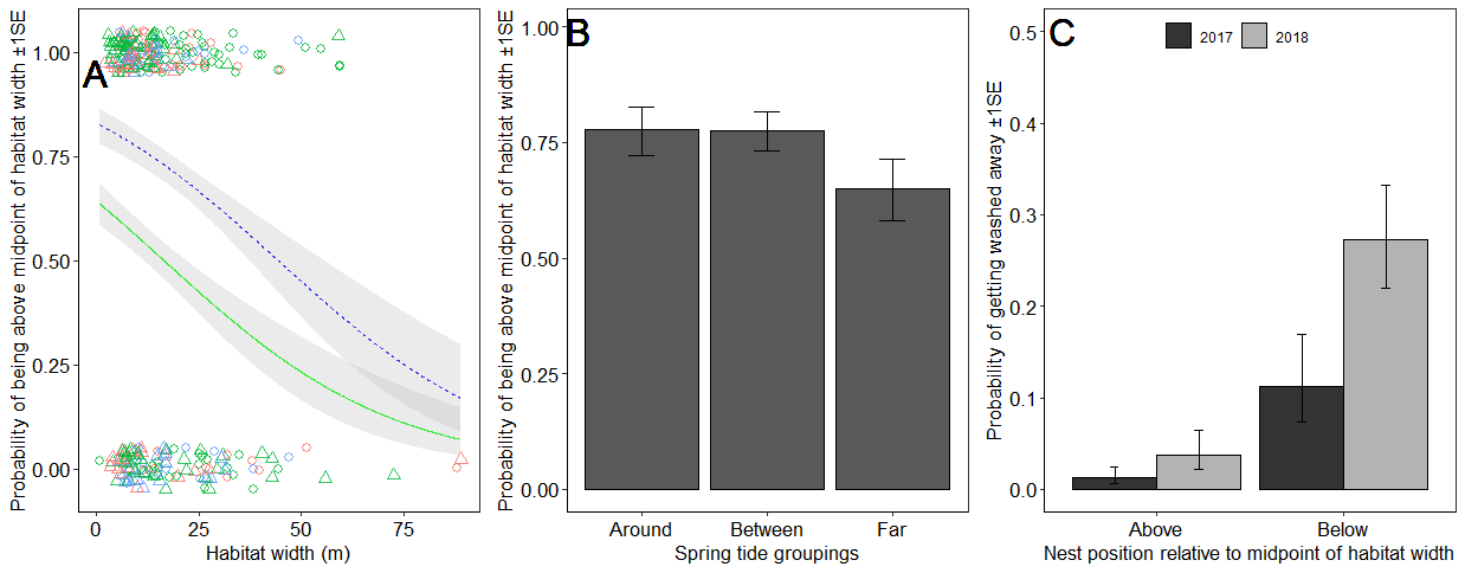


Figure 2.4: The predicted relationship between the probability of a nest occurring above the midpoint of the breeding habitat and the breeding habitat width of oystercatchers on Robben Island over two seasons; colour was based on spring tide group (described in Section 2.25): red = 'Around', green = 'Between', blue = 'Far'; broken blue line = 2017, unbroken green line = 2018; circles represent 2017 and triangles represent 2018 data points (Panel A). The predicted differences in the probability of a nest occurring above the midpoint of the breeding habitat among the different spring tide groups in 2017 and 2018 (Panel B). The predicted values for Panels A & B are from the model in Table 2.2A with season set at 2017. In Panel A, spring tide group was set at 'Between'. In Panel B, habitat width was set at the median value. Panel C shows the predicted differences in the probability of a nest getting washed away by storm surge between oystercatchers' nests occurring above or below the midpoint of the breeding habitat in 2017 and 2018 on Robben Island. The predicted values are from Table 2.2B.

2.4 Discussion

The results from this study show that oystercatchers synchronised the onset of clutches with the timing of the spring tides such that incubation started for more nests between days 2–9 post a new or full moon date than at other times (Table 2.1; Figure 2.3, Panels A & B). Oystercatchers were more likely to place their nests in the upper half of the breeding habitat in narrow beaches than in wider ones (Table 2.2A; Figure 2.4, Panel A). The nests for which incubation started -2 to +2 days of new or full moon dates and those initiated between 3–9 days post new or full moon dates had a slightly higher probability of occurring in the upper half of the breeding habitat than those initiated 10–13 days post new or full moon dates, but the difference was not significant (Table 2.2A; Figure 2.4, Panel B). Nests

located below the midpoint of the beach were more likely to get washed away by storm surges (Table 2.2A; Figure 2.4, Panel C).

2.41 The onset of incubation by oystercatchers relative to the semilunar spring tide cycle

If a bird could predict the timing of occurrence of a potentially threatening event during incubation, it might potentially time the duration or onset of incubation away from the threat to maximise nest success (Lack 1968; Lima 2009). For example, birds could increase incubation attentiveness to maintain high incubation temperature, which hastens the development of the embryos and reduces the incubation period (Hepp et al. 2005; Durant et al. 2013). By decreasing the incubation period, the length of time for which the nests are exposed to threatening conditions is reduced, consequently increasing nest survival probability (Du & Shine 2015). The synchronisation of the onset of clutches with the timing of the spring tides, such that incubation started for more nests between days 2–9 post a new or full moon date by oystercatchers as detected in this study, could be an adaptation to minimise the set of spring tides they would experience during their nearly 30 days of incubation. By starting a nest around or soon after a new or full moon date, the clutch would experience only one set of spring tides (instead of two) and by the time the next potentially dangerous set of spring tides arrives the eggs would have hatched, and mobile chicks could easily avoid the danger. Alternatively, given that some breeding pairs of oystercatchers make several scrapes within their territory before eventually choosing one in which to lay (Hall 1959): could it be that they make such scrapes and watch to see which ones gets washed by the storm surges of spring high tides and which ones are sufficiently above the reach of such storms before choosing to lay in the latter? Testing this alternative hypothesis would require that the number of scrapes in each territory be determined and their positions relative to the mean high watermark be measured. These scrapes could then be monitored before and after spring tide events as well as before and after the commencement of egg laying to see which were destroyed by storm surges and in which the birds eventually lay their eggs.

Several examples exist of fish species using the semilunar periodicity to time their breeding activities (Korringa 1957). For example, Brackish Damselfish *Pomacentrus taeniometopon* spawns twice a month around the semilunar spring tide periodicity in the wild (Pisingan et al. 2006). But under experimental conditions which lacked the semilunar spring tide

periodicity, the fish were observed to spawn sporadically, indicating that they required the tidal stimuli in their natural habitat to entrain reproductive activities (Pisingan et al. 2006). There are examples of birds using the periodic nocturnal illumination associated with the new moon to time biological activities (Yamamoto et al. 2008; Pinet et al. 2011; Cruz et al. 2013). However, few studies have focused on how birds make use of the semilunar spring tide cycle to time reproduction as detected for the oystercatchers in this study. Some of the studies with similar observations to those of the oystercatchers include the ones by Shriver et al. (2007) and Plaschke et al. (2019). Shriver et al. (2007) found that Saltmarsh Sparrows *Ammodramus caudacutus* initiated their nests mostly around 2.9 days post new moon dates and that the probability of nest success was dependent on the timing of nest initiation relative to new moon spring tide dates. They found that nests initiated between 0–9 days post a spring tide date had over 60% chance of success while those initiated afterwards had below 60% chance of success (Shriver et al. 2007). They concluded that the Saltmarsh Sparrows tightly synchronised their nest initiations with the spring tides as an adaptation to reduce the risk of nest flooding because such synchronised nests usually hatch before the timing of the next new moon spring tides. Plaschke et al. (2019) found that Snowy Plovers *Charadrius nivosus* initiated the highest number of nests around spring tides and noted that the plovers could have tracked the actual high tide levels and used the associated water line to inform the selection of safe nest positions.

Tracking and synchronising nest initiations around the timing of the spring high tides may come at the cost of losing time, and perhaps not many breeding pairs would rely on this strategy. For example, birds renesting after a failed first attempt or those laying their first clutch of the season towards the middle or end of the breeding season may be unable to afford further delaying egg-laying and perhaps would lay at any time their state/condition permits, irrespective of the spring tide periodicity (Plaschke et al. 2019). Hence, it is likely that only good condition birds which can breed earlier in the season (van De Pol & Verhulst 2006) and increase nest attendance to hatch their nests after 27–29 days of incubation would take advantage of the synchronisation of nests with the semilunar spring tide periodicity.

2.42 The impact of breeding habitat width on nest-site selection by oystercatchers

Like most coastal breeding birds (Benvenuti et al. 2018), oystercatchers need to balance the placement of their nests to minimise the risk of predation (distance away from the uppermost part of the breeding habitat, which may harbour nest predators), and that of nest losses to storm surges (distance away from the ocean) (Hall 1959). However, the capacity to adequately manage both risks may depend on the width of the breeding habitat. The breeding habitat width of the oystercatchers in this study was 17.34 ± 0.80 m on average and ranged between 1–89 m. As anticipated, the nest-site selection of oystercatchers was influenced by habitat width: they were more likely to place their nests in the upper half of the breeding habitat in narrow habitats than in wider ones (Table 2.2A; Figure 2.4, Panel A). This result shows that oystercatchers in wide habitats were able to trade-off the risk of predation with that of getting washed away by placing nests away from the uppermost part of the habitat without increasing vulnerability of nest losses to storm surges. In contrast, individuals in narrow habitats placed their nests in the upper part of the breeding habitat (minimising the risk of nest losses to storm surges but increasing predation risk) (Chapter Five), probably because they perceived storm surges to be the greater threat. This makes sense because, while placing a nest closer to the vegetation in the upper part of the beach would increase predation risk it is not a given that such nests would get predated as some may become lucky and escape predation. However, any nest placed too close to the mean high watermark likely have no chance of surviving even a single large storm surge event.

Poor availability of sufficiently wide breeding habitats may constitute an important constraining factor for the oystercatchers given that they are territorial birds, particularly as climate change-induced coastal flooding and erosion further reduce breeding habitat width (Reynolds et al. 2015). For example, Chapter Six of this thesis shows that oystercatchers' nests that were located between 10–20 m from the mean high watermark were more likely to succeed compared with those closer or further away. Yet, the widths of many territories were less than 10 m. In the early 2000s, the minimum breeding habitat width estimated in the same site as this study was 5m (Tjørve 2006). In the current study, it is 1m wide—some areas were even narrower than a meter, and oystercatchers avoided those altogether. The reduction in the width of the breeding habitat may have resulted from the impact of coastal erosion exacerbated by the flooding action of increased magnitude and frequency of storms

on the higher shoreline as a result of climate change (Thorne 2012; Widlansky et al. 2015; Vousdoukas et al. 2016). However, given the increase in oystercatcher population size on the island (Chapter Six), some pairs may be using narrower habitats which were not occupied in the early 2000s when there were fewer breeding pairs.

2.43 The impact of the spring tide cycle on nest-site selection by oystercatchers

One of the explanations for the synchronising of nest initiations around the timing of spring tides is that birds might be able to track the storm surge levels associated with spring high tides and use those to inform the selection of safe nest-sites which are sufficiently high into the beach and beyond the reach of the storm surges from subsequent high tides (Plaschke et al. 2019). This is because the storm surges associated with the spring high tides are usually highest and extend further into the beach than at other times (Shriver et al. 2007; Bulla et al. 2017). In this study, the nests of oystercatchers for which incubation started around a spring tide date -2 to +9 days post a spring tide date had a slightly higher probability of occurring higher up in the beach than those initiated 10—13 days post a new or full moon date, but the difference was not significant ($p=0.08$) (Table 2.2A; Figure 2.4, Panel B). This result, therefore, does not provide evidence to support the idea that individuals starting their nests around the time of spring tides may have better information about spring tide storm surge levels compared to those starting later. However, the non-significant result may have occurred probably because the sample size was insufficient to detect such effects or because the exact date of clutch initiations was not used in this study. Future studies using more samples and the exact nest initiation dates (rather than the onset of clutch incubation alone) may be able to detect a significant effect of the use of spring tide water levels by coastal birds to inform nest-sites which are beyond the reach of subsequent high tides.

2.44 Oystercatchers' nest placement relative to the middle of the breeding habitat affects the risk of nest losses to storm surges

In this study, oystercatchers' nests which were located above the midpoint of the beach were more likely to escape being washed away by storm surges compared with those below it (Table 2.2A; Figure 2.4, Panel C). This result suggests that oystercatcher's nest-site selection was adaptive such that the individuals which were able to site their nests further away from the ocean had greater success than others (Chapter Six). This supports the

findings from other studies that coastal breeding birds probably use nest-site selection to minimise the risk of nest losses to storm surges (Benvenuti et al. 2018; Bailey et al. 2019). The risk of nest losses to storm surges (Appendix 2.2) experienced by the oystercatchers was higher in the 2018 breeding season compared to the 2017 breeding season (Table 2.2A; Figure 2.4, Panel C). This between-season variation in the risk of nest losses to storm surges is similar to that reported for other coastal breeding birds (Benvenuti et al. 2018; Plaschke et al. 2019) and may have been due to the stochasticity of weather conditions from season-to-season (Plaschke et al. 2019). For example, there were more storm surge events in the 2018 breeding season than there were in 2017.

2.5 Conclusion

In conclusion, this study showed that oystercatchers use the semilunar spring tide cycle to time the onset of incubation, thus reducing the sets of the spring tide that they experience during incubation to one, instead of two. Nest losses to storm surges were higher for nests closer to the ocean compared to those further away. Oystercatchers used nest-site selection to minimise the risk of losing nests to storm surges. However, the ability to select optimal habitat was constrained by the breeding habitat width. These conclusions may apply to other coastal nesting bird species and their general implications are that these species are well adapted to life in the dynamic habitat where they breed. Nevertheless, the reduction of beaches by coastal erosion because of increases in the frequencies and magnitude of storms due to climate change may limit their capacity to cope in the future potentially causing poor breeding outcomes for individuals unable to secure breeding territories in wider areas of the shore.

Appendix



Appendix 2.1: view of some samples of the breeding habitat of the African Black Oystercatchers on Robben Island.

Appendix 2.2: Video footage showing examples of how African Black Oystercatchers' nets get washed by storm surge can be viewed [here](#).

Chapter Three: On-bout thermoregulation behaviours used by African Black Oystercatchers to cope with varying temperatures during incubation



Abstract

The African Black Oystercatcher *Haematopus moquini* (oystercatcher) is potentially vulnerable to climate change-induced heat stress during incubation because of the exposure of its breeding habitat to direct solar radiation, the fact that it breeds at the warmest time of the year, and its minimalistic approach to nest building. However, little is known about how oystercatchers cope with high temperatures and the extent to which they could be impacted by projected climate change-induced rising heat loads. This study examined whether the temperature experienced by incubating oystercatchers in the wild reached levels at which they made use of behavioural thermoregulation. If so, what on-bout thermoregulatory behaviours did they use to cope and did these moderate the nest temperature experienced by their eggs? Over 30 pairs were monitored on their nests using digital time-lapse cameras for two breeding years on Robben Island, South Africa. Nest and local operative temperatures were collected using iButton data loggers. Air temperature was collected from an onsite weather station. Incubating oystercatchers used panting, shading, and increased egg-turning frequency as air temperature increased. They panted for 30 minutes per hour once air temperature reached 22.7°C and panted continuously from 26.6°C. The number of days within the breeding season when air temperature exceeds 26.6°C has increased significantly on Robben Island over the last two decades. During cooler conditions, oystercatchers used the backrest posture (a behaviour used to conserve heat by insulating the bill within the back feathers) for more than 30 minutes per hour once the air temperature fell below 19.0°C. Nest temperature was on average 8.9°C higher than mean air and 6.1°C higher than mean operative temperatures during the coldest hours of the day (19h–09h) but was 7.4 °C cooler than the mean operative temperature during the warmest hours of the day (10h–18h). This study showed that the oystercatchers employed an array of on-bout thermoregulatory behaviours to cope with the varying environmental temperatures prevailing in their breeding habitats during incubation. The study also highlights the ability of the oystercatchers to modulate nest temperature, as they kept the nest significantly warmer than the surroundings during cold environmental conditions and significantly cooler than the surroundings during warm environmental conditions. These behaviours, coupled with other adaptations of the oystercatchers, may potentially help the species to withstand harsh thermal conditions and to buffer their eggs as the temperature continues to rise as predicted under future climate change. Future studies should focus on

establishing the upper thermal tolerance threshold of oystercatchers' eggs and the physiological heat tolerance of adult oystercatchers to enable further understanding of the potential impacts of repeated exposure to high temperatures.



3.1 Introduction

Endothermic organisms maintain body temperatures within normal bounds (“normothermic body temperature”) at minimal energy and water costs when the environmental temperature to which they are exposed is within their thermoneutral zone (Boyles et al. 2011; Lopes & Bicca-Marques 2017). However, when the environmental temperature falls below or rises above the thermoneutral zone, maintaining an optimal body temperature becomes increasingly demanding in terms of energy and water expenditure (Smit et al. 2011; Lopes & Bicca-Marques 2017). An incubating parent faces an even more significant challenge because it needs to maintain its own body temperature and also that of its thermally-dependent eggs (Grant 1982; Webb 1987) while needing to perform other activities such as scanning for predators (Felton et al. 2018). These concurrent thermoregulatory tasks have the potential to put pressure on incubating adults and increase the costs of reproduction, especially as temperatures continue to rise under anthropogenic climate change (Grant 1982; Hepp et al. 2006; AlRashidi et al. 2010, 2011; Cook et al. 2020). Concerns have therefore been raised as to how birds incubating in hot climates will cope (Durant et al. 2019) since the ongoing global warming is predicted to continue throughout the 21st century (Coffel et al. 2018).

Behavioural thermoregulation entails the alteration of body posture, seeking thermally buffered locations and regulating activity patterns to manage environmental heat loads (Huey & Slatkin 1976; Sinsch 1989; Simeone et al. 2004; Lopes & Bicca-Marques 2017; Pavlovic et al. 2019). Behavioural thermoregulation allows animals to conserve or dissipate heat by adjusting the rate of heat exchange between the organism and its environment through a combination of evaporation, radiation, convection, and conduction (Paterson 1981; Lopes & Bicca-Marques 2017). However, changes in behaviour for thermoregulation usually involve significant cost-benefit trade-offs (DeWitt 1967; Huey & Slatkin 1976; Cunningham et al. 2015; van de Ven et al. 2019), suggesting that organisms should make use of behavioural thermoregulation only when the costs of not doing so are greater than those associated with these trade-offs (Herczeg et al. 2006, 2008; Tattersall et al. 2017). Such behaviours could be used to cope with increased heat loads that are associated with rising temperature due to climate change (Wong & Candolin 2015).

One of the vital and often difficult tasks of biological conservation is the timely identification and management of threatening population stressors before they have a detrimental effect on species persistence (Clarke 1995). Behavioural thermoregulation is a response that researchers could observe before changes in physiology, demography or distribution are noticed, thereby allowing climate-change impacts on species to be detected earlier (Beever et al. 2017). Research into the behavioural responses of species to hot weather events could, therefore, become increasingly important in assessing species vulnerability to climate change to inform management decisions (Smit et al. 2016; Conradie et al. 2019).

The behavioural thermoregulation employed by birds can be grouped into heat dissipating behaviours (Smit et al. 2016) and heat conserving behaviours (Pavlovic et al. 2019). The two groups of behavioural thermoregulation entail, in part, the exposure or covering of certain vascularised parts of the body as environmental temperature changes (Simeone et al. 2004; Pavlovic et al. 2019). For example, the avian bill and feet are highly vascularised but poorly insulated making them suitable to function as thermoregulatory structures which birds could use to conserve or dissipate body heat, depending on environmental conditions (Greenberg et al. 2012; Tattersall et al. 2017). Examples of heat-dissipating behaviours include, amongst others, panting to increase evaporative cooling, moving away from an area of high heat to a thermally buffered microclimate (Cunningham et al. 2015; Smit et al. 2016) and the shading of eggs by incubating birds (Ward 1990; Brown & Downs 2003). Heat conservation behaviour includes standing on one leg or sitting in a way that covers the feet to minimise heat loss, and the use of the backrest posture (Simeone et al. 2004; Pavlovic et al. 2019). The backrest posture involves the insulation of the bill in the back feathers by birds to minimise heat loss through the bill (Ryeland et al. 2017; Tattersall et al. 2017). This is because, under conditions of low environmental temperatures, birds can incur a high thermoregulatory cost through the excessive loss of heat from their bills (Ryeland et al. 2017; Tattersall et al. 2017; Pavlovic et al. 2019).

The use of these thermoregulation behaviours may vary with body size. For example, bird species with larger bills relative to their body size are prone to losing more heat from their bills and thus may initiate the use of the backrest posture at relatively higher environmental temperatures compared with smaller billed birds under cold conditions (Greenberg et al.

2012; Ryeland et al. 2017). Also, species with large body sizes are known to initiate evaporative cooling (e.g. panting) at lower environmental temperatures than smaller ones as environmental temperature rises (Weathers 1981; Smit et al. 2016).

Egg-turning behaviour is an essential component of avian incubation that is widespread among birds (Walsh et al. 2007; Weathers & Zaun 2010; Clatterbuck et al. 2017; Blévin et al. 2020). It is vital to the hatchability of avian eggs (Tona et al. 2003; Taylor et al. 2018). It prevents the abnormal adhesion of embryos to the shell membrane and enhances the utilisation of albumen by embryos, thereby improving healthy growth and weight of developing embryos (New 1957; Tona et al. 2005). Egg-turning is also known to improve communication between the developing embryos and incubating parents. For instance, the embryos of Eared Grebe *Podiceps nigricollis* were observed to vocalise more when turned by their parents than when they were at rest (Brua et al. 1996). The rate of egg-turning could be positively influenced by temperature because the risk of dehydration and glueing of embryos to the shell membrane can increase with temperature (Taylor et al. 2018; Veldsman et al. 2020).

The African Black Oystercatcher, *Haematopus moquini*, (hereafter oystercatcher) has black plumage which may absorb and retain more heat compared with lighter plumages (Hochscheid et al. 2002; Sandoval & Barrantes 2019) but this may change depending on postural adjustments (Lustick et al. 1980) and windspeed (Walsberg et al. 1978). Oystercatchers nest in the open and on shelly/rocky ground where there is no shelter for the incubating adult and its eggs from direct solar radiation. Ground-nesting birds with open nests are thought to adjust the size of their nest lining in a way that creates a thermoregulatory insulating layer for their eggs (Gray & Deeming 2017; Kubelka et al. 2019). However, the oystercatchers lay their eggs in simple scrapes with little to no lining (Hockey 1983a; Tjørve 2006). Studies have shown that the ground-level temperature of this type of habitat reaches over 50°C especially during the hottest part of the day (Grant 1982; Amat & Masero 2009) thereby exposing the birds incubating eggs in such open habitats to high thermoregulatory costs (Amat & Masero 2004b; AlRashidi et al. 2010).

These characteristics of the oystercatcher and its natural breeding habitat make it potentially vulnerable to the impact of climate change in the form of increased heat load due to rising temperature. This could potentially have severe consequences for the

oystercatchers' eggs in that they may experience temperatures above lethal thresholds and become inviable (Webb 1987). Incubating adults, on the other hand, may experience high physiological costs when trying to simultaneously balance their body temperature and that of their eggs (AlRashidi et al. 2010).

Despite these evident risks, little is known about how oystercatchers cope with increasing heat loads and therefore, the extent to which they could be impacted by rising temperature due to anthropogenic climate change. Also, while several studies have focused on incubation scheduling (Afton 1980; Reid et al. 2000b; Auer et al. 2007; Tulp et al. 2009; Sládeček et al. 2019; Chapter Four), and some on what incubating birds do during recess while off their nests (Bulla et al. 2015b; Marchi et al. 2015), not many have focused on the array of behaviours used by birds to thermoregulate while present at their nests. This study bridges these gaps by monitoring the behaviour of incubating oystercatchers on their nests in their natural breeding habitat on Robben Island, South Africa. I asked – what air temperature do oystercatchers experience in the wild during incubation and has this shown a trend over the last two decades? Do these temperatures reach levels at which oystercatchers make use of behavioural thermoregulation while present at their nests? If so, what on-bout behaviours do they employ to cope, and do these behaviours help to regulate the nest temperature to which their eggs are exposed?

I predicted that oystercatchers would make use of heat-dissipating behaviours such as panting to increase their rate of evaporative cooling, as well as engage in frequent egg-turning and shading during the hottest part of the day. Since oystercatchers have a relatively large bill (61.4mm–80.8mm) (Kohler et al. 2009) and might, therefore, be vulnerable to heat loss through their bills at low temperatures (Greenberg et al. 2012; Ryeland et al. 2017), I also predicted that oystercatchers would use heat conservation behaviours such as the backrest posture at lower temperatures to minimise heat loss (Ryeland et al. 2017; Tattersall et al. 2017; Pavlovic et al. 2019)). Since body size can potentially influence the use of thermoregulation behaviours (Weathers 1981), and the oystercatcher male and female differ in their body size (Hockey 1981; Kohler et al. 2009), the sex of incubating oystercatchers was included in the analysis to control for any sex-related effects. Similarly, since air temperature can vary by the hour of the day, the hour of the day was also considered in the analysis.

3.2 Methods

3.2.1 Footage analysis and scoring thermoregulatory behaviours

The video footage was analysed using VLC video player on a computer screen (details on video placement and set-up are presented in Chapter One Section 1.244). The identity of the incubating bird was noted as male or female using details of colour rings and the leg on which the rings are worn (details on how oystercatchers were sexed are captured in Section 1.243). The posture or activity of the incubating oystercatcher within an incubation bout was scored as follows "backrest posture" (when oystercatchers sat tightly on their nests, folded their feathers tightly to their body and put their bills underneath their feathers (Ryeland et al. 2017)), "panting" (when they sat on their nests and panted), "shading" (when they squatted or stood with their wings drooping, in a way that lifts their brood patch off their eggs and casts a shadow over the eggs (Clauser & McRae 2017)). These activities are referred to as 'on-bout' thermoregulatory behaviours because they were scored when the oystercatchers were actively tending their nests. This is different from other thermoregulatory behaviours that the birds may engage in during recess and away from their nests. Only the activities scored within incubation bouts (a session of arrival at and departure from the nest by an incubating bird), which were up to an hour-long, were included in this chapter.

The duration of time that oystercatchers spent in each posture was scored to the nearest second, each time any of the postures described above were used. Oystercatchers used different postures and switched between postures several times within an hour. The total duration of time for which oystercatchers were engaged in each posture per hour was summed for each oystercatcher. Shading and panting happened concurrently. The oystercatchers always commenced panting before beginning to maintain shading posture such that by the time shading started, they were already panting continuously. Panting was therefore calculated as the sum of the time spent panting and time spent shading. The frequency of egg-turning per hour was noted. Since an hour-long bout consists of several one-minute videos analysed together, at the beginning of each one-minute video, an oystercatcher is assumed to have maintained the same posture it was engaged in at the end of the preceding footage if it was seen to still be engaged in the same activity. However, if it was observed to be engaged in a different activity, the activity it was engaged in at the start

of the video is assumed to have started 15 seconds earlier and the posture that it was exhibiting at the end of the preceding video also gets 15 seconds added, for footage with an interval of 30 seconds between 1-minute recordings. Observations were made across the 24 hours of the day and each hour of the 24 hours of the day was sampled for an average of 11.38 ± 0.89 (3–19) times. Because the observations were made per hour not the entire footage recorded and analysed were used because short (less than one hour) and interrupted bouts were not included.

3.22 Temperature data collection

Temperature data were collected using iButton DS1922L Thermochron Data Loggers (-40 to +85°C) which were placed in the centre floor of the nest in-between the eggs, in such a way that the bottom of the iButton was in contact with the floor of the nest, and the top and sides maintained some level of contact with the eggs. This placement of temperature logger at the centre of the clutch is similar to that used in Grant (1982); Cresswell et al. (2004); Watson et al. (2006) and Sládeček et al. (2019). The positioning of the iButton among the clutch ensured that it was beneath the incubating oystercatchers, such that each time the incubating birds tended their eggs, the logger was also 'incubated'. The temperature logged by this iButton was referred to as 'nest temperature'. The inner egg temperature is reported to be closely correlated to, but higher by at least 1°C than nest temperature logged in this manner (Purdue 1976; Evans 1995). In some cases, incubating oystercatchers ejected the loggers from their nests; hence the data from any logger found outside the nest scrape at the time of retrieval were not included in this study.

To obtain a comparable measure of temperature with which to examine whether the oystercatchers managed to modulate their nest temperature, a second iButton (of the same resolution, shape size and colour as the one in the nest) was placed simultaneously outside the nest within two meters at ground level in an open, unshaded area. This approach of measuring temperature in an exposed location next to the incubating oystercatcher is similar to that used for other ground-nesting shorebirds by AlRashidi et al. (2010) and Bulla et al. (2016). The temperature logged by the second iButton was referred to as 'operative temperature' in this study only for comparisons between 'nest' temperature and nearby 'operative temperature', not to provide an exact estimate of the temperature experienced by the eggs and adults as differences in the physical properties (e.g., size, shape and colour)

between iButton loggers versus birds and eggs could influence the exact operative temperatures experienced by each of these (Bakken et al. 1985).

Both nest and operative temperature iButtons were set to log data every minute except for the first few nests of the 2017 breeding year, where data was logged every 30 seconds. Air temperature recorded by a weather station based on Robben Island, logging every five minutes, was obtained from the South African Weather Services (SAWS) for 2017 and 2018 breeding seasons. Historical maximum and minimum air temperature recorded daily for Robben Island between 2001 and 2018 were also obtained from SAWS.

3.23 Data analysis

The duration in minutes per hour spent engaging in each thermoregulation behaviour was converted to proportions by dividing the duration by 60 minutes. This means that 1= engaged in the behaviour continuously for an hour and 0= not engaged in the given behaviour at all within that hour. The proportion of time not engaged in the activity was calculated as 1 minus the proportion of time engaged in the behaviour within that hour. To test the relationship between temperature and the use of each of the behaviours scored, generalised linear mixed-effects models (GLMM) with a binomial error distribution and a logit link were implemented using the nlme R package version 3.1-140 (Pinheiro et al. 2019). Following Crawley (2005) the response variable was a column bind of the proportion of time spent using a given behaviour, the proportion of time not engaged in that behaviour, using cbind function in R. The model for each behaviour contained mean air temperature within the hour of observation (continuous), breeding season (two-level factor: 2017 and 2018), sex (two-level factor: male and female) and NestID entered as a random factor to account for repeated measures from the same nests.

The predicted air temperature at which the oystercatchers engaged in each behaviour for 50% of an hour was determined as the temperature value at the point where the median intersects the x-axis (Smit et al. 2016; Cook et al. 2020). The same method was used to determine the threshold air temperature (where the maxima intersects the x-axis) at which oystercatchers panted continuously. To test the relationship between egg-turning frequency and mean air temperature, egg-turning frequency per hour was modelled as for the other behaviours but with a Poisson error distribution. The use of each behaviour by the hour of the day was analysed as above. The quadratic term of the hour of the day was included in

the model because oystercatchers were anticipated to vary their behaviours in a non-linear way (attain maxima) as temperature changes. Hour of day and air temperature were considered separately to avoid collinearity problems. Breeding season was always retained in the models irrespective of whether it was significant or not to account for the unmeasured variation within each season.

To examine how air temperature varied within the day during the breeding season of the oystercatchers on Robben Island, a linear mixed effect model using the lme4 R package (Bates et al. 2015) was used to fit mean air temperature within each hour of the day as a function of the hour of the day, its quadratic and cubic terms, with the date entered as a random factor (Funghi et al. 2019). To examine if the minimum and maximum air temperature during the oystercatchers' breeding season have shown a significant trend over the past two decades, the overall minimum and maximum air temperature within each breeding season since 2001 was modelled as a function of the breeding season (continuous between 2001–2018) using a general linear model. The number of days within each breeding season for which maximum temperature exceeded 26.6°C (the temperature above which oystercatchers panted continuously) was extracted using the 'group-by' and 'summarise' functions of the Tidyverse R package version 1.2.1 (Hadley 2017) and modelled as a function of the breeding season (2001–2018 October of a year to March of the subsequent year) using a general linear model.

To assess the effectiveness of the strategies employed by the oystercatchers in modulating the temperature of their nests, air temperature (from SAWS), nest and operative temperatures were compared between the cooler hours (19h00–23h59; 24h00–09h00) of the day and warmer hours (10h00–18h00) of the day using the Tukey PostHoc HSD test. The relationships between air, operative and nest temperature were explored using ordinary least square regression analysis. The relationships between the hour of the day and temperature (air, nest and operative) were explored utilizing a linear mixed-effect model using the lme4 R package (Bates et al. 2015) with the date of observation entered as a random factor (Funghi et al. 2019). The quadratic and cubic terms of the hour of the day were included in the model because the temperature was expected to vary in a non-linear manner with the hour of the day.

To detect any sex-effect on the use of thermoregulation behaviours, the models above were first examined using the data from the nests where biometrics and eye-fleck data were collected from both parents, enabling the birds to be accurately sexed (details on how biometrics and eye-fleck were used to determine the sex of the oystercatchers are presented in Chapter One Section 1.243). This is because the overlap in the biometrics of male and female oystercatchers could reduce the accuracy of distinguishing between the two sexes (van de Pol et al. 2009) but a within-pair comparison could increase the accuracy of discriminating males from females (Hockey 1981; Kohler et al. 2009). Once sex was observed to not be very important (according to its p-value in the model), sex was removed from the model and the model refitted using a larger sample size (i.e., including data from all parents irrespective of whether biometric data existed for both individuals of a pair). The models with and without sex as an explanatory variable are presented.

All statistical analyses were performed in R statistical software version 3.6.1 (R Core Team 2019). Mean values of variables are presented as the mean $\pm$ standard error (range).

3.3 Results

A total of 273 hours of video footage from 31 incubating oystercatcher pairs was analysed. Air temperature was available for all 273 hours of behavioural data; nest and operative temperature were available for 118 hours of behavioural data from 17 nests (the smaller sample size of the iButton logged temperature was because some pairs ejected the loggers from their nests, as noted in the method section, and those could not be added).

3.31 Thermoregulatory behaviours used by oystercatchers as air temperature changes

The proportion of time spent panting and shading by the oystercatchers increased significantly, while the use of the backrest posture decreased significantly, as air temperature increased (Table 3.1, Sections B1–B3; Figures 3.1, Panels A–C). The use of these behaviours was generally not influenced by sex (Table 3.1, Sections A1–A3). The oystercatchers used the backrest posture for 50% of the time as air temperature fell to 19.0°C and shaded their nest for 50% of the time when air temperature = 34.0°C. They panted for 50% of the time when the air temperature was 22.6°C and panted continuously from 26.6°C. Oystercatchers significantly increased their egg-turning frequency as air temperature increased (Table 3.1, Section B4; Figure 3.1, Panel D).

Table 3.1: Generalised linear mixed effect models testing the relationship between temperature and the on-bout thermoregulatory behaviours used by oystercatchers on Robben Island during the 2017 and 2018 breeding seasons. Models in Section A were based on 152 data points from 16 nests, where parents were able to be reliably sexed (Chapter One Section 1.243). Models in Section B were based on 273 data points from all 31 nests. Nest ID was added as a random term to control for repeated measures from the nests

	Section A: Included sex				Section B: Excluded sex			
	Estimates	SE	t value	P	Estimates	SE	t value	P
Panting:	Section A1				Section B1			
Intercept	-32.14	6.17	-5.21	<0.001	-28.54	5.42	-5.27	<0.001
Temperature	1.39	0.27	5.22	<0.001	1.23	0.23	5.28	<0.001
Sex: male	-0.94	0.89	-1.06	0.29	–	–	–	–
Year 2018	0.45	1.37	0.33	0.74	0.65	0.86	0.75	0.45
Shading:	Section A2				Section B2			
Intercept	-11.93	2.81	-4.25	<0.001	-11.30	2.16	-5.24	<0.001
Temperature	0.36	0.10	3.47	<0.001	0.34	0.086	3.95	<0.001
Sex: male	-0.93	1.08	-0.86	0.39	–	–	–	–
Year 2018	0.49	1.14	0.42	0.67	-0.28	0.89	-0.31	0.75
Backrest:	Section A3				Section B3			
Intercept	15.23	3.01	5.06	<0.001	10.58	1.58	6.70	<0.001
Temperature	-0.78	0.16	-5.01	<0.001	-0.56	0.08	-6.82	<0.001
Sex: male	-0.012	0.50	-0.024	0.98	–	–	–	–
Year 2018	-0.36	0.96	-0.37	0.71	0.10	0.51	0.20	0.84
Egg-turning:	Section A4				Section B4			
Intercept	-1.84	0.30	-6.06	<0.001	-1.75	0.23	-7.57	<0.001
Temperature	0.12	0.012	9.31	<0.001	0.12	0.01	12.06	<0.001
Sex: male	-0.090	0.12	-0.74	0.46	–	–	–	–
Year 2018	0.14	0.19	0.75	0.45	0.02	0.14	0.17	0.87

Sex: female and the 2017 breeding season are represented by the value of the intercept. Significant p-values are presented in bold. Temperature represents mean air temperature in all models.

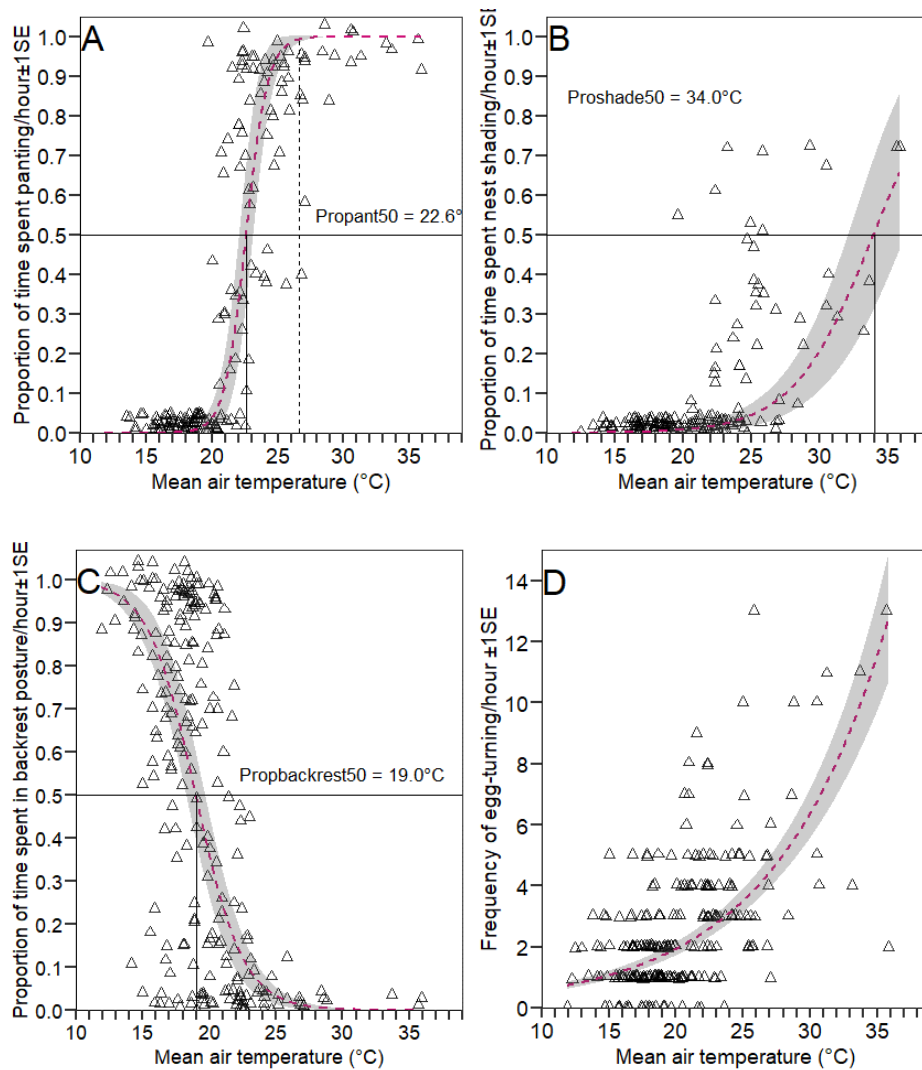


Figure 3.1: The predicted relationships between the proportion of time spent panting (Panel A), shading (Panel B), or in backrest posture (Panel C) and mean air temperature experienced by the oystercatchers on Robben Island over two breeding years. Panel D shows the predicted relationship between oystercatchers' egg-turning frequency and mean air temperature on Robben Island over two breeding years. For Panels A–D, triangular symbols represent raw data points from 2017 and 2018 breeding years. Predicted lines for Panels A–D are from the models in Sections B1–B4 of Table 3.1, respectively. Breeding season was set at 2018 for each of the plots in Panels A–D. In Panels A–C, Proshade50, Propant50, Propbackrest50 are the predicted temperatures at which the oystercatchers shaded, panted, or maintained backrest posture for 50% of the time, respectively. The point at which the broken vertical line in panel A intersects the x-axis (26.6°C) represents the temperature from which oystercatchers panted continuously.

3.32 Thermoregulatory behaviours used by oystercatchers across different hours of the day

Oystercatchers varied their use of thermoregulatory behaviours by the hour of the day; they restricted the use of panting and shading to the hottest hours of the day (08h00–18h00), while the backrest posture was used predominantly during the coolest hours of the day (19h00–07h00) (Table 3.2, Sections B1–B3; Figures 3.2, Panels A–C). Oystercatchers turned their eggs throughout the day but increased egg-turning frequency during the hottest hours of the day (Table 3.2, Section B4; Figure 3.2, Panel D). Overall, oystercatchers turned their eggs 2.27 ± 0.14 (0–13) times per hour. However, average egg-turning frequency during the warmest hour of the day (10h00–18h00) was 3.67 ± 0.28 per hour, and during the coolest hours of the day (19h00–09h00), it was 1.41 ± 0.11 per hour.

Table 3.2: Generalised linear mixed effect models examining how oystercatchers on Robben Island varied their use of different thermoregulatory behaviours by the hour of the day during the 2017 and 2018 breeding seasons. Models in Section A were based on 152 data points from 16 nests, where parents were able to be reliably sexed (Chapter One Section 1.243). Models in Section B were based on 273 data points from all 31 nests.

	Section A: Included sex				Section B: Excluded sex			
	Estimates	SE	t value	P	Estimates	SE	t value	P
Panting	Section A1				Section B1			
Intercept	-48.20	13.00	-3.71	<0.001	-39.06	8.11	-4.82	<0.001
Hour	7.53	1.99	3.78	<0.001	6.05	1.24	4.89	<0.001
Hour ²	-0.28	0.073	-3.82	<0.001	-0.23	0.046	-4.92	<0.001
Sex: male	-0.30	0.89	-0.34	0.73	–	–	–	–
Year 2018	2.24	1.28	1.75	0.080	1.70	0.95	1.78	0.074
Shading	Section A2				Section B2			
Intercept	-130.93	58.94	-2.22	0.026	-32.92	17.92	-1.84	0.066
Hour	17.55	7.91	2.22	0.027	4.42	2.57	1.72	0.085
Hour ²	-0.59	0.26	-2.22	0.026	-0.16	0.09	-1.74	0.081
Sex: male	-3.98	1.97	-2.02	0.043	–	–	–	–
Year 2018	2.79	1.77	1.58	0.11	0.60	0.76	0.79	0.43
Backrest	Section A3				Section B3			
Intercept	3.99	0.91	4.40	<0.001	2.51	0.54	4.62	<0.001
Hour	-0.91	0.16	-5.65	<0.001	-0.68	0.095	-7.12	<0.001
Hour ²	0.037	0.0065	5.67	<0.001	0.027	0.0038	7.16	<0.001
Sex: male	-0.43	0.49	-0.88	0.38	–	–	–	–
Year 2018	-0.95	0.71	-1.34	0.18	-0.069	0.43	-0.16	0.87
Egg-turning	Section A4				Section B4			
Intercept	-0.41	0.23	-1.83	0.068	-0.27	0.18	-1.49	0.14
Hour	0.25	0.036	6.94	<0.001	0.25	0.027	9.12	<0.001
Hour ²	-0.011	0.0014	-7.52	<0.001	-0.011	0.0011	-9.79	<0.001
Sex: male	0.086	0.12	0.71	0.48	–	–	–	–
Year 2018	0.48	0.19	2.46	0.014	0.23	0.15	1.52	0.13

Sex: female and the 2017 breeding season are represented by the value of the intercept. Significant p-values are presented in bold. Temperature represents mean air temperature in all models.

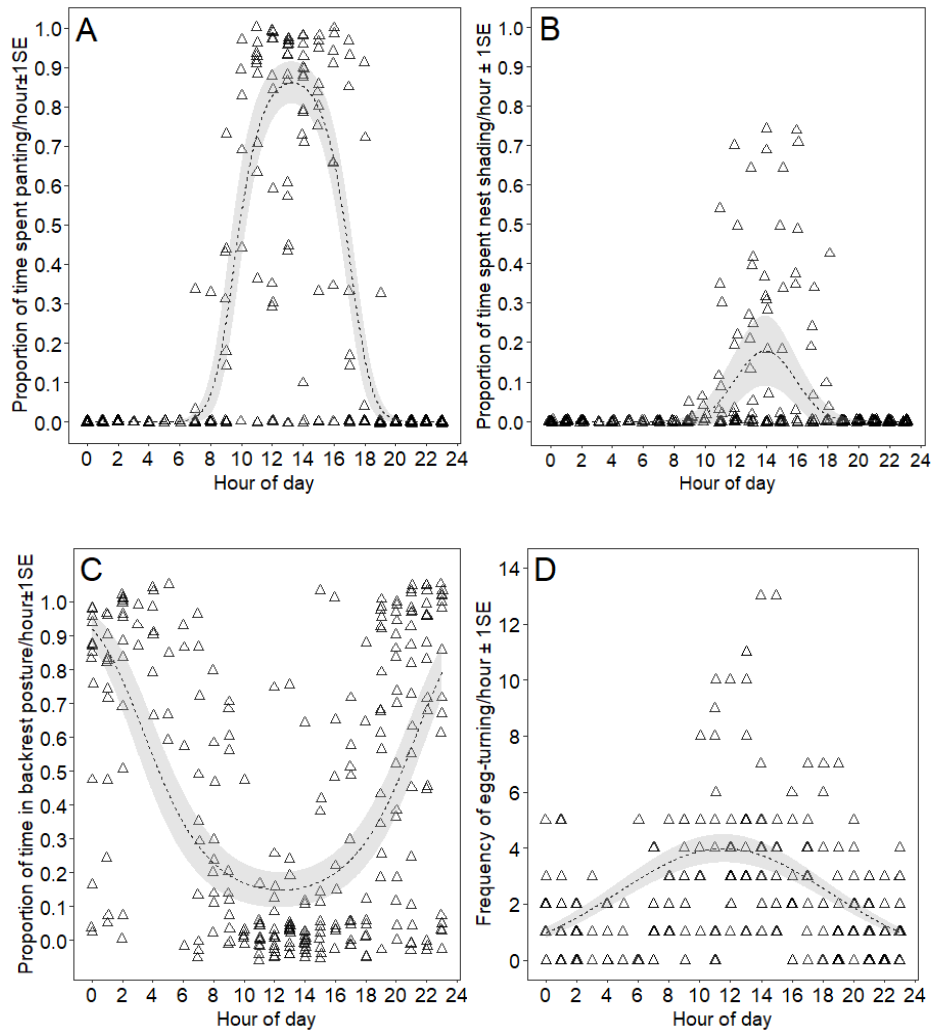


Figure 3.2: The predicted relationships between the hour of the day and the proportion of time spent panting (Panel A), shading (Panel B), or in backrest posture (Panel C) as well as the frequency of egg-turning (Panel D) per hour by the oystercatchers on Robben Island over two breeding seasons. The predicted curves are from the models in Table 3.2 Sections B1, B2, B3 & B4 respectively for the 2018 breeding season. The triangular shapes represent raw data points for the 2017 and 2018 breeding seasons in all panels.

3.33 Temperature variation within oystercatchers' breeding season

Air temperature followed a diurnal pattern; it was lowest during the early hours of the day and increased from about 10h00 then started to decline from about 16h00 (Figure 3.3, Panel A). The daily minimum and maximum air temperature on average during the breeding season of the oystercatchers on Robben Island over the last two decades were mean 14.26 ± 0.04 (4.2 – 15.8°C) and 23.99 ± 0.07 (13.60 – 40.8°C), respectively. The minimum and maximum air temperature within the breeding season did not show a significant change with year (Figure 3.3, Panel B). On average, 39 ± 2 days out of the 181 days within a breeding

season (1 October–31 March) experience maximum temperature values above 26.6°C. This has increased significantly over the last two decades with the minimum being 26 in 2008 and maximum being 54 in 2015 and 2017 breeding seasons (Figure 3.3, Panel C).

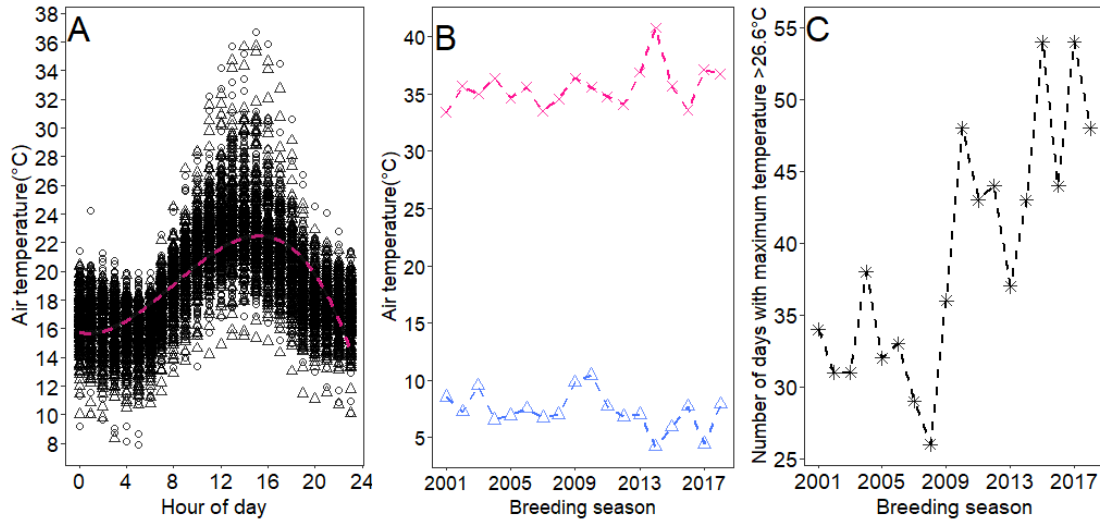


Figure 3.3: Daily pattern of air temperature (Panel A), trends in the minimum (blue) and maximum (pink) air temperature (Panel B) as well as the number of days with a maximum temperature of >26.6°C (Panel C) during the breeding season of the oystercatchers on Robben Island. The predicted line in Panel A was plotted for 2018 from the model in Table 3.3, Section D. The circles and triangles in Panel A, represents the hourly mean air temperature for the 2017 and 2018 breeding seasons, respectively. Panels B & C represent data between 2001–2018 breeding seasons. Although minimum temperature during the breeding season appeared to have declined over time, the linear model indicated that the decrease is not significant ($F_{1,16} = 2.44$, $p = 0.14$, $\beta = -0.11$, $SE = 0.07$). Similarly, the increase in the maximum air temperature within the breeding season is not significant ($F_{1,16} = 2.65$, $p = 0.12$, $\beta = 0.12$, $SE = 0.08$). However, the number of days with maximum air temperature >26.6° during the breeding season has increased significantly since 2001 ($F_{1,16} = 24.47$, $p < 0.001$, $\beta = 1.23$, $SE = 0.0014$).

3.34 Comparisons among air, nest, and operative temperatures

Air temperature and operative temperature were significantly correlated ($F_{1,116} = 263.6$, $\beta = 0.29$, $p < 0.001$, $R^2 = 0.69$). Nest temperature was significantly related to operative temperature ($F_{1,116} = 78.2$, $\beta = 0.22$, $p < 0.001$, $R^2 = 0.40$), and air temperature ($F_{1,116} = 60.23$, $\beta = 0.58$, $p < 0.001$, $R^2 = 0.34$). Nest temperature significantly differed from the operative and air temperature at all hours of the day (Figure 3.4). It was significantly higher than mean air (TukeyHSD, difference = $8.9 \pm 1.52^\circ\text{C}$, $p < 0.001$) and mean operative (TukeyHSD, difference = $6.1 \pm 1.57^\circ\text{C}$, $p < 0.001$) temperatures during the hours of the day with the coolest air

temperature (19h00–09h00) but significantly lower than the mean operative temperature (TukeyHSD, difference= $-7.4 \pm 2.91^{\circ}\text{C}$, $p < 0.001$) during the warmest part of the day (10h00–18h00). Further summaries of the three temperatures and the distribution of nest temperature observed are presented in Appendices 1&2.

Table 3.3: Linear mixed effect models examining how nest, operative and air temperatures varied by the hours of the day during the oystercatchers breeding season on Robben Island for the 2017 and 2018 breeding seasons. Sections A, B & C were based on 118 observations from 17 nests. Section D is based on 6504 data points from 271 days between November–February of 2017 and 2018 breeding seasons.

	Estimate	SE	DF	t value	p	Estimate	SE	DF	t value	p
Section A: Nest temperature						Section B: Operative temperature				
Intercept	26.06	1.38	70.63	18.87	<0.001	12.18	3.02	58.46	4.04	<0.001
Hour	0.13	0.44	112.97	0.29	0.77	2.98	0.89	112.64	3.36	0.0011
I(Hour^2)	0.083	0.045	111.41	1.86	0.065	0.027	0.089	110.11	0.31	0.76
I(Hour^3)	-0.0038	0.0012	109.42	-3.05	0.0029	-0.0072	0.0025	107.86	-2.91	0.0044
Year2018	0.19	1.05	14.02	0.18	0.86	2.83	2.69	15.62	1.05	0.31
Section C: Air temperature						Section D: Overall air temperature				
Intercept	16.4	1.14	59.89	14.41	<0.001	15.85	0.19	381	81.64	<0.001
Hour	0.080	0.34	112.7	0.24	0.81	-0.16	0.031	6230	-5.23	<0.001
I(Hour^2)	0.098	0.034	110.3	2.92	0.0043	0.11	0.0032	6230	33.82	<0.001
I(Hour^3)	-0.0046	0.00094	108.10	-4.87	<0.001	-0.0045	0.000091	6230	-49.18	<0.001
Year2018	1.34	1.01	15.97	1.33	0.20	-0.10	0.24	269	-0.43	0.67

The value of the intercept represents 2017 breeding season. Significant p-values are presented in bold.

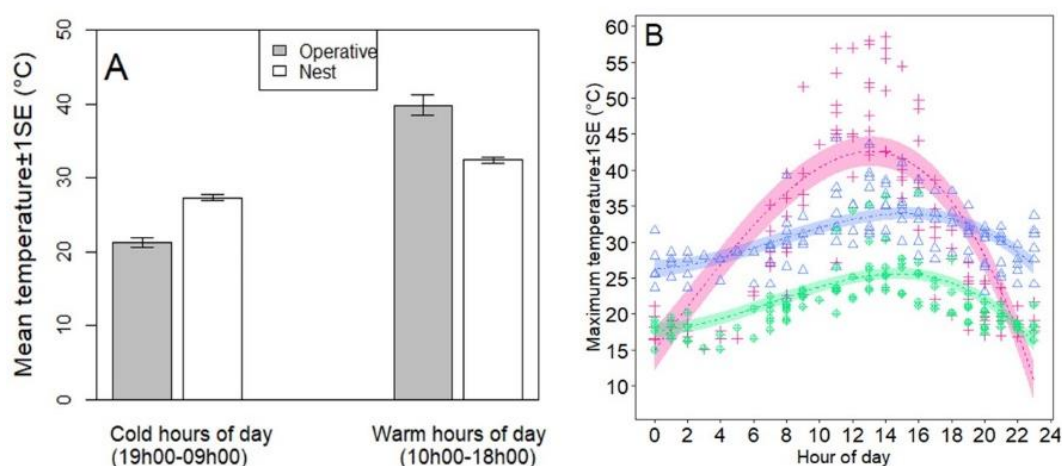


Figure 3.4: A: Oystercatchers nest temperatures and nearby operative temperatures by the hour of day. B: the predicted maximum nest (blue), operative (pink), and air (green) temperatures during each hour of the day plotted for 2018 from the models in Table 3.3 Sections A, B & C, respectively. The points represent raw data recorded within the hours of the day during the oystercatcher breeding seasons in 2017 and 2018 on Robben Island.

3.4 Discussion

The air and operative temperatures recorded during the periods over which oystercatchers had active nests rose as high as 37°C and over 58°C respectively during the hottest part of the day and fell to 11.3°C and 14.6°C respectively during the coldest hours of the day. Incubating oystercatchers made use of heat-dissipating behaviours during the hottest part of the day and heat conserving ones during the cooler hours of the night, as predicted. The use of these behaviours by oystercatchers suggests that the environmental temperatures they experienced could have been thermally stressful such that the costs of not thermoregulating (e.g., overheating adults and eggs which could lead to lethal hyperthermia) exceeded that of active thermoregulation (e.g., the exposure to the risk of dehydration while panting). The thermal conditions they experienced also varied by the hour of the day, and they used different types of behaviours across the different times of day as the temperature changed. Incubating oystercatchers modulated the temperature of their nests significantly by maintaining warmer nest conditions under low environmental temperature and cooler nest conditions under high environmental temperature.

3.4.1 Heat dissipating behaviours used by oystercatchers under elevated evaporative cooling demand

Panting

The predominant heat-dissipating behaviour used by the oystercatchers at their nests to cope with increasing heat loads was panting. The proportion of time spent panting by oystercatchers increased with temperature. They panted for 50% of the time on average when mean air temperature reached 22.6°C and did so continuously when the air temperature exceeded 26.6°C (Figure 3.1, Panel A). Panting, as a respiratory heat dissipation behaviour carries with it the benefit to lose metabolic and dry heat quickly through evaporative cooling (Weathers 1981). However, the use of evaporative cooling incurs a high risk of dehydration as it leads to a high rate of water loss (Bartholomew & Cade 1963; McKechnie & Wolf 2010; McKechnie et al. 2016). The risk of dehydration is a considerable threat to the survival of birds because extended exposure to dehydration under high environmental temperatures can be lethal (Albright et al. 2017; Sharpe et al. 2019; Conradie et al. 2020). Birds and mammals in desert habitats where water is exceptionally limiting have been reported to delay their use of evaporative cooling behaviours, by raising their

body temperature above normal levels through facultative hyperthermia, to minimise the risk of lethal dehydration (Van Sant et al. 2012; Gerson et al. 2019). However, the risk of lethal dehydration under high environmental temperatures is reduced in scenarios where drinking water and food is available (Angilletta Jr. et al. 2010; Mitchell et al. 2018; Cooper et al. 2020).

Panting for 30 minutes per hour when the air temperature reaches 22.6°C and continuously from 26.6°C, in an open habitat where air and operative temperatures reach the maximum of 37°C and over 58°C, respectively, could have exposed incubating oystercatchers to considerable risk of dehydration. However, the proximity of the oystercatcher's breeding ground to the ocean may reduce these risks to some extent. Incubating oystercatchers were observed to shorten their bout lengths, thus increasing the number of trips they made to the ocean as air temperature increased (Chapter Four). Even though the oystercatchers may not be able to directly drink seawater because of the salt content; they may benefit by increasing their foraging rate in the intertidal area to replace the water that they lose through evaporative cooling from the water content of their prey. This is because birds can access a considerable amount of water from the food they eat and supplement that with oxidative water (water produced as a by-product of oxidation of organic compounds containing hydrogen) (Bartholomew & Cade 1963). They may also benefit from their frequent trips to the ocean by belly-soaking, bathing and putting their feet in water thus losing heat to the water and could even take water in their wet belly feathers to cool their eggs as seen in Kentish Plover *Charadrius alexandrinus* (Amat & Masero 2004b, 2007, 2009). These possibilities could be very important in terms of the ability of the oystercatchers to balance their heat and water budgets and could have significantly reduced the dehydration costs associated with the use of evaporative cooling by the oystercatchers. However, the increasingly frequent trips between the ocean and the nest undertaken by the oystercatchers as temperature increases (Chapter Four), may increase parent activity around the nest and potentially increase the risk of nest predation by visually-cued predators (Martin et al. 2000).

No sex difference was found in the use of panting behaviour by oystercatchers. Body size affects the rate of water loss during evaporative cooling with smaller birds being more at risk of dehydration and therefore often delaying their use of evaporative cooling compared

with large birds (Weathers 1981; Smit et al. 2016; Thompson et al. 2018). It was thus anticipated that the use of panting by the oystercatchers might vary by sex since females are generally larger than males (average adult body mass of 665 g (male) and 730 g (female)) (Hockey 1983b; Kohler et al. 2009). The lack of a sex difference may suggest that both sexes perceived the thermal conditions that they experienced in their breeding habitats in a similar way, hence the reason for both sexes responding in the same manner. The observations reported by the authors cited above were based on interspecific comparisons rather than intraspecific. Hence, the body size effect may be too small to be detected at an intraspecific level within the same population, and larger sample sizes may be needed.

Shading

Incubating oystercatchers used shading only during the hottest hours of the day (Figure 3.2, Panel B) and significantly increased the proportion of time that they spent shading as air temperature increased (Figure 3.1, Panel B). Shading was used 50% of the time when air temperature reached 34°C: a significantly higher temperature than for panting. The oystercatchers may have used shading for a combination of reasons to benefit both incubating adults and their eggs, as discussed below.

Shading may have been initiated by oystercatchers in response to an increase in the temperature of their eggs under high environmental conditions. The traditional behaviour of avian incubation where birds sit on their eggs to permit an intimate contact between their highly vascularised brood-patch and their eggs to facilitate direct heat transfer from the parents to warm their eggs (Hanson 1959) is vital under conditions with low to moderate environmental temperature. However, during extreme air temperature, eggs may need to be kept cool rather than warm such that maintaining constant brood-patch contact with eggs may increase the risk of overheating the eggs (Grant 1982; Brown & Downs 2003) and increasingly so under the current scenarios of global warming (Durant et al. 2019; Stillman 2019). The oystercatchers may have lifted their brood-patch off their eggs to prevent the direct transfer of body heat to the eggs to keep them cool as environmental temperature increased (Downs & Ward 1997). This is because the body temperature of adults (Brown & Downs 2003; Amat & Masero 2007) and even egg temperatures (Purdue 1976; Clauser & McRae 2017) are known to increase as environmental temperature increases, especially

during the warmer part of the day. Also, depending on the stage of incubation, avian embryos begin to produce metabolic heat which contributes to the core temperature of the eggs (Lourens et al. 2006). Purdue (1976) observed that mean egg temperature was significantly lower (39.58°C) when incubating Snowy Plovers *Charadrius alexandrinus* shaded their nests compared with when sitting on them (40.07°C) when the air temperature was $>36^{\circ}\text{C}$ and concluded that shading might be a more effective way of keeping eggs cool than sitting under high environmental temperature.

The egg-cooling mechanism may be through the convective cooling effect of moving air. The oystercatchers may have protected their eggs from direct solar radiation by using their body to block solar radiation from reaching the eggs (Clauser & McRae 2017) while permitting convective cooling of the eggs as air flowed over the eggs under shading conditions (Grant 1982). However, given that the air itself could be warm under high environmental temperatures, there is a possibility of heating the eggs if parents maintain shading for an extended period because of the complex nature of heat flux between the eggs and the environment (Mitchell et al. 2018). This may explain why the oystercatchers did not normally engage in prolonged shading bouts. They usually interrupted the shading bouts with egg-turning, brief sitting and then back to shading while panting heavily. This may explain why the nest temperature recorded during incubation shows some pattern of small increases and decreases, which mimics that of when the nest was left unattended (Appendix 3.2).

The oystercatchers may have used shading behaviour to reduce their own risk of overheating if the ground on which they sat to incubate becomes very hot and contributes to the heat load that they experience (Downs & Ward 1997; Brown & Downs 2003). Lifting themselves off the ground into a shading posture may temporarily disconnect them from the heat load from the ground and permit convective cooling through increased airflow (Brown & Downs 2003; Mitchell et al. 2018). Also, by shading rather than sitting, the oystercatchers exposed their uninsulated feet and legs as well as holding their wings away from their bodies (wing-drooping) thereby increasing the surface area from which to rapidly lose heat (Grant 1982; Pavlovic et al. 2019). An oystercatcher always initiated panting before eventually starting to use shading, which suggests that it may have used this posture as the need to dissipate more heat increased under mounting environmental heat loads.

The shading behaviour observed here in the oystercatcher further confirms other studies on ground-nesting birds, e.g. Least Terns *Sternula antillarum athalassos* (Andes et al. 2020), Black-winged Plover *Vanellus melanopterus* (Ward 1990), Crowned Plover *Vanellus coronatus* (Brown & Downs 2003) and King Rail *Rallus elegans* (Clauser & McRae 2017), that have shown that birds initiate shading behaviour at high environmental temperatures and increase the amount of time spent in the posture as environmental temperature increases.

Egg turning

Oystercatchers turned their eggs significantly more often during the hottest hours of the day (Figure 3.2, Panel D) and significantly increased egg-turning frequency as air temperature increased (Figure 3.1, Panel D). Egg-turning improves hatching success because it prevents abnormal adhesion of embryos to the shell membranes, enhances albumen utilisation and communication between incubating parents and their embryos (New 1957; Brua et al. 1996; Tona et al. 2005). Given that the heat loads experienced by incubating birds and their eggs increase as environmental temperature increases (Brown & Downs 2004; Amat & Masero 2007), the possibility of some part of an egg getting warmer than the others if left unturned for an extended period should also increase as environmental temperature increases. Incubating oystercatchers may have increased their egg-turning frequency as temperature increased to ensure an even distribution of heat across the eggs and the entire clutch (Boulton & Cassey 2012).

New (1957) suggested that egg-turning could reduce the risk of desiccation and prevent the abnormal adhesion of avian embryo through the supply of a fresh layer of watery albumen over the drying regions of the membranes when turned. New (1956, 1957) explained that the mechanism behind abnormal embryo adhesion to the shell membrane in an avian egg is the rapid evaporative water loss from the albumen through the shell surface and the blastoderm especially at the early stages of incubation. This suggests that the risk of dehydration and therefore, abnormal embryo adhesion to the shell membranes may increase with temperature if the rate of water loss through evaporation occurred faster as temperature increased. Interestingly, temperature was found to explain 40% of the variance in the rate of water loss from avian eggs, with eggs losing water faster as temperature increased after controlling for ambient humidity and eggshell thickness (Veldsman et al. 2020). The oystercatchers in this study may have been reducing the risk of desiccation and

the abnormal adhesion of their embryos to the shell membranes (Appendix 4.1 in Chapter Four) by increasing their egg-turning frequency as temperature increased. Conversely, as temperature decreases during the cooler hours of day, the risk of overheating, desiccation and abnormal embryonic adhesion to the shell may have also reduced and may explain the decreased egg-turning frequency by oystercatchers during these periods.

The findings of previous studies on the impact of temperature on egg-turning frequency in birds exhibiting egg-turning behaviour are varied. Walsh et al. (2007) observed no significant relationship between egg-turning frequency and environmental temperature in Meadow Pipits *Anthus pratensis*. Walsh et al. (2007) may have failed to detect the impact of temperature on egg-turning frequency because their study periods were restricted to only night-time minimum temperatures (which ranged from 1 to 11°C) rather than the entire 24 hours of the day. Other studies which explored the entire daily pattern of egg-turning frequency, e.g. Weathers & Zaun (2010); Clatterbuck et al. (2017); Taylor et al. (2018); Blévin et al. (2020) did not directly examine the effect of environmental temperature on egg-turning frequency. However, Taylor et al. (2018) observed a significant positive relationship between egg temperature and egg-turning frequency, while Blévin et al. (2020) observed no such relationship. Some studies reported a lower average egg-turning frequency during the night compared with the day, e.g. Clatterbuck et al. (2017) for Western Gull *Larus occidentalis* and Laysan Albatross *Phoebastria immutabilis* and Taylor et al. (2018) for Forster's Tern. Some of these studies recorded higher environmental temperatures during the day than at night. Although increased activities of birds during daylight hours may contribute to the observed patterns (Taylor et al. 2018), the environmental temperature may also have contributed at least in part to explain why egg-turning frequency was higher during the day than at night.

3.42 Heat conservation behaviours: backrest posture

Incubating oystercatchers in this study used the backrest posture predominantly during the cold hours of the night (Figure 3.2, Panel C). They significantly increased the proportion of time that they spent in backrest posture as temperature decreased and maintained this posture for 50% of the time as the air temperature fell to 18.8°C (Figure 3.1, Panel C).

The use of backrest posture is predominant among species that have longer bills relative to their body size because of their higher vulnerability to heat loss from their large bills

(Ryeland et al. 2017; Tattersall et al. 2017; Pavlovic et al. 2019). Oystercatchers are characterised by very large bills and likely save a substantial amount of body heat by using the backrest posture at low temperatures. In addition to minimising heat loss through their bill, incubating oystercatchers sitting tightly on their eggs with their wings tightly held close to their bodies (in contrast to shading and wing-drooping under hot environmental conditions) may have minimised heat loss from their equally uninsulated feet and legs (Pavlovic et al. 2019). These may have maximised the retention of endogenous heat, reduced heat exchange with the environment thereby reducing the energetic costs associated with maintaining normal body temperature through metabolic means and keeping eggs warm as the environmental temperature dropped (Bartholomew & Dawson 1979; Vleck 1981). This result further validates the findings from other studies, e.g. Ryeland et al. (2017) that birds use the backrest posture to minimise the thermoregulatory and energetic costs imposed by cold environmental conditions.

Birds using the backrest posture to thermoregulate may incur a thermoregulation–predation trade-off if their ability to promptly escape from potential predators is inhibited (Carr & Lima 2012; Ryeland et al. 2017; Tattersall et al. 2017). However, such risk may have been low for the oystercatchers in this study because the period of low environmental temperature when they used the backrest posture occurred mostly at night and the predation of their nests usually occur during the day by a diurnal predator, the Mole Snake *Pseudaspis cana* (Chapter Five).

3.43 Were the oystercatchers able to modulate the temperature of their nest?

The oystercatchers, on average, kept their nests significantly warmer by 8.9°C and 6.1°C than the air and operative temperatures respectively during the coldest hours (19h00–09h00) of the day. They maintained nest conditions which were significantly cooler by 7.4°C than the operative temperature during the warmest part (10h00–18h00) of the day (Figure 3.4). The significant difference between the nest temperature *versus* air and operative temperature during periods of temperature extremes shows the excellent ability of the oystercatchers in modulating nest temperature. The oystercatchers may have possibly prevented their eggs from hypothermia or reaching physiological zero (a temperature below which no development occurs (Webb 1987)) under cold conditions as well as prevented the eggs from hyperthermia under high environmental conditions. This suggests that the array

of on-bout behaviours used by the oystercatchers plus their high nest attentiveness (Chapter Four) appeared to have helped to significantly buffer their eggs from temperature extremes.

The pattern maintained by the oystercatchers in this study follows very closely the findings of Carroll et al. (2018) where a similar approach to that of the current study was used to compare the temperature of incubated eggs to that of an area of the ground next to the nests of two ground-nesting species – Northern Bobwhite *Colinus virginianus* and Scaled Quail *Callipepla squamata*. Both species kept their eggs significantly colder than the conditions outside the nest during the hottest period of the day (Carroll et al. 2018). They also kept their eggs significantly hotter than ambient conditions during the coldest period of the day (Carroll et al. 2018). Similarly, Snowy Plovers *Charadrius alexandrineus* buffered their eggs from extreme temperatures by significantly keeping them warmer than the ambient unincubated eggs under cold conditions and reversed this pattern under warm ambient conditions (Purdue 1976). These observations agree with the findings from other ground-nesting species (Amat & Masero 2007; AlRashidi 2016) that parent birds are generally capable of regulating the thermal conditions of their nests using varying behavioural adjustments and other adaptations as environmental condition changes.

3.44 Implications of the increasing number of days with high air temperatures within the breeding season

The number of days within the breeding season experiencing maximum air temperature higher than that at which the oystercatchers continuously pant heavily has increased significantly on Robben Island over the last two decades (Figure 5.3, Panel C). To experience temperature values above which they panted continuously on more days than usual may pose a new challenge for the oystercatchers. This is because these observations are suggestive of increased heat loads which could potentially become highly thermally demanding. However, the physiological heat tolerance of oystercatchers is unknown and the extent to which experiencing these temperatures repeatedly during each breeding season and over several breeding seasons as a long-lived species breeding in exposed habitat is not clear. Future research should focus on establishing the physiological responses to heat and heat tolerance limits of the oystercatchers so that the implications of repeated exposure to high air temperatures on adults could be better understood.

The behavioural thermoregulatory responses of oystercatchers to the increase in the number of days on which they pant heavily may potentially impact their overall breeding success (Chapter Five). This is because as air temperature increases, oystercatchers respond by shortening their bout length to make frequent trips to the intertidal for thermoregulatory activities, presumably to minimise their risk of dehydration (Chapter Four). Such frequent trips may increase nest predation risk through increased parent activities around the nest (Cresswell 1997a; Martin et al. 2000). Since the predation activity of snakes as ectotherms are influenced by environmental temperature (Cox et al. 2013), and Mole Snake *Pseudaspis cana* was identified as the major predator of oystercatchers nests (Chapter Five), the increase in the number of days with high temperature through its effects on predator activity and that of the incubating adults may result in higher nest predation thus influencing overall breeding success (Chapter Five).

The maximum nest temperature recorded in some nests (44.6°C), although rare, is a value that is considered risky for many avian eggs (Appendices 3.1&3.3). Most avian eggs experience temperatures between 30–40°C during incubation (Webb 1987). The average egg temperature for several shorebird eggs as assembled by Webb (1987) is 34.3°C. Adams et al. (1999) measured African Black Oystercatcher egg temperature using instrumented eggs which were added to clutches that were naturally incubated by adult oystercatchers and unincubated artificial scrapes around the nest. The average and maximum egg temperature of the oystercatcher's eggs in incubated nests were 34.4±0.7°C and 38°C, respectively; while the temperature of unincubated nests which were exposed to direct solar radiation was 40.1°C during the day (Adams et al. 1999).

Given that the core temperature of eggs is typically higher than the surface egg temperature by at least by 1°C (Vleck 1981; Evans 1995), the nest temperature recorded during the day in this study (32.43±0.43), which is quite close to that reported by Adams et al. (1999) for the oystercatchers and by Webb (1987) for shorebirds, may represent a lower temperature compared to the egg temperatures of oystercatchers in this study. If so, the maximum nest temperature observed in the nests of oystercatchers in this study (44.58°C) could be lower than the actual egg temperature. A single exposure of the eggs of most birds to temperatures above 40.5°C is reported to be lethal (Webb 1987; Conway & Martin 2000b; Clauser & McRae 2017). In one of the nests where iButton logged very high temperatures

>44°C, one of the eggs got damaged. The nest temperatures reported here were logged while the oystercatchers were actively tending their nests. If the temperature reaches potentially lethal levels under the active care of the parents, it may be indicative of some level of thermal risk especially as the number of days with high air temperature within a breeding season increases. However, the upper thermal tolerance limit for oystercatchers' eggs is unknown, making it unclear to what extent they could be impacted if they repeatedly experience temperatures over 40.5°C. Future research should ascertain the extent to which oystercatchers' eggs can tolerate exposure to temperatures above 40.5°C.

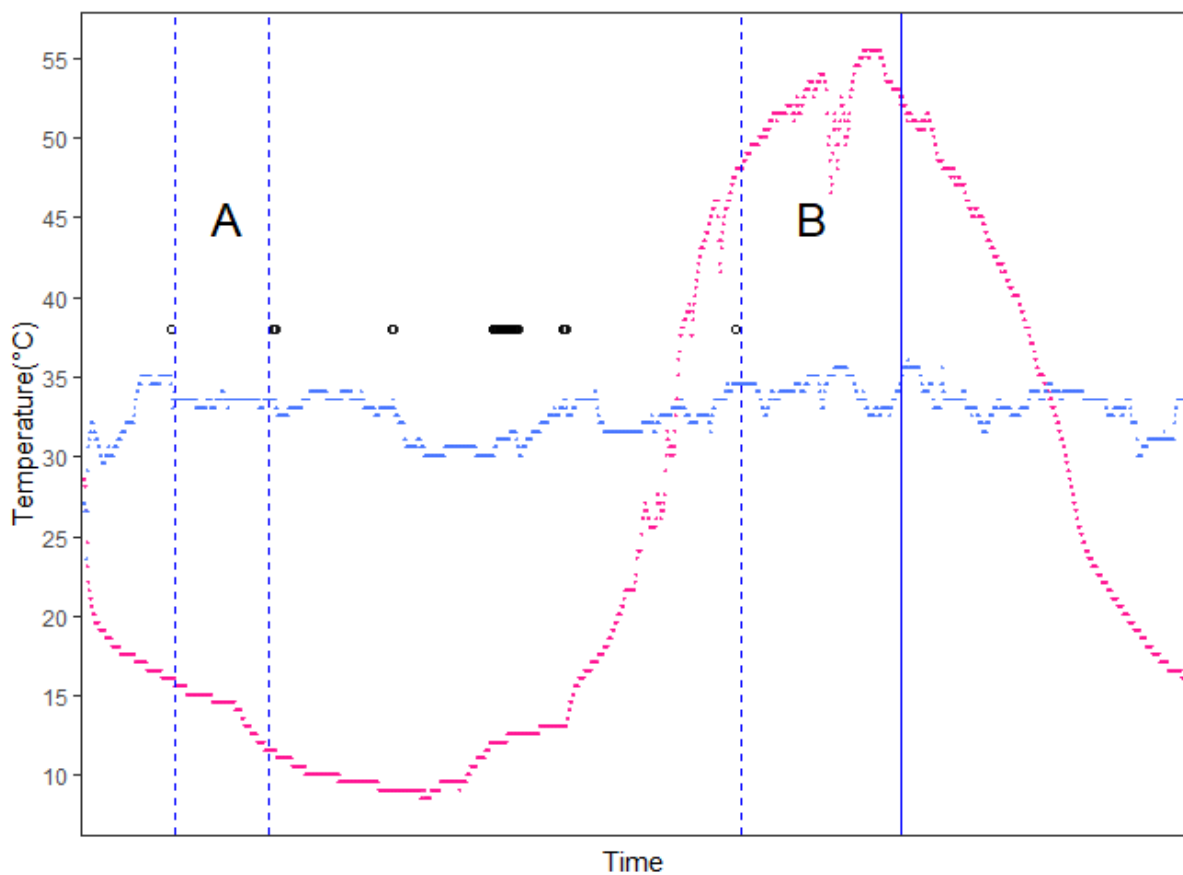
3.5 Conclusions

Oystercatchers experienced thermal conditions that varied significantly within 24 hours. They employed an array of thermoregulatory behaviours to cope with these temperature variations (examples of these behaviours can be viewed [here](#)). Oystercatchers used behaviours favouring heat retention during the cold hours of the day and employed those enhancing the dissipation of heat during the hot hours of the day. The oystercatchers always modulated the temperature of their nests significantly such that the variation in the thermal condition within the nest was less than that outside the nests. The costs associated with the use of these behaviours such as the increased risk of predation associated with the use of the backrest posture during the cold hours of the day and the risk of dehydration associated with heavy use of evaporative cooling appeared to have been minimised by the lack of nocturnal predators on Robben Island and the proximity of oystercatchers' breeding habitat to the ocean, respectively. The array of thermoregulatory behaviours used by the oystercatchers probably helped the oystercatchers to balance their heat budget and buffered their eggs from experiencing temperature extremes. The number of days within a breeding season on which air temperature exceeds that at which the oystercatchers would pant continuously has increased significantly on Robben Island over the last two decades. This suggests a potential increase in the heat load experienced by the oystercatchers and their eggs; however, the physiological heat tolerance of adult oystercatchers and thermal tolerance of the oystercatcher eggs are currently unknown. It is, therefore, recommended that future studies should focus on establishing the upper thermal tolerance threshold of oystercatchers' eggs and the physiological heat tolerance of adult oystercatchers to enable an understanding of the potential impacts of repeated exposure to high temperatures.

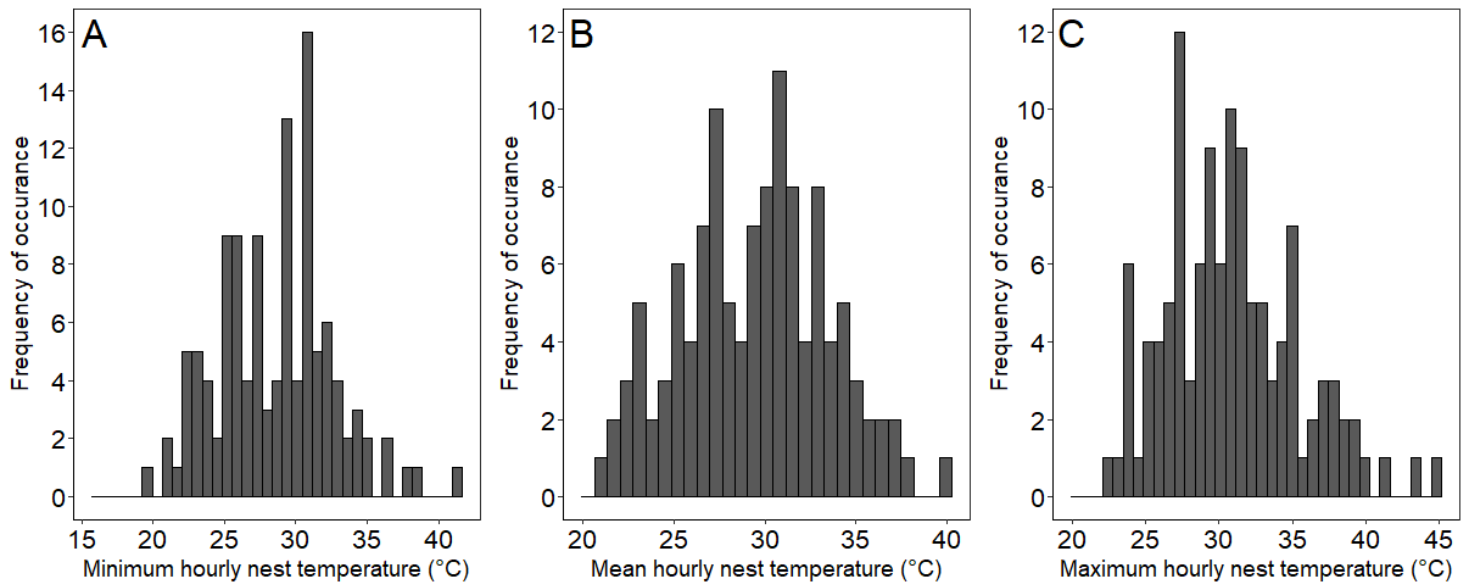
Appendix

Appendix 3.1: Summary of the air, operative and nest temperatures during the period observations were made on the Breeding African Black Oystercatchers on Robben Island over two breeding years

	19h-09h			10h-18h		
	Air °C	Operative °C	Nest °C	Air °C	Operative °C	Nest °C
Minimum	11.30	14.60	19.95	16.30	17.82	24.45
Mean	17.76±0.16	21.21±0.68	27.34±0.39	23.71±0.36	39.85±1.33	32.43±0.43
Maximum	27.30	51.60	39.26	36.90	58.52	44.58



Appendix 3.2: Nest (blue) and operative (pink) temperature from nest B18004 in the 2018 breeding season on Robben Island. This record started on 12-12-2018 by 19h19 and ended on 13-12-2018 by 20h25. Video footage indicates that the nest was being attended continuously by the parent in Sections A and B. The decreases and increases in nest temperature are more evident in Section B than in A. This may be because of increased shading and egg turning activities by the parent under high environmental temperature during the hotter hours of the day. The section after the unbroken vertical line in Section B represents the period when the video camera had stopped recording. The small circles and the thick black line represent the time when no parent was at the nest for about a minute and greater than one minute, respectively.



Appendix 3.3: The frequency of occurrence of hourly minimum (A), mean (B) and maximum nest temperature of the oystercatchers' nests from the 2017 and 2018 breeding seasons on Robben Island.



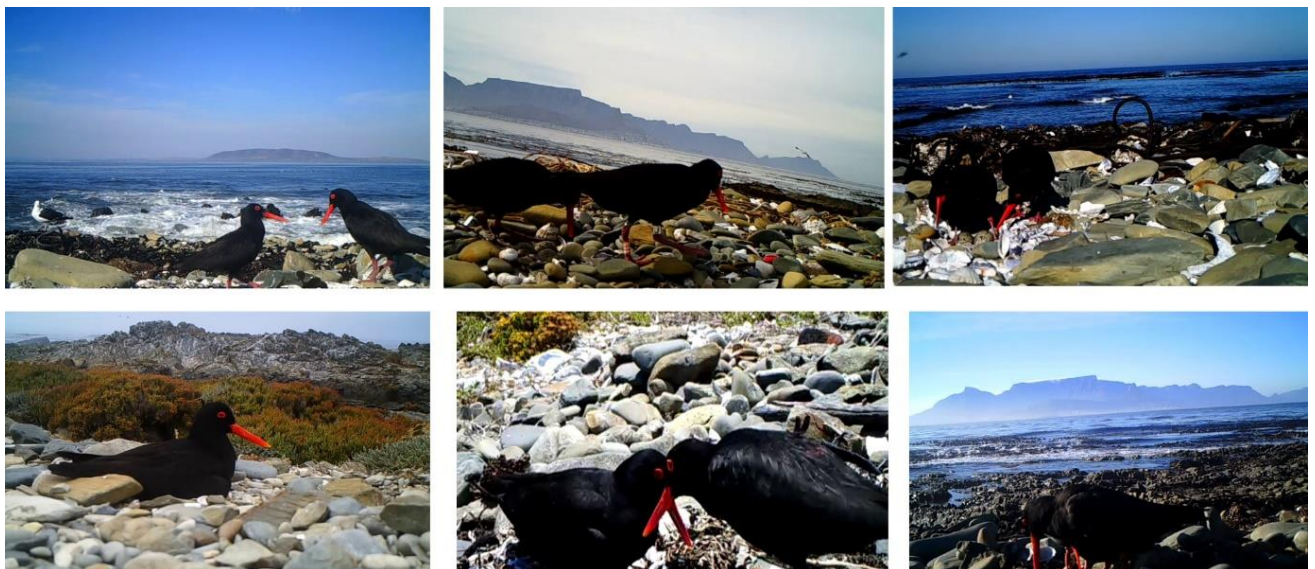
Chapter Four: Incubation scheduling by African Black Oystercatchers: Effects of weather, tide phase, and time of day



Abstract

Constant nest attentiveness, which benefits avian embryos, and body maintenance activities (e.g., foraging trips) by incubating parents are mutually exclusive activities. To balance these competing needs, parents need to schedule the time spent on and off their nests according to a wide range of environmental conditions which potentially interact to affect their energy demands and the temperature of their eggs. This study used incubation data from 39 nests monitored with time-lapse cameras over two breeding seasons on Robben Island, South Africa to examine how the African Black Oystercatchers *Haematopus moquini* (oystercatchers), a biparental incubator, varied incubation bout lengths in relation to important environmental variables that would have affected energy budgets: tide phase, air temperature, windspeed and time of day (day versus night). The study also described the rate of incubation bout interruptions, the duration of nest exposure and the corresponding changes in nest temperature. Oystercatchers' overall nest attentiveness was 95%. Incubation bout length was higher at high tide and at night than at low tide and during the day. Increases in air temperature resulted in the shortening of incubation bout length. However, time of day explained more of the variation in incubation bout lengths than air temperature. Incubation bout lengths increased sharply with windspeed and plateaued at high windspeed during the day, whereas incubation bout lengths increased slightly with slight increases in windspeed but declined from moderate to high windspeed at night. Over 50% of bouts were interrupted by the activities of humans, conspecifics, and other wildlife. Nest exposure duration (0.9 ± 0.1 minutes) during duty exchanges between parents and the associated increase in nest temperature ($0.7 \pm 0.1^{\circ}\text{C}$) was significantly lower compared to that associated with interrupted bouts (exposure duration: 4.5 ± 0.4 minutes, temperature increase: $1.7 \pm 0.2^{\circ}\text{C}$). The minimum and maximum nest temperature recorded at any nest during adults being absent from the nest were 19.0°C and 47.0°C when local operative temperatures (iButton-logged temperature in an exposed area next to the incubating bird) were 16.0°C and 51.0°C , respectively. These results suggest that oystercatchers optimised foraging efficiency by having shorter incubation bouts during low tide, when food availability was potentially highest, allowing both parents to forage within each low-high tide cycle. The results also indicate that oystercatchers' energetic, thermoregulatory, and hydration needs may have increased with temperature and high heat loads during the day but probably decreased at night and with increased windspeed during the day, and

oystercatchers responded by varying incubation bout lengths accordingly. The proximity of their nests to the intertidal zone, which means shorter travel time and quick access to food, water, and thermoregulatory opportunities, seems to be of vital importance to the effectiveness of incubation schedules and their capacity to deal with increased heat loads. Overall, these results improve our knowledge of how oystercatchers balance their own needs and that of their eggs in response to dynamic environmental variables which potentially interact to alter egg cooling rates and adults' energetic demands. It also highlighted the potential implications of extended nest exposures to high temperatures following interruption of bouts by factors external to the oystercatchers.



4.1 Introduction

Avian eggs need to experience the right temperatures to enable optimum embryo development and post-hatching survival (Webb 1987; Durant et al. 2013). However, avian eggs are ectotherms and depend almost entirely on their parents' nest attentiveness to attain proper temperatures (Conway & Martin 2000b; Reid et al. 2000b; Martin et al. 2007). Constant nest attentiveness by parents is, therefore, beneficial to the embryos (AlRashidi 2016). However, an extended nest attentiveness may result in a high-energy loss for the parents because in addition to regulating egg temperatures they need energy with which to maintain their own metabolic needs (Tulp et al. 2009). To avoid starvation, incubating birds need to forage away from the nest, to replenish depleted energy reserves (Coe et al. 2015; Marchi et al. 2015). These mutually exclusive needs of embryos and parents result in a trade-off between nest attentiveness and foraging by parents (MacDonald et al. 2013). To balance this trade-off, parent birds usually have tight scheduling of time spent on and off their nests (White & Kinney 1974; Afton 1980).

Generally, two systems of incubation exist in birds – the uniparental system where only one parent, usually the female incubates (Manlove & Hepp 2000) and the biparental system where both males and females incubate (Bulla et al. 2015a). In the biparental system both parents relieve each other periodically such that when one parent incubates, the other goes on recess to replace lost energy, making it likely for them to maintain constant nest attentiveness at a relatively lower energetic cost compared to uniparental incubators (Cresswell et al. 2003; AlRashidi et al. 2011; Hoppe et al. 2019). The time difference between when a biparental incubator starts to incubate and the time its partner returns to take over incubation duty can vary extensively among birds in response to dynamic environmental conditions which potentially influence the energetics of parents and the temperature of the eggs (Skutch 1962; Cresswell et al. 2003; Folk & Hepp 2003; Amininasab et al. 2016).

Body reserves of incubating adults are presumably highest at the start of the incubation bout and decrease as the length of the incubation bout increases (Moreno 1989). Biparental incubators may take their cue to end an incubation bout by responding to the depletion of their body reserves (Chaurand & Weimerskirch 1994). An incubation bout may also be scheduled per the arrival time of the returning partner (Yorio & Boersma 1994). However,

the arrival time of the returning off-duty partner may depend on how quickly it can access and handle prey items with which to replenish its depleted body reserve (Chaurand & Weimerskirch 1994). Incubating birds foraging in areas with high food abundance which are close to their nests, may be able to replenish their reserves quickly and therefore take shorter breaks (Vafidis et al. 2018). Hence, local conditions which periodically influence food availability and accessibility could influence the incubation scheduling decisions of incubating birds (Grémillet 1997; Collins et al. 2016; Brambilla et al. 2019). For example, shorebirds nesting in coastal areas next to their intertidal foraging grounds which become periodically inaccessible, depending on the tide height, may be expected to schedule their incubation bouts around tide conditions (Ramli & Norazlimi 2016; Fonseca et al. 2017), with birds likely to have shorter bouts at the time of low tide when food is presumably more abundant and accessible (Spiegel et al. 2012; Marchi et al. 2015).

Temperature is another critical factor which is used as a cue by incubating birds to schedule time on and off their nests (Conway & Martin 2000b; Simmonds et al. 2017; Zhang et al. 2017). In a hot environment, biparental incubators may need to relieve each other more frequently (shorter incubation bout lengths) as temperature increases, for thermoregulation purposes (Grant 1982; AlRashidi et al. 2010). This is because the body temperature of incubating birds may correlate with how long the bird has been tending the nest without being relieved under an increasing load of solar radiation (Grant 1982; Amat & Masero 2007). The cost of adult thermoregulation is, therefore, likely to increase with a prolonged bout duration during high environmental temperatures (AlRashidi 2016). This increased cost of adult thermoregulation may necessitate frequent trips to thermally buffered habitats or water sources to cool off (Marchi et al. 2015), as observed in incubating Kentish Plovers *Charadrius alexandrinus* which took frequent trips to belly-soak to quickly reduce excess body heat as environmental temperature increased (Amat & Masero 2004). The need to stay hydrated (maintain water balance) may also increase as temperature increases, particularly for birds using evaporative cooling thermoregulatory behaviours (Bartholomew & Cade 1963; Dawson 1982), such as panting (Chapter Three). This increased need for water balance as reliance on evaporative cooling increases under rising heat loads may also drive the shortening of incubation bouts as temperature increases (Bourne et al. 2021).

Windspeed may influence the thermal and gaseous environments experienced by incubating birds and their nests (Ar & Rahn 1980; Heenan & Seymour 2012). This is because air movement over a nest and the body surface of incubating adults play an essential role in the rate of heat and water vapour exchange between the nest, adults, and the environment (Hilton et al. 2004; Heenan & Seymour 2012; Dickinson et al. 2019). As windspeed increases, the rate of heat loss and cooling of eggs and adults also increases (Brown & Downs 2004; Dickinson et al. 2019). Incubating birds may respond to increasing windspeed by increasing incubation bouts and reducing off-bout frequency (Klimczuk et al. 2015; Hoppe et al. 2019). For example, windspeed was the most critical weather variable affecting incubation patterns in the White-rumped Sandpiper *Calidris fuscicollis*, with the Sandpipers spending more time on their nests as windspeed increased (Cantar & Montgomerie 1985).

Time of day and the sex of incubating birds are also factors reported in the literature to influence incubation scheduling by birds. While both sexes may contribute equally in some species (Bulla et al. 2014), others may vary contribution by the time of day with one gender contributing more during a particular time of day (AlRashidi et al. 2011). In the Black-billed Gull *Larus bulleri* for example, one of the parents sits uninterruptedly throughout the night, but during the day, the two relieve each other approximately every two hours (Beer 1965). Similarly, female Semipalmated Sandpipers *Calidris pusilla* tended to incubate more at night than males (Cresswell et al. 2003). However, in the American Black Oystercatcher *Haematopus bachmani*, both parents incubated both day and night and nocturnal bouts were nearly two times longer than during the day (Spiegel 2008). One of the explanations for why shorebirds have longer incubation bouts at night compared to the day is the potential effect of light intensity on foraging efficiency. Some shorebirds rely on visual cues to locate their prey, and although they can forage during both day and night low tides using different tactics such as tactile and probing strategies at night (Turpie & Hockey 1993; Rompré & McNeil 1996; Dwyer et al. 2013), they may prefer to forage more during the daytime low tides than at night-time low tides, and may therefore schedule their incubation bouts accordingly. For example, incubating Semipalmated Sandpipers *Calidris pusilla* stayed closer to their nests at night and tended to spend less time feeding than during the day (Bulla et al. 2015b).

The various environmental factors that could potentially influence the scheduling of avian incubation bouts may be interrelated with each other such that they may potentially interact to influence incubation bout schedules. For example, solar radiation and light intensity during the day may contribute to making temperature to vary between daytime and night-time, with daytime temperatures normally warmer than night-time temperatures (Tulp & Schekkerman 2006). Also, windspeed may negatively influence temperature such that as windspeed increases temperature may decrease. But this relationship between windspeed and temperature may depend on the time of day, because as temperatures may already be cooler at night compared to during the day, an increasing windspeed may have different effects on the temperature experienced by incubating birds during the day compared to at night (Cantar & Montgomerie 1985). Birds may therefore need to deal with these complexities and schedule their incubation bouts in manners that protect their eggs from harsh environmental conditions without compromising their own somatic needs (Bulla et al. 2015b).

The nests of biparental incubators are almost always attended by one or the other of the parents such that the duration of exposure of the eggs is almost negligible (Bulla et al. 2015a; Bulla 2016; Pedler et al. 2016). However, there are times that both parents leave the nest exposed in an impromptu manner due to, for example, human disturbance (AlRashidi 2016). An increased frequency and duration of impromptu nest exposure could negatively compromise the incubation process through increased parent activity around the nest which could, in turn, increase the risk of nest predation (Martin et al. 2000; Smith et al. 2012). Additionally, an extended duration of nest exposure following an impromptu exit by incubating parents may result in the cooling (when the air temperature is low) or overheating (during the hottest part of the day) of the eggs (Smith et al. 2012; Bueno-Enciso et al. 2017). The cooling of eggs when exposed may not compromise immediate egg viability but may lengthen the incubation period, compromise immune function, and affect post-hatching survival (Durant et al. 2013; Ospina 2017; Shi et al. 2019). The exposure of eggs to excessively high temperatures ($>40.5^{\circ}\text{C}$) has been reported to be more injurious to the developing embryo because it can cause the immediate death of the embryo or abnormal embryonic adhesions to the shell membrane (Webb 1987; Adams et al. 1999; Clauser & McRae 2017). Hence, the frequency and duration of impromptu nest exposure, especially

during the hottest part of the day, may have significant implications for the success of the incubation process (Prescott 1964; Adams et al. 1999; Martin et al. 2000; McGowan & Simons 2006; Merrill et al. 2020).

Although African Black Oystercatchers *Haematopus moquini* (hereafter oystercatchers) is relatively well studied compared to many other African birds, the aspects of its incubation patterns and variability have not been explored in much detail. In this chapter I asked: (1) What is the rate of interruptions to the incubation bouts of oystercatchers on Robben Island? (2) What is the duration of impromptu nest exposure and the corresponding nest temperature changes during such exposure? (3) What percentage of the time do oystercatchers tend their nests for (overall nest attentiveness)? and (4) How do the oystercatchers vary incubation bout lengths with tide height, temperature, windspeed and daytime versus night-time to maximise foraging opportunities while minimising the costs of leaving the nest? I hypothesized that nest exposure duration and the associated changes in nest temperature following duty exchanges by parents would be less than that associated with forced (impromptu) nest exposures.

Since oystercatchers' foraging grounds, like that of other shorebirds that forage in the intertidal zone (Ramli & Norazlimi 2016; Fonseca et al. 2017; Burger et al. 2018) become flooded and inaccessible at high tide, I hypothesized that incubation bout lengths would be higher at high tide than at low tide to maximise foraging efficiency. I hypothesized that incubation bout length would be inversely proportional to temperature because of the increased energy and hydration demands under increased heat load that is associated with rising temperatures (Grant 1982; Amat & Masero 2004b; AlRashidi et al. 2011; Bourne et al. 2021). For example, incubating oystercatchers began to pant when the air temperature reached 23°C and continuously panted when it exceeded 27°C (Chapter Three). I anticipated that as air temperature approached these temperature values, the oystercatchers would shorten their incubation bout lengths as their need for frequent trips to thermally-buffered areas for thermoregulation purposes may have increased (Amat & Masero 2004b). Since the rate of cooling of both eggs and incubating adults increases as windspeed increases (Hilton et al. 2004; Heenan & Seymour 2012; Dickinson et al. 2019), I hypothesized that incubation bout length would be directly proportional to windspeed, but this may vary by the time of the day (Cantar & Montgomerie 1985; Klimczuk et al. 2015). According to the observation

of Adams et al. (1999) that oystercatchers leave their nests exposed at night, I hypothesized that oystercatchers would attend their nests more during daylight than at night. Since incubation bouts could vary by sex (Klimczuk et al. 2015), the sex of incubating oystercatchers was noted and included in the analysis to control for any sex-related variation.

4.2 Methods

4.2.1 Video data extraction

The video footage (details on cameras settings and placement around oystercatchers' nests have been presented in Chapter One Section 1.244) was analysed using the VLC media player (3.0.6 Vetinari). The total time of observation at each nest is calculated as starting from the time that either the male or female oystercatcher returns to the nest after camera activation (the footage between when the video cameras were activated and the time the birds return to resume incubation were excluded) and ends when either the camera stops recording (due to a technical breakdown or power outage), a predation event occurs, or any other factor that leads to the removal of the incubated eggs such as being washed away by storm surge. The identity of the incubator (male or female, using details of colour rings and/or the leg on which the rings are worn (as explained in Section 1.243)) was noted at the start of every incubation bout. The media player was set on fast playing mode during analysis, stopped and played at normal speed whenever the incubating bird responded either to the arrival of its mate, humans, vehicles, conspecifics or predators, following the example of Spiegel et al. (2012). The length of an incubation bout was determined as the time elapsed in minutes, between an incubator's arrival to tend its nest (either by sitting or shading) and departing from its nest.

Incubation bouts were grouped as follow: **full bouts** (progressed without any interruptions and ended when the relieving partner arrived); **impromptu bouts** (ended by the incubator moving off the nest in an agitated manner in response to disturbance); **break bouts** (ended without the relieving partner's arrival or any agitation); **incomplete bouts** (when an individual leaves the nest after being disturbed and the same individual returns to incubate after which its partner returns to take over; the first section of the individual's time on the nest is noted as an impromptu bout. But the second section is noted as an incomplete bout, because, although the second section ended by its partner's return, it is different from that

of a full bout because of the interruption in-between and the duration of the interruption usually vary, sometimes lasting for minutes); **camera bouts** (camera stopped recording). Nest exposure duration was calculated as the time elapsed in minutes when neither of the parents attended the nest either during duty exchange or following an impromptu or other departure from the nest. All the bouts which were ongoing when the camera stopped recording as well as all other bouts, except full bouts, were excluded in the analysis used to determine how oystercatchers schedule incubation bouts in response to environmental conditions because they could potentially confound the results. Impromptu bouts were, however, used to assess and describe the rates of interruptions of the incubation schedules of oystercatchers. Also, all the incubation bouts (i.e., all the period when the nest was tended) were used to determine the overall nest attentiveness (irrespective of sexes) and by sex (specifically for males and females) as described below in the next paragraph.

Overall nest attentiveness was determined as the percentage of time spent on the nest by both parents over the total period of footage, { i.e., (the sum of all incubation bouts by both parents divided by the total observation time) x 100} (Martin et al. 2007). Male attentiveness was calculated as the percentage of the total observation time for which the nest was incubated by the male following the example from AlRashidi et al. (2011) and Sládeček et al. (2019). Similarly, female attentiveness was calculated as the percentage of the total observation time for which the female incubated the nest. Bouts were grouped as occurring during the day or night by using the details of daily sunrise and sunset timings for Robben Island from the times and date website at <https://www.timeanddate.com/sun/@3362356>. Like Spiegel et al. (2012), if over 50% of an incubation bout occurred during the day or night (i.e., bouts occurring during the transition from day to night and vice versa), the bout was assigned to that time of day category with over 50% of the bout.

4.22 Weather data and tide data

Air temperature recorded every five minutes, and windspeed recorded hourly through a weather station on Robben Island was obtained from the South African Weather Services (SAWS) for the period of this study. Nest and local operative temperatures were measured using iButton temperature loggers which were placed in the centre floor of the nest in-between the eggs and within two meters of the nest, respectively. The two iButton loggers

were set to take temperature readings every minute (these iButton-logged temperatures were not used in the main analysis but used to compare nest temperature fluctuations when the nests were being attended and when left exposed). The iButtons were placed only in the nests where cameras were placed and were retrieved at the same time as the cameras. Not all deployed iButtons provided useful data because some pairs ejected the loggers and the data from such loggers were not used because they were found outside the nest at retrieval. Predicted hourly tide height data for Cape Town Harbour, located about 11 Km from Robben Island (Figure 1.1) was supplied by the South African Navy.

4.23 Data analysis

Air temperature (taken every five minutes), windspeed (hourly), and predicted tide height (hourly) data corresponding with the start time and end time for each bout were noted. The mean air temperature, maximum windspeed, maximum tide height occurring during each bout were calculated and linked to each bout accordingly. Maximum tide heights <1 m was categorised as low tide, while maximum tide heights >1 m were grouped as high tide because it was assumed that the birds may have had access to the intertidal feeding area at tide heights of <1 . This grouping of tide height was not based on the traditional low tide-high tide times (which are normally about six hours apart), but on the hourly tide heights. Tide heights of <1 m represent about half of the highest tide heights and were grouped as low tide because the birds may access their feeding grounds as the tide ebbs (Hockey 1983a; Leseberg 2001). The nest (temperature logged by iButton placed in the floor of the nest) and local operative temperatures (ground-level temperature logged by iButton placed within 2 m of incubating oystercatchers) at the start of each nest exposure (the time when an incubating bird moved away from the nest) and at the end of each nest exposure (the time that the exposure ended either by the return of the same individual or its partner taking over incubation duty) were noted. The change in nest temperature during nest exposure was calculated as the nest temperature at the end of the exposure period – the nest temperature at the start of the exposure.

As explained in Section 3.21 above, only full bouts were included in the analysis of how oystercatchers vary their incubation bouts in relation to environmental variables. Incubation bout length was modelled as a function of tide phase (two-level factor: low and high), time of day (two-level factor: day and night), sex (two-level factor: male and female) and

maximum windspeed (continuous) using a linear mixed-effect model in the lme4 package (Bates et al. 2015). Because the various environmental variables could potentially interact to influence the incubation bout lengths of oystercatchers, two-way interaction terms between the time of day and sex, time of day and windspeed, time of day and tide phase were included in the model. The quadratic term of windspeed was added to the model because it was anticipated that the effect of windspeed on temperature and, therefore, incubation bout length might be non-linear. Nest ID was included as a random variable because of the repeated bout measurements from the same nests. The year (breeding season) of observation was retained to account for uncaptured variation in both breeding seasons monitored. Incubation bout length was log-transformed to meet model assumptions. Time of day and temperature were analysed in separate models to avoid collinearity problems and to compare their relative performance using AIC and the amounts of variation R^2 explained by their respective models. Hence to examine the effects of air temperature on Incubation bout length, the same model structure as above was repeated but with the time of day replaced by the mean air temperature. Non-significant interaction terms and quadratic terms were removed from both the time of day and air temperature models. AIC was used to compare the models to select the model with the smallest AIC. Air temperature and the interaction term between the time of day and temperature was, however, introduced to the time of the day model with the smallest AIC value and time of day as well as the interaction term between the time of day and temperature was added to the air temperature model with the smallest AIC to examine how they performed together. To ensure that any sex-effect on incubation bout length was detected, the models were first based on the full incubation bout data (128 incubation bouts) from 20 nests where biometrics and eye-fleck data existed for both parents (details on how biometrics and eye-flecks were used to sex oystercatchers in this study has been presented in Chapter One Section 1.243). This is because there is a small overlap in the biometrics of male and female oystercatchers, but a within-pair comparison could increase the chance of correctly discriminating males from females (Hockey 1981; Kohler et al. 2009). Once sex was seen not to be very important (as indicated by the p-value of 'sex' in the model), sex was removed from the model and the model refitted to a larger sample size (223 incubation bouts from 34 nests i.e., including full incubation bout data from all parents irrespective of whether biometric data existed for both individuals of a pair). A single point was considered an

outlier after initial analysis and was therefore omitted from further analysis. Both the models with and without sex as an explanatory variable are presented. A visual inspection of the standardised residual versus fitted values and quantile-quantile (Q-Q) plots of the models showed no obvious violation of model assumptions. To examine the relationship between air temperature and windspeed and the time of day, a linear mixed effect model was fitted. Mean air temperature during each of the bouts examined was set as the response variable while time of day, windspeed, the quadratic and cubic terms of windspeed were added as explanatory variables. Breeding season was entered as a random variable. To examine if the nest exposure duration associated with impromptu exits from the nest differs significantly from that associated with duty exchanges by parents, Welch Two Sample t-tests were used to test the difference between their means. The same method was used to test whether the temperature increase or decrease during nest exposure differed significantly between impromptu exposures and parents' duty exchange exposures. All data analyses were conducted in the R statistical software version 3.6.1 (R Core Team 2019). Mean values of variables are presented as the mean $\pm$ 1 standard error (range).

4.3 Results

Seven hundred and six incubation bouts totalling 623 hours from 43 pairs of oystercatchers were scored, of which 164 incubation bouts were excluded from further exploration. These bouts were excluded because they were either incomplete, from a nest where only the female incubated (the male was never seen again and the reason for its disappearance is unknown), from nests with only 1–4 hours of recording or were bouts which were ongoing at the time that the camera stopped recording. The mean air temperature during the incubation bouts was 22.16 ± 0.18 (9.66 – 36.78) °C, maximum tide height was 1.13 ± 0.02 (0.20 – 1.90) m, and maximum windspeed was 3.31 ± 0.07 (0.0 – 11.50) m/s.

4.31 Bout interruptions, nest exposure and associated changes in nest temperature

Oystercatchers were disturbed by the activities of humans, conspecifics, predators, and other wildlife (some examples of these disturbances can be viewed [here](#)). Of the 542 incubation bouts totalling 462 hours from 39 nests explored further in this study, 59% (319 of 542) ended in an impromptu manner. Eighty-seven percent (279 of 319) of all impromptu bouts occurred during the day, while 13% (40 of 319) occurred at night. The limited field of

view of the cameras used (less than 360°) did not permit the identification of the exact cause of departure from the nest by oystercatchers during all impromptu escape from the nests.

The nest exposure duration associated with full incubation bout exchanges between pairs was significantly lower (0.87 ± 0.09 (0–7.62) minutes) compared to that associated with impromptu bouts (4.48 ± 0.36 (0.22–80.23) minutes); (Welch Two Sample t-test: $t = -9.71$, $df = 357.39$, $p\text{-value} = <0.001$).

The temperature increase associated with nest exposure during full incubation bout exchanges between pairs was significantly smaller (0.65 ± 0.12 (0.03–1.99) °C) than the temperature increase associated with impromptu nest exposure (1.70 ± 0.22 (0.06–11.95) °C); (Welch Two Sample t-test: $t = -4.27$, $df = 94.74$, $p\text{-value} = <0.001$). Temperature decrease associated with nest exposure during full incubation bout exchanges between pairs was -1.17 ± 0.22 (-3 to -0.50) °C and was similar for impromptu nest exposure (-1.33 ± 0.22 (-8.99 to -0.06) °C; Welch Two Sample t-test: $t = -0.54$, $df = 40.35$, $p\text{-value} = 0.59$). The minimum and maximum nest temperatures recorded (by the iButtons in the nest) at any nest following exposure were 19°C and 47°C when the local operative temperature (logged by the iButton outside the nest within 2 m of the incubating bird) was 16°C and 51°C, respectively.

4.32 Overall nest attentiveness and sex contributions

Overall nest attentiveness was 95 ± 0.58 % (87–100 %) for 38 nests observed for a total of 644 hours. Each nest was observed for an average duration of 16.95 ± 1.02 % (8.2–30.9 %) hours. There was a single nest where only the female incubated. Her total nest attentiveness was low (22 %) and was excluded from the calculation of overall mean nest attentiveness. She eventually abandoned the nest.

Female oystercatchers had an overall nest attentiveness of 51.73 ± 2.32 % (35–81 %), while male nest attendance was similar at 43.68 ± 2.18 % (16–62 %). One hundred and twenty-eight full bouts of 157 hours from 20 nests where biometrics and eye-fleck data exist for the two individuals of a pair allowing accurate discrimination between males and females showed that female incubation bout length was 78.56 ± 7.63 minutes (11.37–339.48) minutes from 68 bouts, and similar to that of the males with bouts of 68.35 ± 7.11 minutes

(11.03–271.33) minutes from 60 bouts (Table 4.1B). Also, incubation bout length did not differ significantly between sex by day or at night (Table 4.1A).

Table 4.1: Linear mixed-effect models examining the factors influencing log-incubation bout lengths of the oystercatchers on Robben Island during the 2017 and 2018 breeding seasons using only the data where the identity/sex of both individuals in a pair is known. Sample size = 128 full incubation bouts from 20 nests where biometrics and eye-fleck data exist for the two individuals of a pair. Nest identity was added as a random variable.

	A= With relevant interaction terms				B= non-significant interaction and quadratic terms removed			
	Estimate	SE	t	p	Estimate	SE	t	p
(Intercept)	3.44	0.30	11.50	<0.001	3.50	0.22	15.90	<0.001
Tide Low	-0.29	0.13	-2.28	0.025	-0.21	0.11	-1.90	0.060
Windspeed	0.19	0.12	1.64	0.10	0.14	0.046	3.08	0.0026
Windspeed ^2	-0.0054	0.011	-0.49	0.63	–	–	–	–
Time of day: night	0.99	0.32	3.05	0.0029	1.17	0.24	4.77	<0.001
Sex: male	-0.15	0.12	-1.21	0.23	-0.16	0.10	-1.64	0.10
Tide Low*Time of day: night	0.29	0.24	1.21	0.23	–	–	–	–
Maximum windspeed* Time of day: night	-0.10	0.059	-1.73	0.087	-0.13	0.054	-2.38	0.019
Time of day: night *Sex male	-0.062	0.22	-0.28	0.78	–	–	–	–
Breeding season: 2018	0.18	0.19	0.92	0.37	0.15	0.18	0.81	0.43

High tide, daytime, female and 2017 breeding season are represented by the value of the intercept. Windspeed represents maximum windspeed. Significant p values are in bold.

4.33 Environmental factors influencing oystercatchers' incubation bout lengths

Two hundred and twenty-two full bouts of 281 hours from 34 nests were included in the analysis seeking to understand how oystercatchers scheduled their incubation bouts in relation to environmental variables (air temperature, time of day, tide height, windspeed and two-way interaction between them). Full incubation bout length on average was 75.98 ± 3.827 (11.03–339.48) minutes. Oystercatchers' incubation bout length was significantly longer at high tide and during the night than at low tide and during the day in most of the models considered (Tables 4.2&4.3; Figure 4.1A). The difference between the incubation bout length of oystercatchers during low and high tide did not differ by time of day (Table 4.2, Section 1A). Incubation bout length decreased as temperature increased (Table 4.2, Section 2B, Figure 4.2A).

Table 4.2: Linear mixed-effect models examining the factors influencing log-incubation bout lengths of the oystercatchers on Robben Island during the 2017 and 2018 breeding seasons. Sections 1 = model accounting for time of day but not temperature, 2 = model accounting for temperature but not time of day. A = full model, B = smallest AIC model. Sample size: 222 full incubation bouts from 34 nests. Nest ID was added as a random term in the models.

Section 1	A: (marginal $R^2 = 0.29$, overall $R^2 = 0.41$, AIC = 430.50)				B: (marginal $R^2 = 0.29$, overall $R^2 = 0.40$, AIC = 428.78)			
	Estimate	SE	t	p	Estimate	SE	t	p
(Intercept)	2.97	0.27	11.19	<0.001	2.95	0.26	11.22	<0.001
Tide: Low	-0.24	0.10	-2.30	0.023	-0.20	0.085	-2.37	0.019
Windspeed	0.36	0.11	3.42	<0.001	0.36	0.11	3.46	<0.001
Windspeed ²	-0.021	0.010	-2.13	0.035	-0.021	0.010	-2.15	0.033
Time of day: night	1.21	0.21	5.75	<0.001	1.26	0.19	6.60	<0.001
Windspeed*Time of day: night	-0.14	0.05	-3.02	0.0029	-0.14	0.045	-3.09	0.0023
Tide Low*Time of day: night	0.11	0.18	0.60	0.55	–	–	–	–
Breeding season: 2018	0.16	0.14	1.17	0.25	0.15	0.13	1.11	0.28
Section 2	A: (marginal $R^2 = 0.23$, overall $R^2 = 0.36$, AIC = 459.13)				B: (marginal $R^2 = 0.22$, overall $R^2 = 0.34$, AIC = 455.52)			
(Intercept)	5.85	0.65	8.94	<0.001	6.13	0.62	9.96	<0.001
Tide Low	-0.04	0.37	-0.12	0.91	-0.17	0.091	-1.89	0.061
Windspeed	-0.16	0.23	-0.70	0.48	-0.32	0.19	-1.68	0.094
Windspeed ²	-0.014	0.010	-1.30	0.20	–	–	–	–
Temperature	-0.11	0.031	-3.51	<0.001	-0.11	0.030	-3.57	<0.001
Windspeed *: Temperature	0.019	0.0093	1.99	0.048	0.019	0.0093	2.09	0.038
Tide: Low* Temperature	-0.0054	0.016	-0.34	0.74	–	–	–	–
Breeding season: 2018	0.10	0.15	0.68	0.50	0.11	0.14	0.80	0.43

High tide, daytime, and 2017 breeding season are represented by the value of the intercept in the models where tide, time of day and breeding season are present. Windspeed represents maximum windspeed; temperature represents mean air temperature. Significant p-values are in bold.

The interaction term between the time of day and temperature was not significant (Table 4.3, Section 1A). The comparison of the performance of air temperature and time of day in explaining the variation in the incubation bout length of oystercatchers showed that time of day consistently explained more of the variation in the data, when considered in separate models (Table 4.2, Sections 1&2). But, when air temperature was added to the time-of-day model with the smallest AIC, the R^2 increased by about 1% (Table 4.3, Section 1B). Windspeed significantly influenced air temperature in a non-linear way and varied by the time of day (Table 4.4, Figure 2B). Similarly, windspeed had a significant non-linear effect on the incubation bout lengths of oystercatchers which also varied significantly by day and night (Table 4.3, Section 1A). During the day, incubation bout lengths increased sharply as windspeed increased and attained a maxima at high windspeed, but at night incubation

bout lengths increased slightly as windspeed increased, but declined at moderate to high windspeed.

Table 4.3: Linear mixed-effect models examining the factors influencing log-incubation bout lengths of the oystercatchers on Robben Island during the 2017 and 2018 breeding seasons. Models accounting for both time of day and temperature: Section 1 = the addition of temperature and an interaction term between temperature and time of day to the smallest AIC model from the time of day controlled model (i.e., the model in Table 4.2 Section 1B)), Section 2 = the addition of time of day and an interaction term between the time of day and temperature to the smallest AIC model from the temperature-controlled model (i.e., the model in Table 4.2 Section 2B)). A = full model, B = smallest AIC model. Sample size: 222 full incubation bouts from 34 nests. Nest ID was added as a random term in the models.

A: (marginal $R^2 = 0.31$, overall $R^2 = 0.41$, AIC = 424.72)					B: (marginal $R^2 = 0.30$, overall $R^2 = 0.41$, AIC = 422.81)			
Section 1	Estimate	SE	t	p	Estimate	SE	t	p
(Intercept)	3.23	0.38	8.55	<0.001	3.20	0.37	8.71	<0.001
Tide Low	-0.20	0.087	-2.33	0.021	-0.20	0.085	-2.32	0.022
Windspeed	0.38	0.11	3.52	<0.001	0.38	0.11	3.58	<0.001
Windspeed2	-0.023	0.010	-2.25	0.026	-0.023	0.010	-2.29	0.023
Time of day: night	0.95	0.76	1.25	0.21	1.17	0.21	5.48	<0.001
Temperature	-0.013	0.012	-1.04	0.30	-0.012	0.012	-1.00	0.32
Windspeed*Time of day: night	-0.14	0.048	-2.85	0.0048	-0.13	0.046	-2.91	0.0040
Temperature *Time of day: night	0.013	0.045	0.29	0.77	–	–	–	–
Breeding season: 2018	0.14	0.13	1.03	0.31	0.13	0.13	1.02	0.32
A: (marginal $R^2 = 0.28$, overall $R^2 = 0.40$, AIC = 431.16)					B: (marginal $R^2 = 0.28$, overall $R^2 = 0.40$, AIC = 429.16)			
Section 2	Estimate	SE	t	p	Estimate	SE	t	p
(Intercept)	5.40	0.64	8.43	<0.001	5.38	0.60	8.95	<0.001
Tide Low	-0.20	0.088	-2.21	0.028	-0.19	0.087	-2.24	0.027
Windspeed	-0.42	0.19	-2.24	0.026	-0.41	0.18	-2.31	0.022
Temperature	-0.085	0.030	-2.80	0.0057	-0.084	0.029	-2.90	0.0042
Time of day: night	0.56	0.78	0.71	0.48	0.62	0.12	5.10	<0.001
Windspeed*Temperature	0.024	0.0091	2.68	0.0081	0.024	0.0088	2.73	0.0069
Temperature*Time of day: night	0.0037	0.045	0.083	0.93	–	–	–	–
Breeding season: 2018	0.16	0.14	1.14	0.26	0.16	0.14	1.14	0.26

High tide, daytime, and 2017 breeding season are represented by the value of the intercept in the models where tide, time of day and breeding season are present. Windspeed represents maximum windspeed; temperature represents mean air temperature. Significant p-values are in bold.

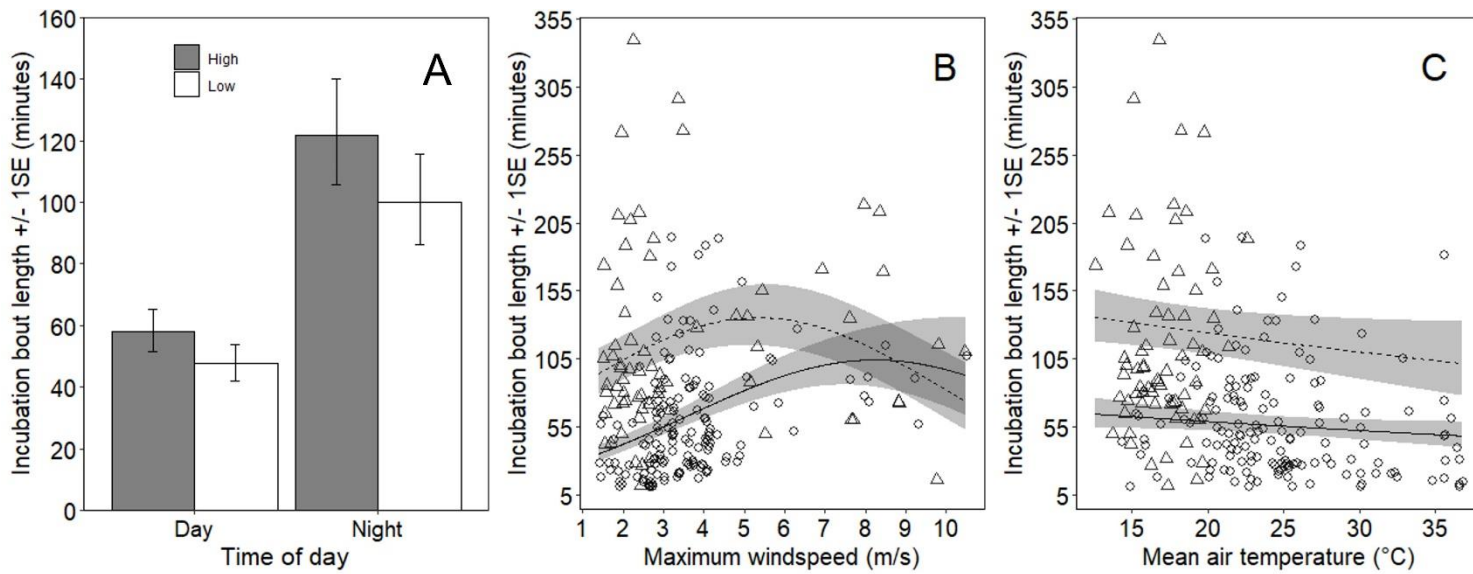


Figure 4.1: The predicted difference between incubation bout length during the day and at night by tide height (low = tide height <1m; high = tide height >1m) (Panel A). The predicted relationships between maximum windspeed (Panel B) as well as mean air temperature (Panel C) and incubation bout length of oystercatchers on Robben Island by day and by night in the 2017 & 2018 breeding seasons. In Panels B&C, the circular and triangular symbols represent raw data points from both breeding seasons by day and at night, respectively; the unbroken and broken lines represent day and night-time, respectively. For all three panels, back-transformed predicted values were plotted for the 2018 breeding season from the model in Table 4.2, Section 3B. In Panel A, the median value was set for windspeed, windspeed² and mean air temperature. In Panel B, the median value was set for mean air temperature and tide phase set at high tide. In Panel C, the median value was set for windspeed, windspeed² and tide phase set at high tide.

Table 4.4: A linear mixed effect model exploring the relationship between air temperature and windspeed by the time of day experienced by the oystercatchers during incubation on Robben Island in the 2017 and 2018 breeding seasons. Breeding season was entered as a random variable. Sample size: 222 data points.

	Estimate	SE	t	p
(Intercept)	16.77	3.35	5.00	<0.001
Maximum windspeed	6.00	2.19	2.74	0.0067
Maximum windspeed ²	-1.29	0.45	-2.90	0.0041
Maximum windspeed ³	0.074	0.03	2.73	0.0069
Time of day: night	-9.93	1.34	-7.42	<0.001
Maximum windspeed* Time of day: night	0.90	0.31	2.86	0.0047

Daytime takes the value of the intercept. Temperature represents mean air temperature. Significant p-values are in bold.

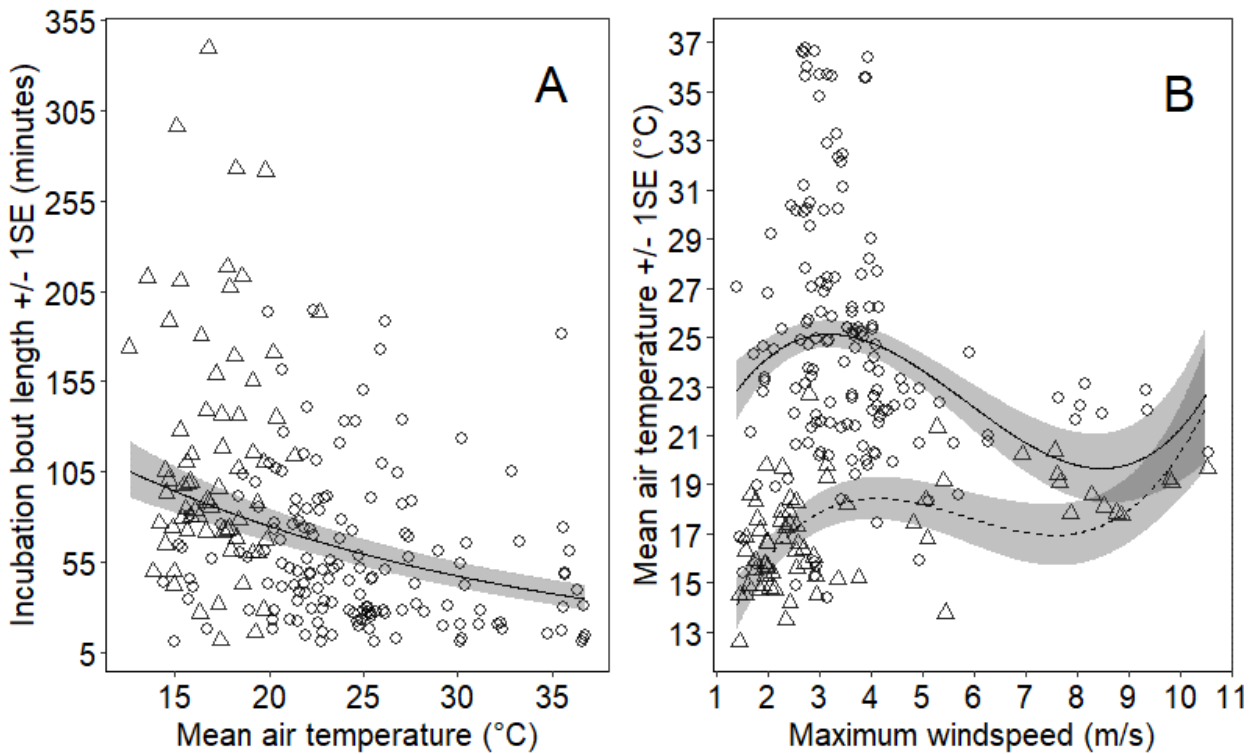


Figure 4.2: The predicted relationship between mean air temperature and incubation bout length of oystercatchers on Robben Island without accounting for time of day (Panel A). The predicted relationship between mean air temperature and the windspeed experienced by oystercatchers on Robben Island during incubation by day and at night (Panel B). In Panels A&B, the circular and triangular symbols represent raw data points from both breeding season by day and at night, respectively. The unbroken and broken lines in Panel B represent day and night-time, respectively. Back-transformed predicted values were plotted for 2018 breeding season from the models in Table 4.2, Section 2B (Panel A) and Table 4.3 (Panel B). In Panel A, the median value was set for windspeed, and tide phase set at high tide.

4.4 Discussion

The results from this study showed that oystercatchers' incubation bout length was significantly influenced by tide phase, air temperature, windspeed and time of day (Table 4.3, Section 1B). Incubation bout length was higher at high tide and at night than at low tide and during the day (Figure 4.1A). Incubation bout length decreased as temperature increased, but the time of day explained more of the variation in the incubation bout lengths of oystercatchers than temperature (Table 4.2). Windspeed had a significant non-linear effect which differed by the time of day on temperature (Table 4.4, Figure 4.2A) and on the incubation bout lengths of oystercatchers (Table 4.3, Section 1B, Figure 4.1B). Male and female oystercatchers scheduled their bouts in a way that maintained an overall high nest attentiveness. The incubation bout length of the females was not significantly different from those of the males and remained so irrespective of the time of day (Table 4.1). Nest exposures and the associated rise in nest temperature following interrupted bouts were significantly higher than those associated with duty exchanges between incubating parents.

4.41 Factors influencing oystercatchers' incubation bout lengths:

Effects of tide phase on incubation bout lengths

In this study, oystercatchers scheduled their incubation bout lengths around the tidal phase. They had significantly longer incubation bout lengths during high tide than at low tide, and this pattern was maintained both by day and at night (Table 4.3, Section 1B; Figure 4.1A). By having shorter incubation bout lengths at low tide, the oystercatchers may perhaps be optimising their foraging efficiency, thereby reducing the risk of starvation and/or dehydration. This is because, at high tide, their foraging ground is flooded and prey become temporarily inaccessible (Hockey 1983a). However, as the tide ebbs, the foraging ground and the prey items become increasingly available (Hockey 1983a; Leseberg 2001). If the oystercatchers have extended incubation bout lengths at the time of low tide (when the prey items on which the oystercatchers forage are potentially available and accessible in a larger quantity than at high tide), only one individual (the off-duty partner) would be able to forage sufficiently to meet its energy and hydration requirements per low-high tide cycle. This may result in starvation, dehydration, or loss of body condition for the on-duty individual. However, by having shorter incubation bout lengths during low tides, both parents have the opportunity to forage within each low-high tide cycle, thereby potentially

meeting their energy requirements and minimising the risk of starvation while still attending their nests (Leseberg 2001; Ramli & Norazlimi 2016; Fonseca et al. 2017; Burger 2018). Also, the proximity of the nests of oystercatchers to the foraging ground means that the off-duty partner has a short travel time between the nest and the foraging ground (Ens et al. 1992). Foraging at low tide and at a site close to the nest, together suggests a more efficient foraging and a faster return to the nest by the off-duty incubator to relieve its partner (Vafidis et al. 2018). The scheduling of incubation bouts to coincide with when food is most available has also been observed in some other bird species. For example, Northern Shoveler *Anas clypeata* cued their incubation schedules around the time when crustaceans on which they forage migrated towards the water surface (Afton 1980). In comparison, Banded Stilts *Cladorhynchus leucocephalus* scheduled incubation bouts in a way that enhanced foraging in areas where food had been concentrated by wind-driven water movements (Pedler et al. 2016). Also, Crab Plovers *Dromas ardeola* (Marchi et al. 2015) and American Black Oystercatchers *Haematopus bachmani* (Spiegel et al. 2012) schedule their bouts in manners that permit a higher proportion of foraging time during low tide than during high tide.

Effects of temperature and time of day on incubation bout lengths

Time of day had a significant effect on the scheduling of incubation bouts: oystercatchers had longer incubation bouts at night compared to during the day (Table 4.2, Section 1, Figure 4.1A). Increases in air temperature resulted in the shortening of incubation bout length (Table 4.2, Section 2, Figure 4.2A). However, time of day explained more of the variation in the incubation schedules of oystercatchers than air temperature (Tables 4.2 & 4.3). Since these results were from the analyses based on full incubation bout data rather than on interrupted bouts, the observed pattern of longer incubation bouts relative to night-time could not have resulted from increased human activity during the day. In some species, this pattern of incubation schedule by the time of day may reflect anti-predatory tactics as they may alter their diurnal behaviour to minimise detection by visually inclined predators (Afton 1980; Ekanayake et al. 2015). However, for the population of the oystercatchers studied here, it is unlikely that the patterns observed have been driven by predator avoidance because the predation of the oystercatchers' nests occurs during the

day mostly by a diurnal snake (Chapter Five), and there are currently no known predators of adult oystercatchers on the study site.

The significant influence of time of day on incubation bout length and its effect in explaining more of the variation in the incubation schedules of oystercatchers than air temperature is probably because temperature itself varied significantly by the time of day (Table 4.4. Figure 4.2B), and the fact that the time of day may also have accounted for other environmental conditions which vary by the time of day, e.g., solar radiation and light intensity (Tulp & Schekkerman 2006), which were not measured in this study. The temperature, light intensity and solar radiation variation between day and night may have influenced the heat load experienced by the oystercatchers by day and at night (Tulp & Schekkerman 2006) and may have been the underlying mechanism driving the incubation scheduling patterns observed in this study.

Temperature increases during the day may have increased the energetic, thermoregulation, and hydration needs of incubating oystercatchers as well as the need to shield their eggs from hyperthermia (Webb 1987). The shortening of incubation bout length under high temperatures and shorter incubation bout length during the day compared to the night may have reflected their need to relieve each other frequently to allow frequent trips to a cooler microclimate for thermoregulation and hydration purposes while still shielding their eggs by maintaining high nest attentiveness through biparental incubation. Oystercatchers were observed to commence panting when air temperature reached 23°C and continuously panted as it exceeded 27°C (Chapter Three). Panting is an evaporative cooling behaviour that is known to be costly in terms of exposure to the risk of dehydration because of the high evaporative water loss incurred during panting (Weathers 1981; Dawson 1982; Gerson et al. 2019). It, therefore, makes sense that the oystercatchers' incubation bout lengths decreased as air temperature increased and was shorter during the day relative to at night because it suggests that as the birds panted more during the heat of the day, their energy and hydration requirements increased, and these needs may have been met as they made frequent trips to forage and thermoregulate in the intertidal zone (Bartholomew & Cade 1963; Section 4.42 below). On the contrary, as temperature drops at night, the adults' need for evaporative cooling, frequent recesses to forage, stay hydrated and/or use other water-related thermoregulation behaviours (e.g., belly-soaking wading) under high heat loads may

have deceased. These may explain the nearly double incubation bout length occurring at night contrasted with that of the day.

Additionally, the longer incubation bout lengths at night compared to the day may also have been driven by the foraging activity of the adults, at least to some small degree. This is because oystercatchers, like some other shorebirds (Ntiamoa-Baidu et al. 1998; Tulp & Schekkerman 2006) are diurnal and, although they are known to forage during low tide, by both day and night (Hockey 1983a), foraging during the day when there is a higher light intensity to see the prey which they extract from rocks may be more profitable. Hence, although they can, and do forage during low tide irrespective of the time of day, they may have scheduled their activities in a way that permitted more foraging time during the daytime low tide period compared to night-time low tide (Tulp & Schekkerman 2006). The longer incubation bout length occurring at night observed here in the oystercatchers compared to the day resembles very closely the pattern observed in the American Black Oystercatchers *Haematopus bachmani* which also exhibited nearly twice as long incubation bouts at night than during the day (Spiegel et al. 2012).

Adams et al. (1999) inferred nests attentiveness from egg temperature measurements using data from three African Black Oystercatchers' nests and observed a substantial decrease in egg temperature at night, in contrast to an almost constant optimal egg temperature during the day. They, therefore, concluded that the oystercatchers deserted their nests for an extended period of up to six hours at night (Adams et al. 1999). This study simultaneously monitored nest temperature and video-monitored incubating oystercatchers: a similar pattern of decreased nest temperature at night compared to the day was observed, but adults were seen tending their nests continuously at night. Egg temperature and nest temperature are correlated (Vleck 1981; Evans 1995). The decline in both temperatures at night may reflect the impact of low environmental temperatures at night. However, egg temperature was not recorded in this study as temperature sensors were only placed inside nest scrape rather than inside a model egg. So, the decline in nest temperature at night may also be a methodological artefact.

Effects of windspeed, temperature and time of day on incubation bout lengths

Incubation bout lengths increased sharply with windspeed and plateaued at high windspeed during the day, while incubation bout lengths increased slightly with slight increases in windspeed but declined from moderate to high windspeed at night (Figure 4.1B). This time-of-day dependent effect of windspeed on the incubation bout schedules of oystercatchers may have been driven through the effect of windspeed on the air temperature experienced by oystercatchers and by implication, the cooling rate of their eggs. Windspeed may negatively influence temperature such that as windspeed increases temperature may decrease, resulting in a faster cooling rate of adults and the eggs (Hilton et al. 2004; Heenan & Seymour 2012; Dickinson et al. 2019). But this relationship between windspeed and temperature may depend on the time of day (Table 4.4, Figure 4.2B), because temperatures may already be cooler at night compared to during the day. Birds incubating under the heat of the day may likely benefit from the cooling effects of an increased windspeed, thus resulting in a reduced need for frequent trips for thermoregulation and hydration purposes, consequentially leading to an increased incubation bout length as windspeed increased during the day. However, at night when temperatures are already cooler, a slight increase in windspeed may result in cold conditions that may also encourage longer incubation bouts because exposing the eggs during frequent duty exchanges at such cold conditions may result in rapid cooling of the eggs and the parents might want to minimise the costs of rewarming the eggs (Cresswell et al. 2004). But if moderate to high windspeed result in very cold conditions and temperature falls significantly below the thermoneutral zones of incubating birds, they may decrease incubation bout length to forage and raise metabolic activities to generate heat (Bulla et al. 2015b). This potential impact of moderate to high windspeed on the temperature experienced by incubating birds may have driven the decline in the incubation bout lengths of oystercatchers at moderate to high windspeed occurring at night. These patterns are similar to some of those reported in the literature (Cantar & Montgomerie 1985; Hilde et al. 2016; Hoppe et al. 2019). For example, Tulp & Schekkerman (2006) noted that the length of the period of continuous incubation increased with decreasing air temperature and/or increasing wind speed in three species of shorebirds. While incubating Semipalmated Sandpiper *Calidris pusilla* were forced to feed more under windy conditions that were energetically stressful (Bulla et al. 2015b).

4.42 Thermoregulation importance of the proximity to the ocean for the oystercatchers and its potential to minimise the risk of nest abandonment under high heat loads

The immediate breeding habitat of the oystercatchers is generally treeless, making a retreat to shady vegetation nearby, as would some bird species under increasing heat loads (Cunningham et al. 2015; Carroll et al. 2018; van de Ven et al. 2019), unavailable to the oystercatchers. However, the proximity to the ocean seems to offset the lack of shaded microhabitat, because oystercatchers wade, belly-soak, and bathe frequently under mounting heat loads by making frequent trips to the adjacent tidal areas. The thermal conductivity of water is known to be up to 25 times that of air (Battley et al. 2003), and these activities are effective thermoregulatory behaviours which result in rapid loss of heat from the bird to the water, without any energy expenditure from the birds themselves apart from that involved in travelling to the water (Grant 1982; Battley et al. 2003; Amat & Masero 2007; Oswald et al. 2008; Marchi et al. 2015). On a few occasions when it was possible to see what the oystercatchers did as they flew to the ocean, they were observed to wade, belly-soak, bath, forage, and even appear to take sips of saltwater (samples of these can be viewed [here](#)). Moreover, the incubating oystercatchers were observed to behave differently when handing incubation duty over to their partners under warmer conditions compared to colder conditions. An incubating bird usually rushed off the nest at the sight of its partner under hot conditions but was reluctant to leave the nest during colder conditions.

Under harsh temperatures, incubating birds may prioritise their survival over their current breeding attempt by permanently or temporarily abandoning their nests if they are unable to cope (Thierry et al. 2013; Bourne 2020). For example, Jacky Winters *Microeca fascians* abandoned their nests when exposed to high environmental temperatures (Sharpe et al. 2019). Similarly, Pied Babblers *Turdoides bicolor* incubating in the Kalahari Desert of South Africa were observed to be more likely to abandon their nests at very high temperatures to minimise the risk of dehydration (Bourne et al. 2021). It may be unlikely that oystercatchers nesting close to the ocean would abandon their nests or leave their nests exposed for an extended period under harsh temperatures as the examples above because of the thermoregulatory benefits that they derive by being close to the ocean. This idea aligns with the observations made by Amat & Masero (2004b) that nest abandonment tendency by

Kentish Plovers *Charadrius alexandrinus* was affected by the proximity of the nest to water. They noted that Kentish Plovers' nests which were close to water were deserted less often and concluded that the susceptibility to thermal stress changed with proximity to water because belly-soaking opportunities enabled a more continuous nest attendance for plovers close to water (Amat & Masero 2004b).

The oystercatchers' dependence on the ocean for thermoregulation in addition to the biparental care system employed by the species may be a vital adaption enabling a continuous nest attentiveness by the species even under the thermally demanding conditions in which they breed. This thermoregulatory dependence on the ocean may contribute in part to the reason why African Black Oystercatchers are yet to colonise and breed in inland habitats like Eurasian Oystercatchers *Haematopus ostralegus* (Buxton 1961; Wilson et al. 2005). Hockey (1983a) noted that the modal distance of oystercatchers' nests from the high watermark at islands was 10–30 m with the furthest being 110 m away. The population monitored here sited their nests on average 17.3 ± 0.80 (1–89 m) from the mean high watermark (Chapters Two & Six). Some of the benefits which the oystercatchers derive from being so close to the ocean, despite the vulnerability of losing their nests to wave-driven storm surges (Chapter Two), include the proximity to the food with which to feed chicks and microhabitats in which to hide them from potential predators (Ens et al. 1992; Ens & Underhill 2014). Breeding in the open close to the ocean, therefore, seems likely to provide several advantages: potentially less predation (Amat & Masero 2004a; Ens & Underhill 2014), shorter distances to guide chicks to safety, quick access to food for chicks and adults (Hockey 1983a; Ens et al. 1992; Tjørve 2006), quick access to belly-soaking, bathing, and wading opportunities under increased heat loads, and shorter travel time between the nests and foraging ground during incubation off-bouts (this Chapter). This proximity to the ocean may therefore contribute to the ability to deal with future temperature increases/heat loads under projected climate change.

4.43 Bout interruptions, nest exposure and the associated changes in nest temperature

The rate of interruption of incubation bouts of the oystercatchers was 59% (319 of 542), with 87% (279 of 319) of all interrupted bouts occurring during the day compared with 13% (40 of 319) at night. The high numbers of interruptions during the day compared to at night, are probably because of increased human activities during the day than at night. As Spiegel

et al. (2012) observed for the American Black Oystercatchers *Haematopus bachmani*, the sources of disturbance to incubating oystercatchers were both natural (conspecifics, predators, tidally driven storm surge, and other wildlife) and anthropogenic (vehicles, pedestrians, cyclists). This suggests that birds already need to deal with natural sources of interruption to their incubation process. Unfortunately, because of the limited field of view of the cameras used, it was not possible to have a 360° view around the nest to distinguish quantitatively how many of the impromptu departures from the nests were caused by humans and which were caused by natural sources. But humans may probably have caused most of the disturbances because the disturbances from natural sources may be negligible.

Oystercatchers in this study left their nests exposed for a significantly longer period when interrupted (4.48 ± 0.36 (0.22–80.23 minutes)) than when they got off their nests in response to the arrival of their relieving partner (0.87 ± 0.09 (0–7.62 minutes)). In most nest handovers, the non-incubating bird arrives before the incubating bird departs the nest, making nest exposures during duty exchanges small. Leaving the nest exposed for an extended period may not constitute a problem under favourable environmental conditions. For example, incubating Crab Plovers *Dromas ardeola* attended their nests only 57% of the time, leaving the nest unattended for the rest of the time because their nests were located in burrows which kept their eggs away from avian predators and provided favourable thermal conditions for their eggs (Marchi et al. 2015). However, extended exposure of nests under unfavourable conditions (e.g. either too cold or too warm) may be injurious to the eggs (Webb 1987). For example, the prolonged exposure of the eggs of Horned Larks *Eremophila alpestris* under very cold conditions resulted in reduced embryo viability and poor hatching success (MacDonald et al. 2013). Also, a complete hatching failure was reported in a king rail *Rallus elegans* nest, which was exposed to direct sunlight and high air temperature for an extended period (Clauser & McRae 2017).

The rise in nest temperature (1.70 ± 0.22 (0.06–11.95°C)) when oystercatchers left their nests following an interruption by an external stimulus was significantly higher than that (0.65 ± 0.12 (0.03–1.99°C)) associated with nest exposures during duty exchanges between parents, with nest temperature reaching 47°C when the local operative temperature was 51°C. Like the observations of Clauser & McRae (2017) above, the oystercatchers appear to have been impacted at least to some extent following the exposure of their nests to

excessive solar radiation and high temperatures. This is because some nests failed partially (only one or two eggs affected) or completely (all eggs in the nest) to hatch because the embryo was glued to the shell membrane, and the shell looked broken and dried (Appendix 4.1). For the 2017 and 2018 breeding seasons combined, 3.54% (11 of 311) of nests were observed to fail because of the glueing of embryos to the shell membranes. Although some of the embryos survived until hatching, they could not survive the hatching process. The mechanism behind these observations is not clear. However, Adams et al. (1999) suggested that repeated exposure to high temperatures may result in critical dehydration under high environmental temperatures resulting in the glueing of embryos to the shell membrane (New 1956; Veldsman et al. 2020). Future studies should seek to understand the mechanisms behind these observations and attempt to quantify the fitness impacts of prolonged exposure caused by disturbance. Because if glueing is caused by heat exposure, then it is likely to become an increasingly severe problem as the climate warms, and it will be increasingly important for management to put in measures to minimise disturbance of incubating birds

4.44 Overall nest attentiveness and sex contributions

Oystercatchers incubated their nests almost continuously with an overall nest attentiveness of 95 ± 0.58 (87–100%). The high nest attentiveness reflects coordinated cooperation between the male and the female oystercatchers in balancing time on and off their nests in a manner that permitted each member of the pair to carry out body maintenance activities (e.g., foraging and thermoregulating) without compromising their incubation duties. The level of nest attendance maintained suggests that the oystercatchers minimised the energetic costs, which are usually associated with needing to rewarm or cool eggs following low nest attendance (Vleck 1981; Cresswell et al. 2004). This pattern of high nest attentiveness is typical of biparental incubators. For example, American Black Oystercatchers *Haematopus bachmani* maintained a nest attentiveness of 96% (Spiegel et al. 2012) while Lesser Crested Terns *Thalasseus bengalensis* maintained 97% nest attentiveness (AlRashidi 2016). These examples indicate that the biparental system of parental care is necessary to ensure continuous nest attendance, especially for birds nesting under harsh environmental conditions (AlRashidi et al. 2010). This was further supported by the observation from the nest where only the female was observed to incubate. She

incubated the nest for only 22% (5 of 23 hours) of the time and eventually abandoned the nest.

Female incubation bout lengths and overall nest attentiveness were not significantly different from those of male bouts (Table 4.1, Section A). This equal contribution by male and female oystercatchers is like that observed in the Semipalmated Sandpiper *Calidris pusilla* (Cresswell et al. 2003; Bulla et al. 2014) and Black-necked Crane *Grus nigricollis* (Zhang et al. 2017) where both parents had approximately equal nest attentiveness.

4.5 Conclusion

This study showed that oystercatcher males and females incubate equally to maintain high nest attentiveness. They schedule their bouts in response to the environmental conditions which could potentially affect their energetic demands and the temperature of their eggs. They reduced their bouts significantly at low tide, probably to allow both parents to forage sufficiently at each low-high tide cycle probably to minimise the risk of starvation and dehydration. Oystercatchers reduced their incubation bout lengths at high air temperature and during the day probably because an extended bout was energetically and thermally demanding, necessitating the oystercatchers to make frequent trips to the ocean to forage and carry out thermoregulatory activities to cool themselves. They increased their incubation bout lengths as windspeed increased during the day, probably because of the cooling effect of increased windspeed on adults and their eggs. Oystercatchers almost doubled the length of their bouts at night relative to daytime, probably because of the need to buffer the eggs from the cold conditions at night and the reduced need for frequent trips to the ocean for thermoregulation. An essential component of the effectiveness of the oystercatchers' bout scheduling and dealing with increased heat loads could be the proximity of their nests to the intertidal zone, which means shorter travel time and quick access to food, water, and thermoregulatory opportunities. Overall, in the absence of disturbances that result in extended nest exposures, male and female oystercatchers balance the time on their nests with that of their own energy needs through well-coordinated incubation scheduling matching the prevailing environmental conditions. However, when nest exposure occurs because of factors that are external to the oystercatchers, the eggs are exposed to temperatures that may not favour optimal embryonic development. Future studies should attempt to explore the fitness consequences

of extended nest exposures caused by the factors external to the incubating birds. Future studies should also examine the reasons why some embryos survived until hatching but then failed to complete the hatching process successfully due to the adherence to the shell.

Appendix



Appendix 4.1: Observations of eggs with dried and damaged shells. Some of the embryos survived until hatching but were glued to the shell and failed to hatch successfully.

Chapter Five: The relative importance of different nest predators and predictors of nest predation in African Black Oystercatchers



Abstract

Nest predation is the primary cause of failure of avian nesting attempts, consequently impacting the overall productivity and population dynamics of avian communities. Robben Island supports more than 5% of the global population of African Black Oystercatchers *Haematopus moquini*. Kelp Gulls *Larus dominicanus*, whose breeding population on Robben Island has increased significantly were suspected to be the most important predator of oystercatcher nests, however, other possible nest predators do occur on the island including feral cats *Felis domesticus* and Mole Snakes *Pseudaspis cana*. Research into the relative importance of nest predators and the predictors of oystercatcher nest predation was necessary to understand if and what conservation interventions may be needed to reduce the impacts of predation. This study investigated how the predation of oystercatcher nests on Robben Island varied with daily maximum air temperature, clutch size, clutch incubation start date, the distance of nests to vegetation (which could potentially conceal predators), predator activity (the distance of nests to Kelp Gull colony and Mole Snake locations); using data from two breeding seasons including only nests which hatched, or which failed due to predation. Data from a subset of 54 nests monitored using digital cameras, and incidental observations of direct nest predation events were used to determine the identity of different oystercatchers' nest predators. Of 311 nests found, 122 (39%) were predated. The predator responsible for 10 (8%) was determined and in all cases was a Mole Snake. All predation events occurred during daylight. No feral cats were sighted either day or night around any of the nests monitored. There was no evidence to show that gulls predated oystercatchers' nests on Robben Island, despite being present in the vicinity of over 60% of the nests monitored. Nest predation was highest when the maximum air temperature was between 21–27°C and declined sharply at 30°C and was lowest from 33.4°C. Three-egg clutches were the least likely to get predated while one-egg clutches had the highest probability of being predated. Nests initiated in the first 106 days of the breeding season had a lower nest predation probability compared to those initiated later. Nests which were sited 22–40 m away from vegetation had a lower nest predation probability compared to those closer to vegetation. Nests sited near Mole Snake locations experienced higher predation probability than those sited >550 m from a Mole Snake location. Nest predation probability was not significantly predicted by the distance of nests to the Kelp Gull colony. This further suggests that Mole Snakes are the major predators of oystercatchers' nests on

Robben Island, contrary to previous expectations that gulls would be the main agents. This highlights the importance of research in identifying nest predators correctly, as some predators which are conspicuous either because of their body size, plumage, abundance, or behaviour may seem disproportionately responsible for nest predation, compared to more inconspicuous ones which may be the actual cause of nest failures. This also suggests that there is no need to control the Robben Island Kelp Gull population on the account of the oystercatchers. However, the impact of gulls on other species may be different from that reported here for the oystercatchers and may require other management, subject to further research. Given the increasing population size of oystercatchers, the fact that Mole Snakes are indigenous to the island and their predation of oystercatchers' nests is already limited by natural factors like extreme temperatures, the openness of oystercatchers' nest-sites, and the availability of nests, it is recommended that the snakes should not be controlled. However, further studies to understand the biology of the snakes and other ecological roles that they play on the island are recommended. Finally, this study provides useful information on which management decisions and further studies can be based. These results highlight how several factors collectively influence avian nest predation pressure.



5.1 Introduction

Nest predation is the primary cause of failure of avian nesting attempts, consequently impacting the overall productivity and population dynamics of avian communities (Ricklefs 1969; Martin 1993a; Thompson III 2007). Knowledge of the true identity of nest predators, and patterns and predictors of nest predation, are vital to understanding predation pressure and interactions within wildlife communities: information which is essential to conservation interventions (Weatherhead & Blouin-Demers 2004; Lahti 2009; Raine et al. 2020). However, nest predation events are elusive and hard to observe because nest predation usually happens quickly. The actual nest or time at which a predation event would occur is generally unpredictable, making it difficult to quantitatively attribute nest predation to specific predator types (Weatherhead & Blouin-Demers 2004). Traditional methods, such as using the evidence left behind by nest predators, have been reported to be unreliable (Williams & Wood 2002). However, the increasing availability and affordability of improved technology – digital time-lapse infrared video cameras – now makes it possible to capture nest predation events that provide indisputable evidence of nest predator identity, time and date of occurrence (Thompson III et al. 1999; Williams & Wood 2002; Stakel & Cimprich 2003). The use of these cameras has continued to improve our understanding of nest predation and helped to accurately identify nest predators (Cox et al. 2012; Bell 2017; Menezes & Angelo 2017; Li et al. 2019).

Several factors are known to interact to determine the probability, patterns and rates of nest predation (Cox et al. 2013; Kearns & Rodewald 2017). These factors include the characteristics of nest predators such as their identity, population size, and behaviour (Weatherhead & Blouin-Demers 2004; Lahti 2009; Reidy & Thompson III 2013). Weather variables, such as temperature, may also influence nest predation. For example, rates of nest predation by birds and snakes increase as daily maximum temperatures increase (Cox et al. 2013; Oswald et al. 2020).

The characteristics and behaviour of the parent birds can also influence or reflect predation risk; for example, predation risk increases as parental activity around the nest increases (Cresswell 1997a; Matysioková & Remeš 2018). Parent birds may respond to predation pressure by varying their clutch size (the number of eggs laid in a given nesting attempt) as observed by Dillon & Conway (2018) in Red-faced Warblers *Cardellina rubrifrons*: parent

birds invested less in reproduction by laying fewer eggs as the risk of nest predation increased, after controlling for food availability and adult body condition.

Predation pressure may also vary temporally across the breeding season in a nest density-dependent manner (Daan et al. 1990; Götmark 2002). If predators become increasingly successful as the number of nests exceeds a certain threshold during the breeding season, predation pressure may be lower earlier in the season before that threshold is reached (Götmark 2002; Verhulst & Nilsson 2008). Predation pressure may increase as the threshold is reached and more nests become available later in the season such that predators develop a search image (finding the same prey type repeatedly and focusing on the prey), agreeing with the predator search image hypothesis (Cornell 1976; Nams 1997; Verhulst & Nilsson 2008). However, if predation pressure is spread across the number of active nests in such a way that the probability of an individual nest being predated is reduced as the number of nests increases, a dilution effect may occur (Duca et al. 2019). This dilution effect may result in a decreased nest predation probability as more nests become available as the breeding season advances (Vigallon & Marzluff 2005; Duca et al. 2019).

The characteristics of the nest itself, such as its location and habitat features will also influence its vulnerability to predation (Visco & Sherry 2015). The proximity of nests to vegetation may affect nest predation pressure if predators use vegetation as cover from which to attack (Lima & Valone 1991; Amat & Masero 2004a; Cresswell et al. 2010). The proximity of nests to other active nests may influence the predation risk of the nests either by decreasing predation risk if the group of breeding adults could collectively deter predators (Pratte et al. 2016), or increasing predation risk if it makes it easier for predators to locate the nests (Göransson et al. 1975; Shitikov et al. 2018). Similarly, the proximity of nests to locations used by potential predators may influence a nest's vulnerability to predation either by increasing or decreasing predation risk (Vermeer et al. 1992). The proximity to locations used by potential predators could reflect higher predator activity compared to sites which are further away (Lima 2009; Kearns & Rodewald 2017). Increased predator activity in an area could increase the predation risk of the nests located in such a place (Kearns & Rodewald 2017; Oja et al. 2018). However, if the presence of a potential predator serves as a protection from other potential nest predators, the overall risk of nest predation may be reduced (Norrdahl et al. 1995; Bodrati & Cockle 2017).

Robben Island, South Africa is an important breeding site for several seabirds and shorebirds (Crawford & Dyer 2000; Sherley et al. 2011). It is an important conservation area for African Black Oystercatchers (hereafter oystercatchers) and holds more than 5% of the global population of the species (Underhill et al. 2001; Calf & Underhill 2002; Braby & Underhill 2007). Predation has been a significant cause of nest failure of the oystercatchers on Robben Island (Tjørve 2006; Braby & Underhill 2007) and in other sites across its breeding range (Hockey 1983b; Loewenthal et al. 2016). The suspected nest predators of the oystercatchers on the island are feral cats *Felis catus*, Kelp Gulls *Larus dominicanus*, Mole Snakes *Pseudaspis cana* and House Rats *Rattus rattus* (Calf 2004; Tjørve & Underhill 2008). However, the relative importance of these nest predators is unknown (Calf 2004).

Historically, feral cats were thought to be the primary predator of oystercatchers' nests on Robben Island, causing near-total nest failure in 2004 (Braby & Underhill 2007). There have been a series of feral cat culls on the island as management intervention to protect the breeding shore- and sea- birds on Robben Island (Crawford & Dyer 2000; Spiby 2012). The control of feral cats occurred around mid-1980s, and again by the summer of 1998/99 when 107 cats were removed (Crawford & Dyer 2000). It was repeated in 2005 and again in 2009 (Spiby 2012). Between 2009 and 2016, a total of 106 cats were removed (Christopher Wilke Unpublished data). The current (2019) number of cats on the island is less than ten (Christopher Wilke pers. comm). Following the culling of feral cats, Kelp Gulls are suspected to be the most important predator of oystercatchers' nest contents because of their increasing numbers on the island (Underhill 2014). Kelp Gulls bred on Robben Island for the first time in 2000 when five nests were reported (Calf et al. 2003). They have increased rapidly, reaching about 483 breeding pairs in 2007 (Crawford et al. 2009) and over 2500 pairs in recent years (Whittington et al. 2016). Because of the suspected impact of the gulls on the oystercatchers and other avian species breeding on the island, a recommendation was made that the gull population might need to be controlled (Calf et al. 2003; Braby & Underhill 2007). Research into predation of oystercatcher nests was recommended (Calf 2004; Underhill 2014).

In this chapter, I asked: what are the predictors of oystercatcher nest predation on Robben Island? I also asked what is the identity and the relative importance of different predators of the nests of oystercatchers on Robben Island? I used data from nests which hatched and

those which failed due to predation to answer the first question and used time-lapse digital cameras to monitor incubating oystercatchers on their nests to address the second question.

I hypothesised that nest predation probability would increase as the breeding season advanced because as nests become numerous, predators may find it easier to locate them thereby increasing overall nest predation probability (Verhulst & Nilsson 2008), but a dilution effect is also possible (McKinnon et al. 2014; Duca et al. 2019). Higher air temperature occurring later in the season may also affect predation rates through its effects on the activities of nest predators (Cox et al. 2013; Oswald et al. 2020). If oystercatcher nest predation pressure increases as the season advances as predicted, then I expected that oystercatchers would reduce their clutch size over the course of the season (Slagsvold 1982; Dillon & Conway 2018). I hypothesised that nest predation probability would decrease with distance from predator-dominated areas, the distance away from vegetation as well as with increased proximity of active nests to other active oystercatchers nests (Pratte et al. 2016). I hypothesised that predation by gulls would be higher than all the other predators because of the potential increased predation pressure as a result of the increasing number of the gulls on the island (Underhill 2014). Finally, I expected that nest predation by feral cats would be low following the decrease in the number of cats on the island.

5.2 Methods

5.2.1 Nest searching and monitoring

From October to March during the 2017 and 2018 breeding seasons, the entire coastline of Robben Island was searched on foot to locate oystercatchers' nests. Nests were found by watching for oystercatchers that were either sitting, walking off their nests or returning to their nests after being flushed as well as by opportunistically searching the area above the mean high watermark (Beintema & Muskens 1987; Jackson 1988; Tjørve 2006). After discovering a nest for the first time, the exact location was recorded on a GPS (Garmin GPSMAP 64st). The eggs were uniquely marked using a black marker to write an I, II or III on the egg according to the number of eggs in a clutch. The marking on eggs allowed each egg to have an identity against which their measurements were recorded. Additionally, for clutches found before the completion of egg-laying, the marking enabled the differentiation between the egg(s) processed on previous visits and the newly laid egg(s) on subsequent

visits. The marking was very similar to the natural dark markings on the eggs (Appendix 5.1A), did not make the eggs more obvious and was therefore unlikely to increase the eggs' risk of predation. Similarly, each nest was marked using a black permanent marker to write an inconspicuous unique nest number on one of the stones found around the nest (Appendix 5.1B).

Nest age was determined by the date of clutch completion or by weighing eggs for complete clutches. Eggs were weighed to the nearest 0.1 g, using an electronic balance and their length measured to the nearest 0.1 mm using a vernier calliper. To determine an index of egg volume despite asymmetry in the eggs, two breadth measurements were taken to the nearest 0.1 mm at right angles to each other over the widest part of the egg using a vernier calliper (Tjørve 2006). Dates and time when measurements were taken were noted. Based on the principle that eggs, in general, lose about 16% of their mass during incubation, due to water loss by diffusion (Ar & Rahn 1980), the fresh egg mass (mass at the time of laying) can be estimated from egg dimensions and mass measurements taken at the time an egg was first discovered (Green 1984; Underhill & Calf 2005). The number of days for which an egg has been incubated is then estimated based on the rate of mass loss (Underhill & Calf 2005). The fresh egg mass and the duration for which each oystercatcher egg had been incubated were determined by inputting the egg dimensions taken above into the equations specified in Underhill & Calf (2005) for the population of oystercatchers on Robben Island. Once the length of incubation, in days, was calculated, the incubation-start-date for each egg was determined by counting days backwards, starting from the date the egg was first observed and measured (Underhill & Calf 2005). The incubation start date of a clutch is taken as the incubation start date of the oldest egg in the clutch (Underhill & Calf 2005). This date was converted to a Julian date and standardized as the number of days since 1 September for each nest. Given that on average, the incubation period of the oystercatchers is 30 days (Hockey et al. 2005), the potential hatch date was estimated as the clutch incubation start date plus 30 days. Nests were monitored at an interval of between 3-7 days. Clutch size was recorded as the total number of eggs in each nest and confirmed for most nests after a second visit.

Nests were scored as predated if eggs disappeared several days before the expected hatch date, a direct predation event was observed, a broken egg was seen, or parent behaviour

indicated the nest had failed (nests which failed for other reasons aside from being predated, e.g., washed away by high spring tides or abandoned were noted but not included here because the focus of this chapter is strictly on nest predation). Nests were scored as hatched if chicks were observed, eggshells from hatched chicks were found around the nest, or parents behaved in a manner suggesting they had chicks hidden in the vicinity. Both male and female oystercatchers show great aggressiveness and use distracting displays to try and lure potential predators or pedestrians away from their chicks (Allan & Hockey 1984; Ens & Underhill 2014; Tjørve & Tjørve 2016). They generally do not display these behaviours when they have lost their eggs or chicks instead they are quiet and show no aggression (Allan & Hockey 1984; Ens & Underhill 2014; Tjørve & Tjørve 2016). Some pairs of oystercatchers re-nested after a failed initial attempt. The repeat clutches were noted in the analysis as being from subsequent attempts to account for any variation that may arise for such clutches. The distribution of nests scored as hatched and predated are presented in Figure 5.1.

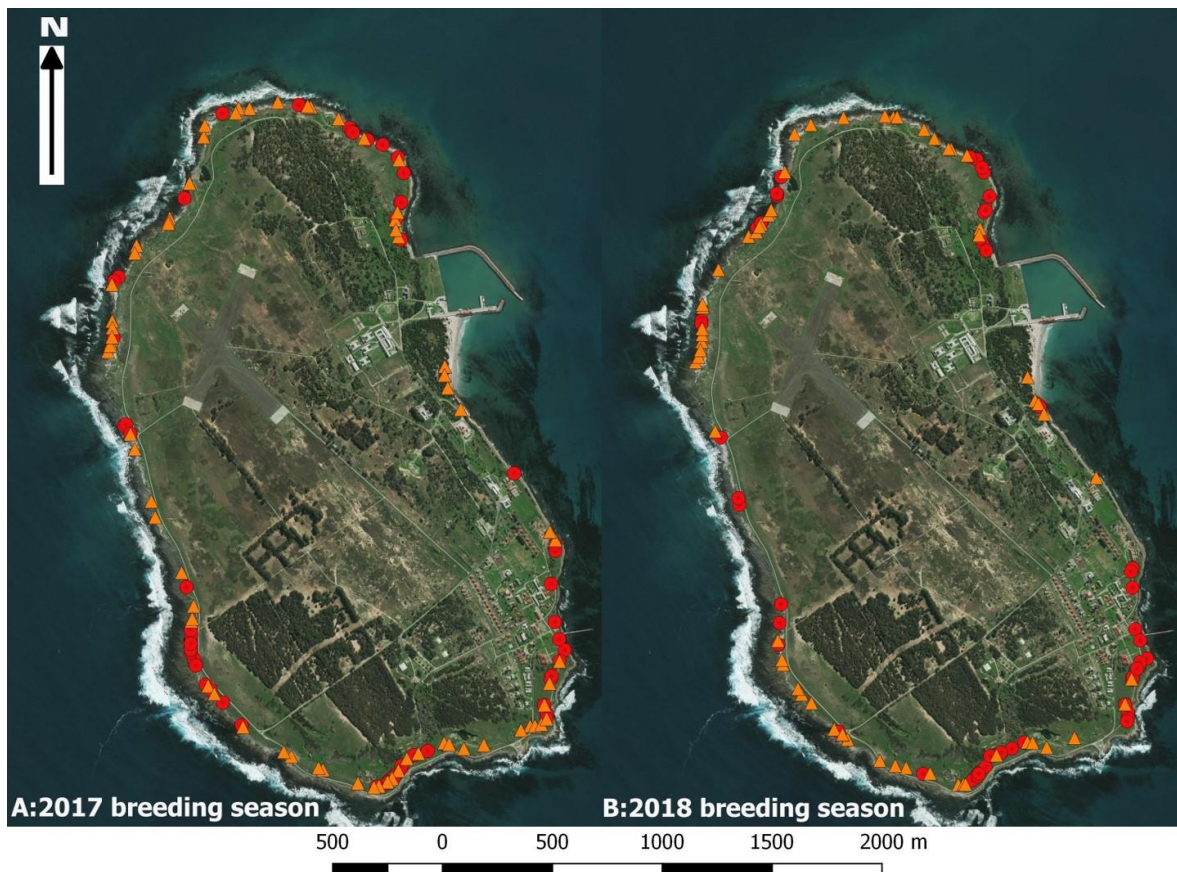


Figure 5.1: Oystercatchers' nests which were predated (red circles) and hatched (orange triangles) in the 2017 (the map on the left) and 2018 (the map on the right) breeding seasons on Robben Island

5.22 Habitat measurements as predictors of nest predation

Since the location of a nest can significantly influence its risk of nest predation (Visco & Sherry 2015), the distance of each nest to the nearest vegetation above it (i.e., the distance to the top of the beach), and the mean high watermark below it (which could potentially harbour reptilian predators as discussed further below) were measured in meters using a laser range finder (Nikon, LASER 550). Distances less than 10 m were taken using a 10-meter measuring tape. The centroid coordinates of the harbour and Alpha 1 (the part of the island used by tourists) were stored on a GPS. The GPS FIND function was used to determine the distance between each nest and the harbour and Alpha 1 as proxies for proximity to areas with human presence as well as the distance between each active nest to another active nest at the time the nest was first found (Watson et al. 2006).

Temperature

Air temperature logged every five minutes and overall daily maximum air temperature from a weather station based on Robben Island were obtained from the South African Weather Services (SAWS). The maximum air temperature during the exposure period (the date a nest was found to the date it hatched or failed) of each nest was extracted and linked to each nest following Oswald et al. (2020). Exposure was used to describe the period over which the nests were active and therefore exposed to harm such as being predated. The maximum air temperature during when a nest was active may not be a very sensitive indicator of the temperature experienced by the eggs, the incubating adults, and the foraging predator. But it was used as a rough estimate of how extreme the air temperature was during the period the eggs were active.

Indices of predator activity

A proxy for predator presence and activity was measured for Kelp Gulls and Mole Snakes. For Kelp Gulls, the distance of each oystercatcher's nest to the Kelp Gull colony and a point count of individual Kelp Gulls (excluding flying birds) within a 50m radius around each nest on the first visit was recorded. For Mole Snakes, during each monitoring visit in the 2017 breeding season, each sighting of a Mole Snake along the shoreline of Robben Island (the breeding habitat of the oystercatchers) and each location where predation by a Mole Snake was known to have occurred (either captured on camera or witnessed) was noted and saved

on a GPS as a “Mole Snake location” (Figure 5.2). Mole Snakes are diurnal and are encountered quite frequently on Robben Island (Dyer 1996). The distance between each nest and the nearest Mole Snake location was determined at the end of the 2017 breeding season when all the Mole Snake locations observed had been noted. The same process was repeated in the 2018 breeding season, and Mole Snakes were again seen mostly in the same areas as 2017 except for two additional locations. When another snake sighting was made where a previous one had been made, the sighting was not considered a new snake location. The snakes were not marked, but the snakes observed were of different sizes which may suggest that the snakes encountered might have been different snakes.



Figure 5.2: Locations where Mole Snakes were observed/where predation by Mole Snakes was known to have occurred (the star symbols) along the coastline of Robben Island (“Mole Snake locations”) and the core of the breeding area of Kelp Gulls (the green line) on Robben Island. The Kelp Gulls make use of the entire island and can be seen foraging, perching, or flying around the island. However, their breeding colony does not occur across the whole island. They established a colony on the northern part of the island in 2001 which since expanded towards the western area of the island (Calf et al. 2003; Tjørve & Underhill 2008) and has continued extending into the west perimeter of the island. The Kelp Gulls mostly make use of the vegetated area of the coastland and spread across the road into the interior of the island, while oystercatchers only place their nests in the narrow space between the mean high watermark and the start of the vegetation above it as displayed in Figure 5.1.

5.23 Video placement and video-monitoring of nests

Oystercatcher nests were video monitored during the incubation period using Acorn 6510MC/6310MC digital cameras. Cameras were deployed between November 2017 – February 2018 for the first breeding season and November 2018 – March 2019 for the second breeding season. Cameras were deployed on nests that had been incubated for a minimum of seven days to minimize the risk of nest abandonment. In 2017 all the cameras were programmed to take one-minute of video footage every 30 seconds (camera setting one). In 2018 an additional camera setting which required the cameras to take two pictures and 10 seconds of video footage every time an animal passed by the nest (camera setting two) were used. Camera setting two was made to increase the chance of capturing nest predation by potential avian predators.

Cameras were deployed for an overall average of 62.7 ± 15 hours per nest (2017 breeding season average = 17.2 ± 1.4 , 2018 breeding season average = 115.4 ± 29.4). The cameras were retrieved following either egg hatching, predation or when the camera might have run out of power. Cameras were redeployed to other active nests following retrieval and recharging of the batteries. Cameras were deployed across the entire island as active nests which had been incubated for at least seven days became available.

Cameras were placed within 1–3 m of each nest monitored. This distance range is reported not to harm incubating birds and was the exact one used by Perrella et al. (2020) on several bird species including the Yellow-legged Thrush *Turdus flavipes* and Li et al. (2019) on Red-whiskered Bulbul *Pycnonotus jocosus* and within the distance range (0.5–5 m) used by other studies, e.g. Gill et al. (2016) on multiple species including Acadian Flycatchers *Empidonax virescens*; Reidy & Thompson (2018); Troy & Conover (2019) for White-crowned Sparrow *Zonotrichia leucophrys oriantha*. The cameras used in this study were camouflaged using stones from around the area in which they were placed to cover them so that they generally blended in with their surroundings and minimised their conspicuousness to pedestrians and potential predators (Appendix 5.2). The cameras had no-glow 940nm black light LED, which enabled data capture at night but without being visible to most wildlife.

5.231 The potential effect of video deployment and other research activities on nest predation probability

Some studies have reported that the use of cameras to monitor incubating birds (Thompson III et al. 1999; McKinnon & Bêty 2009; Richardson et al. 2009) or trapping of adult birds on their nests (MaCivor et al. 1990) may not on average increase the chance of the nests getting predated, but some suggest these activities may negatively influence the fate of nests (Götmark 1992; Renfrew & Ribic 2003). Information on the research activities that could potentially influence oystercatchers nest predation in this study was collected so that their potential impact on nest predation could be examined and controlled for during data analyses. These activities include video deployment to monitor incubating oystercatchers on some nests, trapping of some adult oystercatchers on their nest from a minimum of 7–10 days post clutch incubation start date and the deployment of a dummy oystercatcher on a small subset of camera-monitored nests. The dummies were deployed (on 16 nests in 2017 and none in 2018) and retrieved at the same time as the cameras. The dummy deployment and trapping activities are not part of the focus of this chapter at all but were considered here because they were implemented concurrently with the data analysed here as part of other chapters (as is the case with trapping activities) or discontinued oystercatcher studies (in the case of dummy deployment) on the island.

5.24 Data analysis

Predictors of nest predation probability

A correlation analysis was conducted before model building to examine collinearity. Some of the variables were correlated and so were not retained for further analysis as follows: Distance to Alpha 1 was correlated with the distance of nest to the harbour (correlation coefficient = -0.62, $p < 0.001$) and the number of Kelp Gulls around a nest correlation coefficient = 0.58, $p < 0.001$). Distance to Alpha 1 was, therefore excluded from the model building phase. Similarly, the number of Kelp Gulls around a nest was correlated with the distance of the nest from the Kelp Gull colony (correlation coefficient = -0.66, $p < 0.001$). The distance of nests from the Kelp Gull colony was retained as it may be a more reliable indicator of exposure of the nests to Kelp Gulls, since the number of Kelp Gulls around a nest may change with time. However, the distance to the colony remains constant. The number of active nests per week increased as the season increased and declined towards

the end of the season (Appendix 5.3). The rate of predation per week also increased as the weekly count of active nests increased (the statistics and figures for the correlation are in Appendix 5.3). The date on which incubation started for each nest relative to the number of days since the start of the breeding season was used as the 'time' variable instead of weeks in the full model. Since the number of active nests increased as the breeding season advanced (Appendix 5.3), the 'time' variable in the full model was also used as a proxy for the number of active nests.

The probability of nest predation (predated=1, hatched=0) was analysed using a Generalised Linear Model (GLM) with a binomial error structure. Given the nature of the breeding habitat and behaviour of the oystercatchers on Robben Island, it was assumed as Tjørve & Underhill (2008), that most nesting attempts were found and discovered closer to when they were initiated rather than later, such that the use of a binomial method is unlikely to have biased the results. Also, the comparison of a nest survival model implemented in programme MARK (White & Burnham 1999; Dinsmore et al. 2002) which accounted for the detectability bias and a binomial regression model, which did not, yielded similar outcomes for the population of oystercatchers studied here (Chapter Six). Also, the application of programme MARK to the data analysed here yielded similar results to that of the binomial model (Appendix 5.8).

The full model contained the following explanatory variables: Clutch incubation start date (continuous) + Maximum air temperature during nest exposure (continuous) + Breeding season (two-level factor: 2017 and 2018) + Clutch size (continuous) + Nesting attempt (two-level factor: first attempt and re-nesting attempt) + Distance of a nest to the harbour (continuous) + Distance of a nest to vegetation (continuous) + Distance of a nest to the Kelp Gull colony (continuous) + Distance of a nest to the nearest active nest (continuous) + Distance of a nest to a Mole Snake location (continuous) + Distance of a nest to the mean high watermark (continuous) + Trap: whether a trapping attempt was made at the nest or not (1,0) + video: whether the nest was video-monitored or not (1,0). The variables 'trap' and 'video' were included in the full model to examine whether trapping activity and video monitoring had a significant impact on the fate of nests.

The quadratic terms of distance of a nest to vegetation and distance of a nest to the mean high watermark were included in the model because nests that are closer to vegetation may

experience a higher risk of predation, so nesting further away from the vegetation should reduce nest predation risk (Amat & Masero 2004a). However, in the context of the breeding habitat of the oystercatchers, the farther away a nest is from the vegetation, the closer it gets to the mean high watermark, another area that could potentially harbour reptilian predators in the dried kelp accumulated there and risk nest destruction due to wave-driven storm surges (Chapter Two). So, the oystercatchers are expected to increase the distance of their nests away from the vegetation, but this should plateau at some optimum distance after which predation risk should rise again. Similarly, if the Mole Snake locations found in this study represents a close-to-true measure of the presence/activity levels of Mole Snakes, nests closer to a Mole Snake location should experience higher nest predation probability compared to those further away from a Mole Snake location. The quadratic term of Mole Snake location was therefore included in the model to determine whether there is a certain distance away from a Mole Snake location at which nests may experience a flattened predation risk. Also, the quadratic term of maximum air temperature was included in the models because I expect an optimum temperature for poikilothermic predator activities.

To arrive at the best model from which to illustrate results, the variables that were not significant at $p=0.05$ were removed one at a time starting with the variable with the highest p -value. The regular Akaike's information criterion (AIC) of all the models created at each step was then compared, and the model with the lowest AIC was selected as the best. Since the data analysed were collected over two breeding seasons, breeding season (two-level factor: 2017 and 2018) was always included in all models (irrespective of whether the breeding season was significant at $p=0.05$ or not). This was to account for the variation within each season that was not measured. Estimates from the full and best models are presented to show that model simplification did not change the results in any material way.

To explore how oystercatchers vary their clutch size within a season, clutch size was converted into a binomial variable following Akresh et al. (2017). To test the probability of occurrence of large (3-egg clutches) across the season, nests with one or two eggs were scored as 0 and nests with three eggs as 1. To examine the probability of occurrence of small (1-egg clutch) across the season, one-egg nests were scored as 1 while two- and three-egg nests were scored as 0. A GLM with a binomial error distribution was then used to fit a

logistic relationship with the binomial clutch size as the response variable and clutch incubation start date and season as the predictor variables, following Akresh et al. (2017).

Data from only the nests monitored with cameras

A data set unique to the nests on which cameras were deployed was analysed to examine which factors influenced the status of the nests (predated=1, active=0) at the time of camera retrieval. The status of a nest at the time of camera retrieval (Predated=1, active=0) was modelled as a function of camera setting type (two-level factor: camera setting one and camera setting two); dummy oystercatcher (two-level factor: dummy present and dummy absent); duration of time for which camera was deployed in hours (continuous) and season (two-level factor: 2017 and 2018) using a GLM with binomial error distribution. All data analyses were conducted in the R statistical software version 3.6.1 (R Core Team 2019).

5.3 Results

5.31 The predictors of nest predation

A total of 311 nests of oystercatchers were found across 2017 and 2018 breeding seasons combined, of these 251 with fate as hatched (133) or failed due to predation (118) were used in the analysis of the predictors of nest predation (the remaining 60 were not included in the analysis because they were abandoned, of unknown fate, failed due to other reasons other than predation or had incomplete data across the explanatory variables). Air temperature logged every five minutes was on average, 19.14 ± 0.013 (7.8–37.1) °C on Robben Island during the period of data collection. The maximum air temperature during the exposure period of each nest was 32.41 ± 0.21 (21–37.1) °C. Nests were located on average 7.5 ± 0.58 (0–65.5) m from vegetation. The average incubation start date was 112.8 ± 1.6 (17–180) days from 1 September. Nests were located 214 ± 14.3 (0–972) m from Mole Snake locations and 1317 ± 62.0 (0–3340) m from the Kelp Gull colony.

The maximum air temperature during the exposure period of each nest significantly influenced nest predation probability. Nest predation probability was 100% between 21–27 °C and declined sharply to 62% at 30°C and further declined to 17% from 33.4°C but increased slightly again when air temperature approached about 36°C (Table 5.1; Figure 5.3, panel A). The probability of a nest being predated decreased with increasing distance away from vegetation, but the relationship was non-linear (Table 5.1; Figure 5.3, panel B). Nest

predation probability achieved a low at moderate distances to vegetation (Table 5.1; Figure 5.3, panel B). Three-egg clutches had the lowest probability (7%) of getting predated followed by two-egg nests with a 21% chance of getting predated and one-egg clutches which had the highest (43%) probability of getting predated (Table 5.1, Figure 5.3, panel E).

The probability of nest predation increased significantly as the breeding season advanced such that earlier nests were the least likely to be predated (Table 5.1, Figure 5.3, panel D). Nests initiated within the first 106 days of the breeding season had between 2–20% chance of getting predated while those initiated between 106 to 180 days into the breeding season had between 21–66% chance of getting predated (Table 5.1, Figure 5.3, panel D). Oystercatchers were more likely to lay three-egg clutches earlier in the season than later and more likely to lay one-egg clutches later in the season than earlier (Table 5.2, Figure 5.4).

The nests closest to Mole Snake locations had the highest chance of getting predated with nest predation probability declining from 46–18% between 0–300 m away from a Mole Snake location. Nests located <550 m from a Mole Snake location had the lowest probability (< 10%) of getting predated (Table 5.1, Figure 5.5, panel C). The distances of a nest to the nearest active nest, to the Kelp Gull colony, and the harbour were not statistically related to the probability of nest predation in this study (Table 5.1). Although the mean high watermark was not significant, its retention in the model decreased the AIC of the model, hence its retention in the best model (Table 5.1).

Table 5.1: Results from the binomial models (full and the one with the smallest AIC) exploring the explanatory variables that predict the probability of nest predation of oystercatchers on Robben Island for the 2017 & 2018 breeding seasons. Sample size = 251 nests

Full model					Smallest AIC model + season			
	Estimate	SE	z value	P	Estimate	SE	z value	P
(Intercept)	139	39.81	3.49	< 0.001	134	38.45	3.48	< 0.001
Incusdate	0.034	0.0093	3.69	< 0.001	0.027	0.0080	3.44	< 0.001
MaxT	-8.17	2.39	-3.42	< 0.001	-7.82	2.31	-3.39	< 0.001
I(MaxT^2)	0.12	0.036	3.36	< 0.001	0.11	0.034	3.33	< 0.001
Season 2018	-0.67	0.42	-1.60	0.11	-0.64	0.38	-1.70	0.089
Clutch size	-0.99	0.41	-2.42	0.015	-1.07	0.39	-2.71	0.0068
Trap	-0.029	0.64	-0.046	0.96	–	–	–	–
Nestatt2&3	-0.63	0.58	-1.08	0.28	–	–	–	–
Video	-0.35	0.58	-0.59	0.55	–	–	–	–
DNH	-0.00019	0.00034	-0.56	0.58	–	–	–	–
DTENV	-0.15	0.049	-2.98	0.0029	-0.14	0.046	-3.11	0.0019
I(DTENV^2)	0.0024	0.0010	2.41	0.016	0.0023	0.00094	2.43	0.015
DKC	-0.000062	0.00024	-0.26	0.79	–	–	–	–
DNN	0.00075	0.00090	0.83	0.40	–	–	–	–
MSLD	-0.0058	0.0024	-2.42	0.015	-0.0057	0.0022	-2.58	0.010
I(MSLD^2)	0.0000035	0.0000030	1.17	0.24	0.0000039	0.0000027	1.45	0.15
DHWL	-0.12	0.088	-1.35	0.18	-0.10	0.081	-1.22	0.22
I(DHWL^2)	0.0047	0.0027	1.74	0.082	0.0040	0.0025	1.58	0.11

The first nesting attempt and 2017 breeding season are represented by the value of the intercept. Incusdate = incubation start date, MaxT and I(MaxT^2) = maximum temperature and its quadratic term during the exposure period for each nest, Nestatt2,3 = re-nesting attempts 2 & 3, DNH=distance of a nest to the harbour, DTENV=distance of a nest to vegetation edge, I(DTENV^2) = the quadratic term of the distance of a nest to vegetation, DKC=distance of a nest to Kelp Gull colony, DNN=distance of a nest to the nearest active nest, MSLD = distance of nest to a Mole Snake location, I(MSLD^2)= quadratic term of the distance of a nest to a Mole Snake location, DHWL=distance of the nest to the mean high watermark, I(DHWL^2) the quadratic term of the distance of nest to the mean high watermark. Significant p-values are in bold.

Table 5.2: Binomial models examining the probability of occurrence of large (three-egg) clutches compared to a two- or one- egg clutch (Section A) and small (one-egg) compared to a two- or three- egg clutches (Section B) of oystercatchers across the breeding season on Robben Island for the 2017 & 2018 breeding seasons. Sample size = 251 nests.

	Section A				Section B			
	Estimate	SE	z value	p	Estimate	SE	z value	p
Intercept	1.42	1.22	1.17	0.24	-4.19	0.88	-4.78	< 0.001
Clutch incubation start date	-0.039	0.012	-3.22	0.0013	0.021	0.0070	3.07	0.0021
Season 2018	-0.40	0.56	-0.71	0.48	0.45	0.33	1.36	0.17

The 2017 breeding season takes the value of the intercept. Statistically and biologically significant p-values are in bold

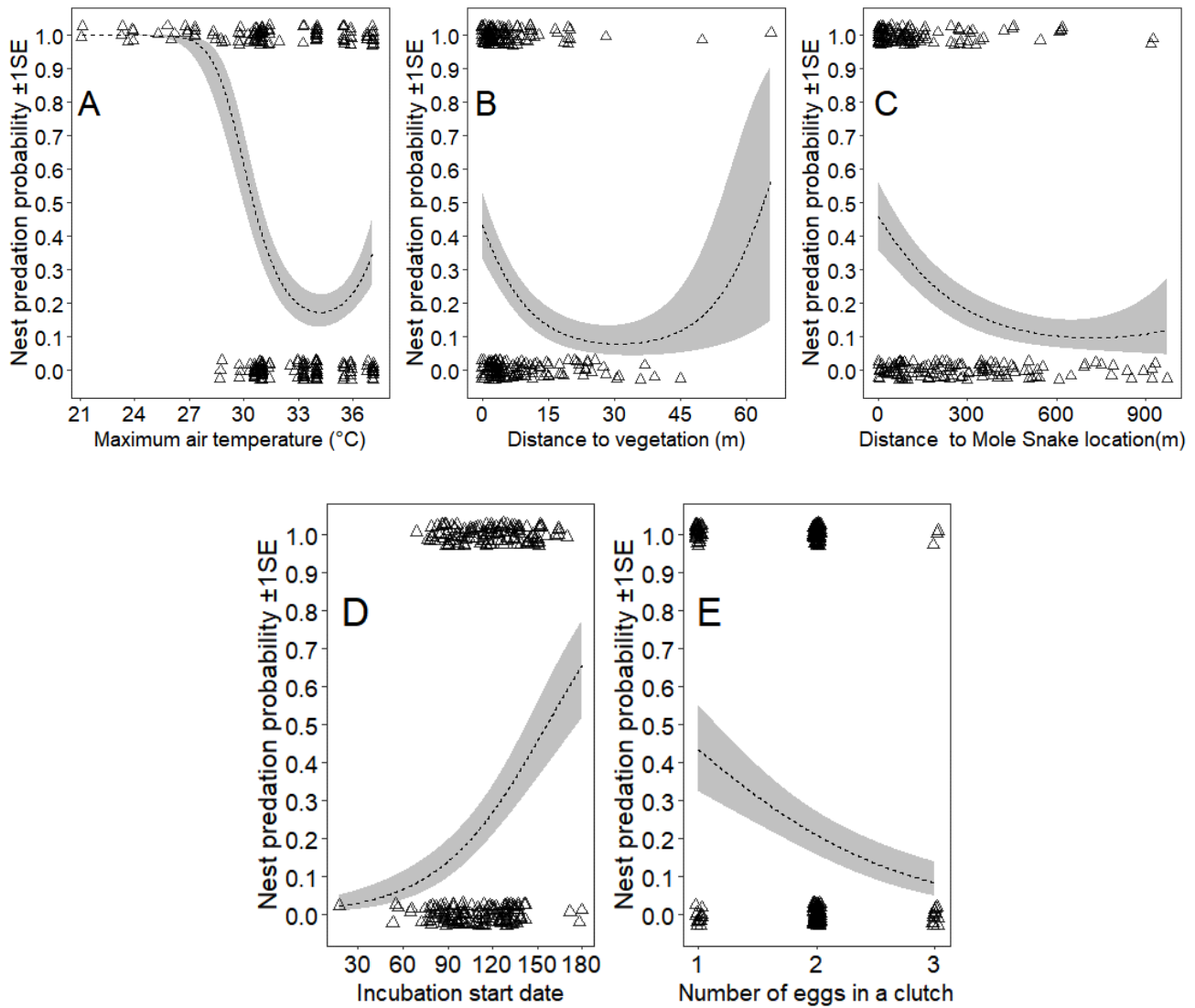


Figure 5.3: The predicted relationships between the maximum air temperature during exposure period of each nest (A) distance of a nest to vegetation (B), the distance of a nest to a Mole Snake location (C), the incubation start date of a nest (D), clutch size (E), and the probability of oystercatchers nest predation on Robben Island. Triangular symbols are raw data points for 2017 & 2018 breeding seasons. Back-transformed predicted values plotted for 2017 from the model with the lowest AIC in Table 5.2, with mean values set for the other predictors in the model.

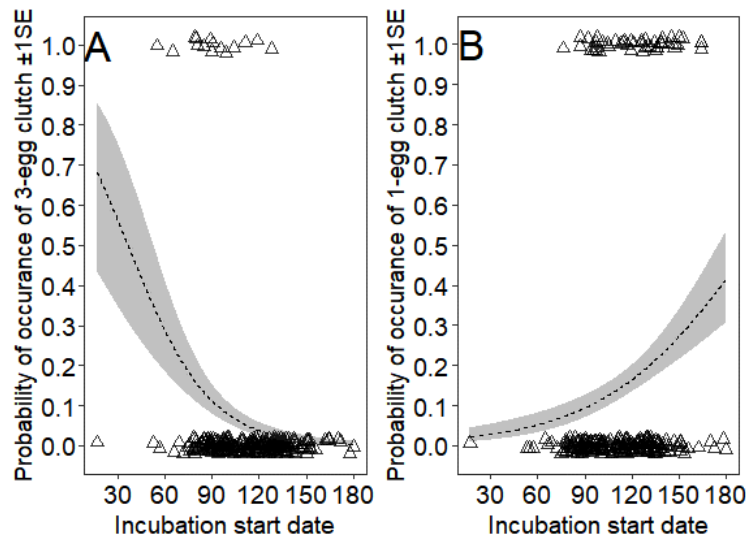


Figure 5.4: The predicted probability of an oystercatcher's nest having A: a large (three-egg) clutch compared to a two- or one- egg clutch, B: smaller clutch (one-egg clutch) compared to a two- or three- egg clutch, as a function of the clutch incubation start date on Robben Island. Triangular symbols are raw data points for 2017 & 2018 breeding seasons. Back-transformed predicted values plotted for 2017 from the models in Table 5.2.

5.32 Camera monitored nests

A total of 17.4% of all the nests found (54/311) were camera-monitored for a total of 3385 hours. Of these nests monitored with cameras, 85% (46 of 54) remained active as of the time the cameras were retrieved, 7.4% (4 of 54) were predated, 7.4% (4 of 54) were lost due to other factors (the two eggs from one nest were picked up by a child, another nest lost both eggs to wave-driven storm surge, another was displaced by Cape Cormorants *Phalacrocorax capensis*, and another appeared to have been affected by an ungulate). The binomial model examining the factors which affected the status (predated, active) of camera monitored nests at the time of camera retrieval showed that none of the factors considered (Camera setting type, presence of a dummy oystercatcher, footage duration and breeding season) affected nest status significantly (Table 5.3).

Direct evidence of nest predation was incidentally observed at six nests outside the regular camera monitoring (footages and photos of these are noted below in Section 5.42). One occurred during a trapping attempt, two predation events were directly observed during nest monitoring, and predators were observed to be moving away from three nests that had just been predated bringing the total number of nests where the predator identity was known to ten.

The footage from the cameras with camera setting two was activated by birds like Cape Wagtails *Motacilla capensis*, European Common Starlings *Sturnus vulgaris*, Cape Turtle Doves *Streptopelia capicola*, Chukar Partridges *Alectoris chukar*, African Penguins *Spheniscus demersus*, and other birds. Most of these birds are much smaller in size compared to the Kelp Gulls, so the assumption that the camera would be activated by the gulls if there was predation by them appears to be supported. It was also triggered by oystercatchers' bout exchange activities, ungulates, and Mole Snake predation events.

Table 5.3: The binomial model examining the factors affecting the status (predated, active) of camera monitored nests at the time of camera retrieval. Sample size = 58

	Estimate	Std. Error	z value	p
(Intercept)	-2.40	1.05	-2.29	0.022
Camera setting two	19.15	2874	0.0070	0.99
Dummy present	-0.21	1.47	-0.14	0.89
Footage duration	-0.0055	0.0073	-0.76	0.45
Season 2018	-17.08	2874	-0.0060	1.00

The 2017 breeding season, camera setting one, dummy absent take the value of the intercept

5.33 Predator identity and the proportion of nests predated by each predator type

No feral cats were detected in all the footage (both day and night). Although the footage pooled from both camera settings showed that Kelp Gulls were present at 67% (36 of the 54) of the nests monitored (excluding gulls flying over), none of the known predation events recorded was caused by Kelp Gulls. Of the 311 nests found for both 2017 and 2018 seasons, 39.2% (122 of 311) were predated. The predator type responsible for 8.2% of predation events (10 of 122) was determined and in all cases was a Mole Snake.

All the predation events reported occurred during daylight (Appendix 5.4) and occurred while at least one parent oystercatcher was around the nest. Some oystercatchers responded to the Mole Snakes by quietly moving off the nest without resisting; others showed distraction behaviour attempting to lure the Mole Snake away from their nest but with no success. At one nest, the parent tried to stop the Mole Snake but got an aggressive response from the snake, which eventually predated the nest. Mole Snakes completely swallowed all the eggs in the nests predated with no evidence left behind to inform that a predation event had occurred. This lack of evidence at the nest is similar to those observed on nests not monitored with camera as predated nests without camera looked as intact as

the predated nest with cameras. The presence of other birds, e.g., African Sacred Ibises *Threskiornis aethiopicus* during a predation event did not deter the Mole Snake.

5.4 Discussion

Oystercatcher nest predation probability was predicted by the distance of a nest to vegetation, clutch incubation start date, clutch size, the maximum air temperature over the exposure period of each nest, and by the distance of a nest to a Mole Snake location. However, the distance of a nest to a Kelp Gull colony was not a significant predictor of predation probability. Contrary to expectation, the results from both the predictors of nest predation and camera monitored nests showed that the main predator of the nests of oystercatchers on Robben Island was the Mole Snake and not the gulls.

5.41 Predictors of nest predation of oystercatchers

The position of nests with respect to vegetation

The probability of oystercatchers' nests getting predated had a quadratic relationship with distance away from vegetation with the lowest predation risk being 8% at 22–40 m from vegetation (Figure 5.3, panel B). The non-linear nature of the effect of distance to vegetation and nest predation risk in this study shows that the rate of and direction of change in predation pressure is not even across the shoreline where the oystercatchers breed. This may have occurred from the interaction of factors like habitat type, nest concealment strategy, predator hunting strategy and early predator detection. Oystercatchers rely on nest camouflage (Hockey 1982) rather than vegetation concealment as do some shorebirds (Laidlaw et al. 2020). Their breeding habitat on Robben Island is the bare (without vegetation) area between the mean high watermark and the vegetation above it (Figure 5.1). The effectiveness of nest camouflage is reported to increase with how closely the eggs matched their surroundings and with the openness of the breeding habitat i.e., reduced vegetation concealment (Lee et al. 2010; Troscianko et al. 2016). Reduced proximity to vegetation, and thus increased openness of the location of the nest, may also benefit incubating oystercatchers if it promotes early predator detection (Amat & Masero 2004a). The benefit of being further away from the vegetation may increase if it keeps nests far from the reach of potential predators, e.g. reptiles which use vegetation as a cooler microclimate to escape high solar radiation during the heat of the day (Weatherhead & Blouin-Demers 2004) or as a place to hide from being detected either by their prey or by

potential predators (including humans) (Lima & Valone 1991; Lima 2009; Cresswell et al. 2010). These potential benefits suggest that the further a nest is from the vegetation, the better (Gómez-Serrano & López-López 2014).

However, the further away an oystercatcher sites its nest from the vegetation, the closer it gets to the mean high watermark where nests are vulnerable to being destroyed by wave-driven storm surge (Jeffery 1987; Calf & Underhill 2005; Schmechel & Paterson 2005). Mole Snakes, which have been identified as an important predator of the oystercatchers' nests in this study, also appear to camouflage themselves in the washed-up dried kelp around the mean high watermark (Appendix 5.4), thereby potentially increasing nest predation risk around the mean high watermark. The higher nest predation probability of oystercatchers' nests closer to the vegetation, the decline to a minimum nest predation risk at 22–40 m from vegetation and a subsequent increase in nest predation risk beyond 40 m may reflect the need of oystercatchers to balance the placement of their nests at an optimal site which minimises the closeness to both the vegetation and the mean high watermark (Chapter Two).

The high nest predation probability experienced by oystercatchers' nests closest to the vegetation may also reflect the impact of limited habitat availability. The oystercatchers which nested closer to the vegetation mostly did so when the space available to them was narrow, i.e., the space between the mean high watermark and the vegetation above it is too narrow to permit the selection of an optimum nest-site. This narrowness means that the area where predators need to search is small and could potentially make it easier for the predator to locate nests in those narrow areas faster compared to those located in larger areas of the shore. Additionally, Mole Snakes may avoid nests located in larger areas of shore if it increases the time they spend hunting in the open away from vegetation or washed-up dried kelp in which to hide from approaching humans, because the snakes are not known to have natural predators on Robben Island (Dyer 1996; Crawford & Dyer 2000). Hunting in the broader area of the shore which is typically rocky, shelly and warm during the day may also expose the snakes to high thermal risks and they may instead forage in narrow areas close to colder vegetated microclimates (Weatherhead & Blouin-Demers 2004).

Time since the start of the breeding season

The probability of nest predation varied significantly within the breeding season; with the nests initiated earlier having the least chance of being predated compared to those initiated later (Table 5.1, Figure 5.3, panel D). This temporal variation in nest predation probability may have been driven by the increased rate of nest predation which is associated with the increased number of active nests as the season advanced (Appendix 5.3) and may be explained by the optimal foraging and the predator search image hypotheses. The optimal foraging hypothesis predicts that predators would avoid prey items that: (a) have great mobility, (b) are difficult to capture and (c) require greater search time to find because of their low density; especially if the net amount of energy gained from such prey is small (MacArthur & Pianka 1966). The predator search image hypothesis predicts that mobile predators which can move among several foraging patches where prey species occur in different relative proportions in time and space should have a flexible learned search image of their prey items which enables them to switch from a low-density prey to a higher density prey as condition changes (Cornell 1976). A predator's switch from a low-density prey to a higher density one subjects the prey items to density-dependent predation pressure, such that predation pressure is greater at higher prey densities than lower (Nams 1997).

The hunting strategy of Mole Snakes, the main oystercatcher nest predator identified in this study, and the characteristics of the oystercatchers and their eggs seem to fit into both hypotheses. Mole Snakes on Robben Island are known to prey on the eggs of several bird species, e.g. Helmeted Guinea-fowl *Numida meleagris*, Hartlaub's Gull *Larus hartlaubii* and the abandoned eggs of African Penguins (Dyer 1996; Crawford & Dyer 2000). These bird species have different breeding seasons and habitats such that their nest density peaks at different temporal and spatial scales within the island (Dyer 1996; Crawford & Dyer 2000). The Mole Snakes on Robben Island may have formed a learned search image of each of its prey species and then flexibly switch from the eggs of one species to another in a density-dependent manner as the nests become increasingly available at different times of the year.

Oystercatchers' nests are likely to be profitable prey for Mole Snakes. The oystercatchers on Robben Island arrange their nests in a somewhat linear fashion along the shoreline (Figure 5.1) making it potentially easy for a predator to find the nests by systematically following a linear trail along the coastline. While an African Penguin pair were able to successfully

defend their nests against predation by a large Mole Snake on Robben Island (Underhill et al. 2009), no oystercatcher pair succeeded in defending their nest from being predated by Mole Snakes in this study. This suggests that it is relatively easier for the Mole Snakes to prey on the more vulnerable oystercatcher's nest because the snakes do not need to expend much energy to displace oystercatcher parents and gain access to their nest contents. The eggs of the oystercatchers are immobile and presumably high in nutrients, suggesting that the net amount of energy gained by Mole Snakes per unit time will be high.

The likely factors that may limit the predation of oystercatchers' nests by Mole Snakes could be weather (e.g., temperature as discussed further below) and the availability of active nests in high density (Appendix 5.3, panel C). At low nest density, the available nests may be too sparsely distributed, requiring much search effort and time for the Mole Snakes to find. But as oystercatchers' nests become increasingly available as the breeding season advances and nests reach certain density thresholds, the search effort and time needed to find them may become smaller, thereby potentially increasing predation pressure (Cornell 1976; Nams 1997; Verhulst & Nilsson 2008). This may have explained the observed increased nest predation probability as the breeding season advanced in this study and supports the predator search image hypothesis (Cornell 1976; Nams 1997) and the optimal foraging hypothesis (MacArthur & Pianka 1966).

This result corroborates those of other shorebirds, e.g. Redshank *Tringa totanus* (Ottvall et al. 2005) and Kentish Plover *Charadrius alexandrinus* (Que et al. 2014) where predation pressure was higher for nests initiated later in the breeding season. It, however, differs from the pattern observed for the nests of Black-tailed Godwit *Limosa limosa* and Common Snipe *Gallinago gallinago* which were more visible earlier in the season when concealing vegetation was low and consequently suffered greater predation rates compared to later in the season when concealment increased (Laidlaw et al. 2020). The difference is likely explained because oystercatchers do not rely on such vegetation concealment but on camouflage (Hockey 1982) to reduce the detectability of their nests by potential predators.

Clutch size

Nest predation probability of three-egg clutches was lower compared to one- and two- egg clutches (Figure 5.3, panel E). This may have been because oystercatchers are more likely to

lay three-egg clutches earlier in the season rather than later (Paijmans et al. 2015; Figure 5.4A) and thereby escape the higher nest predation occurring later in the season. The higher occurrence of smaller (one-egg) clutches as the season advanced may reflect the reduction of reproductive investments by oystercatchers under high nest predation risk. This idea is supported by the following examples: Red-faced Warblers for which the perception of nest predation risk was experimentally heightened responded by laying smaller clutches than those in the control group (Dillon & Conway 2018). A similar response was observed in another study where Collared Flycatcher *Ficedula albicollis* in an experimental group which experienced a high rate of nest predation significantly decreased their clutch size compared to the control group (Doligez & Jean Clobert 2003). A reduced clutch size response could potentially reduce actual nest predation probability by reducing the parental activity around a nest and by decreasing the period over which a nest is susceptible to predation (Slagsvold 1984; Cresswell 1997a; Martin et al. 2000; Doligez & Jean Clobert 2003). For example, a smaller clutch size means a shortening of the egg-laying period, a potential decrease in the length of incubation and a reduced amount of incubation constancy (Slagsvold 1982, 1984; Martin 1995). A reduced clutch size could spread the risk of nest loss across multiple clutches laid separately (Slagsvold 1984; Griebeler et al. 2010) or conserve energy for future nesting attempts should the first and even the second attempts fail (Roper 2005; de Heij et al. 2006).

However, several factors other than predation risk could be responsible for the occurrence of larger clutches earlier and smaller ones later in the season. For example, individuals starting to breed earlier and having larger clutches may have secured higher quality territories, be of higher quality themselves (Perrins & McCleery 1989), or older and more experienced compared to those laying smaller clutches later (Nisbet et al. 1984; Weimerskirch 1990; Fowler 1995; Janiszewski et al. 2017). The conditions for breeding (e.g. food availability and weather conditions) may generally be more favourable earlier in the season such that larger clutches are the optimum option compared with later in the season when breeding conditions deteriorate and smaller clutches become the ideal option (Crick et al. 1993; Tortosa et al. 2003; Brooke 2019; Kaliński et al. 2019).

Air temperature

The maximum air temperature during the exposure period of nests significantly influenced the nest predation probability of oystercatchers in this study (Figure 5.3, panel A). The maximum daily temperatures on the days of actual Mole Snakes' predation events ranged from 21–37.1°C whereas the actual air temperature at the time of predation ranged between 13.7–35.1°C (Appendix 5.4). Oystercatchers' nest predation probability was highest when the daily maximum air temperature was between 21–27°C (Figure 5.3, panel A). Interestingly, the incubating oystercatchers used evaporative cooling behaviour (panting) heavily around these temperature values (panted for 30 minutes per hour from 22.7°C and continuously from 26.6°C) and relieved each other frequently to enable frequent trips to the ocean for thermoregulation purposes (Chapters Three & Four). Increased parental activities (e.g., the increased movement of the head and bill under panting conditions) may have made the nests more obvious to predators, thereby interacting with the increased activity of snakes as temperature increased to escalate overall nest predation (Conway & Martin 2000b). Being ectotherms, snake activities are known to increase as temperature increases (Cox et al. 2013; George et al. 2015; Putman & Clark 2017), and although they generally depend on chemical cues and increased tongue-flicking, some snakes have eyes and also use visual cues to locate their prey (Mullin & Cooper 1998; Saviola et al. 2012). Mole snakes are diurnal (Dyer 1996) and have eyes (Branch 2002). These characteristics make it likely that increased parental activity around a nest during the day could have increased nest predation, especially under shading and panting conditions (Chapter Three) and frequent back and forth trips between the nest and the foraging ground (Chapter Four).

Nest predation probability subsequently declined as temperature increased beyond 30°C and was lowest from 33.4°C (Figure 5.3, panel A). This decline in nest predation probability at extreme temperatures may have reflected a decrease in Mole Snakes activity level and their need to retreat to colder microclimates. This is because, although snake activities generally increase as temperature increases, their activity is limited by temperature extremes and they respond by minimising or altogether avoiding activities at high temperatures (Henderson 1982; Weatherhead et al. 2012). Ground-level temperature logged by an iButton on Robben Island during summer shows that temperature can be as high as 58.5 during the day (Chapter Three). This suggests that the temperatures which the

Mole Snakes experienced on the ground could be much higher than the air temperature range reported here. The slight increase in nest predation probability at about 36°C (Figure 5.3, panel A) may likely still be attributed to the effect of increased activities by oystercatchers because they used shading behaviour for 50% of the time from air temperature of 34°C which may have increased their being more visible to predators. Also, oystercatchers with nest-sites close to the vegetation in narrow beaches may still be vulnerable to nest predation by Mole Snakes even at high temperatures because of the thermoregulatory benefits such vegetated sites could provide for the snakes (Weatherhead & Blouin-Demers 2004). The high temperature predicted under climate change may favour higher nest success of the oystercatchers if it reduces the activity time of Mole Snakes and thereby minimise nest predation rates, but this may depend on the availability of wide beaches where oystercatchers could site their nests sufficiently away from the vegetated upper part and lower ends of the beach (Chapter Two). Also, high temperatures may compromise egg-viability (if disturbances force oystercatchers to leave their nests exposed during the heat of the day) and may be thermally demanding for adult oystercatchers (Chapters Three & Four). Management interventions which result in broadened breeding habitats and minimise human disturbance may benefit the oystercatchers in the future.

The temperature range at the time of actual nest predation by Mole Snakes is very similar to that observed for the Boomslangs *Dispholidus typus* (14.2–31.6 °C) in their predation of the nests of Rockjumpers *Chaetops frenatus* (Oswald et al. 2020). The pattern observed between nest predation probability and temperature in this study differs slightly from Cox et al. (2013) and Oswald et al. (2020) in that they observed an increase in nest predation as temperature increased but did not detect a quadratic pattern, probably because of the range of daily maximum temperature prevailing at their respective study sites or differences in sample sizes. However, these studies and the observations reported here together emphasise the importance of temperature on snake activity and its significant implications for avian nest predation.

Predator presence and activity

The distance of nests to Mole Snake locations (but not distance to the Kelp Gull colony) had a significant negative influence on nest predation probability. The nests closest to Mole Snake locations had the highest chance of getting predated while those located greater than

550 m from a Mole Snake location had the least probability ($< 10\%$) of getting predated (Figure 5.3, panel C). The use of the locations where predation have been known to occur may have introduced some bias into the data. However, given that the locations where Mole Snake predation were known to have occurred constitute only 8% of the predated nests, this bias may have been negligible.

The presence and activity of potential predators in an area could be an essential source of information on the pattern of the nest predation (Kearns & Rodewald 2017; Mason et al. 2018). Since proximity to locations used by potential predators could reflect higher predator activity compared to locations which are further away (Lima 2009; Kearns & Rodewald 2017), the predation probability of the nests of oystercatchers was expected to significantly decrease as distance to Mole Snake locations and the Kelp Gull colony increased. This prediction was valid for only one of these distances, distance of nests to Mole Snake locations, reflecting the likely importance of Mole Snakes as the significant predator of oystercatchers' nests, rather than the gulls.

Mole snakes are known to be territorial (Branch 2002) suggesting that the Mole Snakes sighted in a given area on the island may be different from others observed elsewhere within the island. Thus, the Mole Snakes responsible for the predation of oystercatchers' nests within the island are likely to be separate individuals making use of sections of the coastline as foraging patches. The different sizes of the snakes observed also suggested that several local individuals were involved. The significant influence of distance of a nest to Mole Snake locations on nest predation probability may have reflected that the Mole Snake locations recorded in this study are an 'effective' proxy for the activities of Mole Snakes along the coastline of Robben Island.

Like the impact of Mole Snakes' activity on the predation of oystercatchers' nests in this study, Kearns & Rodewald (2017) noted that predator activity explained the patterns of nest distribution, predation and therefore survival of the nests of Northern Cardinals *Cardinalis cardinalis*. They also noted that nest survival of Acadian Flycatchers *Empidonax virescens* declined in areas with high avian predator activity (Kearns & Rodewald 2017). Similarly, Pied Flycatchers *Ficedula hypoleuca* nests in areas occupied by Ural Owl *Strix urala* experienced higher nest predation rates compared with those in areas without Ural Owl (Morosinotto et al. 2012). In the same vein, the chicks of Northern Lapwing *Vanellus vanellus* in areas of high

predator activity experienced more significant predation compared with those in areas of lower predator activity (Mason et al. 2018). The lack of a significant effect of distance of a nest to the Kelp Gull colony on the nest predation probability of oystercatchers observed in this study is similar to that of Virzi et al. (2016). They also expected that American Oystercatchers' *Haematopus palliatus* nests which were closer to gull (*Larus argentatus* and *Larus marinus*) colonies would suffer high clutch and brood predation but were surprised to find that distance from gull colonies did not significantly affect clutch or brood survival rates.

5.42 Predator identity, the relative importance of each predator

The predator responsible for the predation of oystercatchers' nests, where predator identity was known in this study, was the Mole Snake, not the gulls. No feral cats were seen around any of the nests that were camera monitored nor were any observed along the coastline where the oystercatchers breed, throughout this study. This suggests that feral cats are not a current threat to breeding oystercatchers.

Evidence of Mole Snakes' predation:

One of the explanations for why shorebirds breed so close to the shoreline despite the increased risk of losing nests to wave-driven storm surges is that predation risk may be lower closer to the coastline (Ens & Underhill 2014). The Mole Snakes on Robben Island appear to have counteracted this possibility for the breeding oystercatchers. The encounter rate of Mole Snakes on the shoreline of Robben Island has increased over time (Calf 2004) and the several Mole Snake locations recorded in this study (Figure 5.3) suggests that they are still very active along the coastline.

Whether Mole Snakes have suddenly become important because of the culling of the cats is indistinct as it is unclear whether the snakes have always been important nest predators of oystercatchers on the island but remained undetected. Because prior to Calf (2004)'s observation of a Mole Snake wriggling to escape as it swallowed the second of two eggs from a 24-day old oystercatcher nest that had been previously active, Mole Snake predation of oystercatcher eggs had not been previously described. This may perhaps explain why oystercatchers were not considered in the first compilation of the list of bird species whose eggs Mole Snakes predate on Robben Island by Dyer (1996). They captured Mole Snakes

between 1989–1994 and checked by palpation for fresh bird eggs consumed by the snakes using the size, shape, strength of the shell and the timing of breeding to group the eggs into those of different species (Dyer 1996). However, oystercatchers were not considered.

Calf (2004) wondered whether Mole Snake was an important predator of oystercatcher eggs or chicks and recommended the use of time-lapse video photography with infrared light at night to find out. Despite Calf (2004)'s observation and curiosity as to whether the snakes were important nest predators of the oystercatchers on the island, Braby & Underhill (2007) still noted in the subsequent breeding season (2004/2005) that Mole Snakes could not have been responsible partly because of the suspected timing of the predation events. Braby & Underhill (2007) highlighted three of 62 predated nests from the 2004 breeding season to infer nocturnal predation by feral cats. They noted that the three nests were active at 19h40, 16h30, 16h40 and observed to be empty on their respective subsequent days at 08h15, 07h00, 08h15, respectively. Mole Snake predation events recorded in this study occurred at similar times with predation events starting by 16:57, 18:43 and 17:01 and lasting for about ten minutes. Given that the oystercatchers breed during summer when sunset could normally extend to 20h00, using the timing of nest predation to infer that cats are predators does not seem well supported.

In the breeding seasons that followed the cat culls, the snake was still not considered an important nest predator of oystercatcher nests and the gulls were instead suspected (Underhill 2014). In the 2013 breeding season, a similar observation to that made by Calf (2004) was made of a one-egg nest which was active on 29/1/14 but found empty on 8/2/14 with a Mole Snake right next to it (Ms Joana Agudo unpublished data). In the 2016 breeding season, similar observations were also made of Mole Snakes departing from nests which had been predated but were active the last time they were checked (BA personal observation). But it was still generally believed that the snakes could not have been an important nest predator of the oystercatchers and the gulls were instead still suspected to be the main agent. During the two breeding seasons reported here, three observations similar to that made by Calf (2004) were made: one in 2017 and two in 2018 breeding seasons, but nest cameras were deployed for the first time to monitor nest predators at the nests of oystercatchers. The full predation event by a Mole Snake raiding the nests of oystercatchers was first captured from start to end on Robben Island on 7/12/17 in the

2017/2018 breeding season. Other video footage capturing the complete predation events soon followed in 2017/2018 and the 2018/2019 breeding seasons. The video footage of these predation events can be viewed [here](#)). These pieces of evidence permitted a more careful observation of each Mole Snake encountered around the nest of the oystercatchers.

Two of the pieces of evidence made outside of the regular camera monitored nests were possible because it was becoming clear that Mole Snakes were important nest predators of the oystercatchers on Robben Island. The first one was made on 19/01/18 during the 2017/18 breeding season while searching the mean high watermark area for chicks of the oystercatchers at high tide (usually it is almost impossible to find chicks at low tide because they have a vast intertidal area to hide and camouflage in). A Mole Snake was observed amidst the washed-up kelp around the mean high watermark. It was later seen coiling around an egg which it eventually predated in an oystercatcher's nest in the area. Pictures from this event can be observed in Appendix 5.3. The second was made on 27/11/18 in the 2018/19 breeding season during nest monitoring and searching for new nests. A Mole Snake was observed hiding and blending with dried kelp above the mean high watermark (Appendix 5.4). It was a few meters from a new nest which contained only one egg which was sighted seconds after seeing the snake. Not to lead the snake to the nest, the nest was left unprocessed (no egg measurements were made). After about 15 minutes hoping that the snake would have left the area, the researcher returned to process the nest and found the Mole Snake right inside the nest. The predation event was filmed, and the video footage can be viewed [here](#). More observations were made of Mole Snakes hiding some meters away from active nests of oystercatchers which were observed to have been predated on subsequent visits days later. The response of Mole Snakes to an approaching observer appears to be linked with whether they had predated a nest or not. They seem to wriggle away very fast from an already predated nest (Appendix 5.5) but prefer to hide and lay motionless when they are yet to predate the nest in the area (Appendices 5.3 & 5.4). They are probably attempting to avoid being noticed and then likely continue their hunting activities once the observer moves away. Together all these pieces of evidence show that Mole Snakes are more important nest predators of the oystercatchers on Robben Island than previously thought.

Oystercatchers are entirely helpless when it comes to deterring Mole Snakes from preying on their nest because all the Mole Snake predation events recorded on the nest cameras occurred while at least one parent oystercatcher was attending the nest. Although Mole Snakes are not venomous, they are known to be very aggressive constrictors and capable of inflicting intense and painful bites (Crawford & Dyer 2000; Branch 2002). Attempts to aggressively defend a nest against Mole Snakes may jeopardize oystercatchers' current survival and hence future reproductive potential. The presence of other birds, e.g., African Sacred Ibises *Threskiornis aethiopicus* during a predation event did not deter the Mole Snake. An African Sacred Ibis was observed to defend a White-breasted Cormorant *Phalacrocorax lucidus* nest against predation by extracting a Common Egg-eater snake *Dasypeltis scabra* from the nest of the cormorant at Schaapen Island (Underhill et al. 2009). However, during several predation events by Mole Snakes on oystercatchers' nests, several African Ibises surrounded the snake but did not mob the snake, suggesting that Mole Snakes are dangerous even to birds larger than oystercatchers.

Evidence of Kelp Gull predation

It was anticipated that Kelp Gulls would be the primary nest predator of the oystercatchers because of their burgeoning population on the island (Braby & Underhill 2007; Underhill 2014) and their reputation as avian nest predators (Malan et al. 2004; Ludynia et al. 2014). But surprisingly no evidence was found to suggest that the gulls predate the nests of oystercatchers in this study. When after the first breeding season of monitoring, no evidence was observed for gull predation, it was thought that perhaps the predation events by gulls happen too quickly to have been captured on the camera settings used. Consequently, a second camera setting was included in the second breeding season of data collection to enable capture of predation events whenever it occurred. However, still, no gull predation was recorded. The evidence from both the first and second seasons of data collection was very consistent with both nest predation by Mole Snakes and none by gulls irrespective of camera settings, despite gulls being seen in over 60% of the footage. Furthermore, the second camera setting was activated by birds that were far smaller compared with the gulls suggesting that if a predation event occurred involving the gulls, the camera would have been activated. Also, for all camera monitored nests, there was no case where the eggs disappeared without the cause being captured. The lack of evidence of

gull predation in the two seasons of data collection in this study seems very robust: Kelp Gulls may not be a nest predator of the oystercatchers on Robben Island at all or at best could be a minor nest predator of the oystercatchers.

Instead, observations between incubating oystercatchers and gulls suggest that the oystercatchers are capable of chasing gulls away from their prey (kleptoparasitism). Kelp Gulls usually hunt for shelled prey items from the intertidal area which they carry in their bills to an area with a hard surface. They then fly high up in the air and release the shelled prey, so it hits a hard surface and breaks open. Once that happens, oystercatchers have been observed on different occasions to chase the gulls off the prey which they then eat. Given the high nest attentiveness of the oystercatchers (Chapter Four) and their ability to chase gulls away, it would be hard for gulls to predate an oystercatcher's nest. This is because nest predation should be low if the parent's presence and nest defence strategy can successfully deter a predator away from the nest (Cresswell 1997b; Oswald et al. 2020).

The presence of broken eggs of oystercatchers with splashed yolk is usually used to infer predation by gulls on Robben Island (Tjørve 2006; Braby & Underhill 2007; Joana Agudo Unpublished data). The gulls may be responsible in these cases, but my observations of the response of incubating oystercatchers to ungulates and the activities of ungulates along the coastline of the island make it also possible that such broken eggs of oystercatchers with yolk may also have resulted from trampling by ungulates. Ungulates (Fallow Deer *Dama dama*, Steenbok *Raphicerus campestris*, Springbok *Antidorcas marsupialis*) are frequently observed along the coastline where the oystercatchers breed. The number of broken eggs of oystercatchers observed also appear to have dropped following the culling of the Fallow Deer population on the island (Joana Agudo Unpublished data, BA personal observation, Christopher Wilke Unpublished data). This suggests that ungulates may have had an undetected impact on the fate of the nests of oystercatchers on Robben Island.

The lack of evidence to support the initial expectation that gulls should be the most important predator of the oystercatchers' nests is similar to the findings from (Thompson III et al. 1999). Thompson, III et al. (1999) had expected more predation by raccoons, Blue Jays (*Cyanocitta cristata*), and American Crows (*Corvus brachyrhynchos*) because of the abundance of these predators on their study area and because they are known as avian nest predators. However, after conducting field observations using video cameras, they detected

only two predation events by raccoons and none by Blue Jays and American Crows. Oswald et al. (2020) also reported no Corvidae predating the Rockjumper *Chaetops frenatus* nests despite being prevalent in their study sites but observed that Boomslang was responsible for the predation of most nests. These highlight the importance of research to accurately identify nest predators as some predators which are conspicuous either because of their body size, plumage, abundance or behaviour may seem disproportionately responsible for nest predation, compared to more inconspicuous ones which may be the actual culprits (Birkhead 1991; Capstick et al. 2019). Research is also crucial because management interventions implemented without adequate knowledge of nest predator identity and patterns of nest predation will most likely be ineffective (Andes et al. 2019; Capstick et al. 2019).

Evidence of oystercatcher chick predation by Mole Snakes or Kelp Gulls?

The chicks were not camera monitored as the nests were, so no clear evidence of chick predation was observed. A juvenile Mole Snake was observed within 1 m of a nest containing a day-old oystercatcher chick (of about 40 g). The chick was never seen again on subsequent visits to the nest. It remained unclear whether the juvenile snake was capable of predated the chick and perhaps could have been responsible for the disappearance of the chick. Juvenile Mole Snakes on Robben Island are reported to prey on clicking stream frogs *Strongylopus grayii* (Dyer 1996), but there was a report of a young Mole Snake which fed on a Cape Weaver *Ploceus capensis* chick that had fallen from its nest (Dyer 1996). Also, observations have been made of adult Mole Snake preying on the chicks of peafowl and attempting to prey on a gull chick of about 200 g on Robben Island (Calf 2004).

It is possible that Kelp Gulls may be responsible for the predation of oystercatcher chicks, but no evidence was observed to suggest that during the three breeding seasons covered in this thesis. I, however, directly observed Kelp Gulls exhibiting cannibalism on the chicks of their fellow conspecifics.

5.43 The impact of research activities on the fate of oystercatchers' nests

One predation event occurred during a trapping attempt on one nest (the footage can be viewed [here](#)). No such impacts were re-observed at any other nests where adults were trapped. Overall research activities (trapping, video, and dummy deployment on a subset of

nests) did not significantly influence the nest predation probability of oystercatchers in this study (Tables 5.1 & 5.3). The sample size of the number of camera monitored nests that got predated was small suggesting that the results should be interpreted with caution. However, the fact that 54 nests were camera monitored and only four got predated while several nests which were not camera monitored got predated suggests that the impact of the camera and by implication the model placement and trapping on nest predation probability may have been low. Additionally, this is similar to the findings of other studies which also observed no significant effects of video placement (Thompson III et al. 1999; McKinnon & Bêty 2009; White et al. 2010) and trapping of adult birds on their nests (MaCivor et al. 1990) on the fate (predated or hatched) of the species studied (mostly ground-nesting shorebirds).

5.5 Conclusions and management implications

The results from this study show that several factors such as predator identity and behaviour, location of nests, weather and the behaviour of adult birds have an additive effect in determining predation risk of avian nests, suggesting that these factors should be considered together when attempting to understand patterns of avian nest predation. The results also suggest that there is no need to control the Robben Island Kelp Gull population on account of the oystercatchers. However, the impact of gulls on other species breeding on the island may be different from that reported for the oystercatchers in this study.

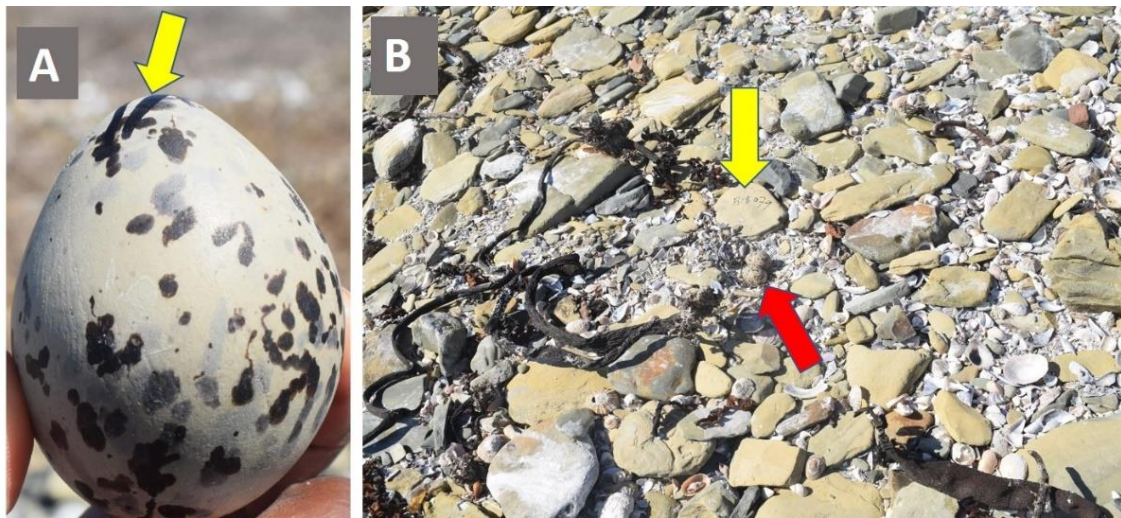
Managing the predation risk from Mole Snakes on the oystercatchers requires careful consideration. Mole Snakes were afforded legal protection in South Africa in 1956 because of their value to farmers as constrictors which control rodent populations (Crawford & Dyer 2000). They are widespread throughout mainland South Africa but occur only on Robben Island of all the 22 islands in the country (Dyer 1996; Branch 2002). While the mainland populations feed on small mammals and reptiles, Robben Island Mole Snakes are known to prey on avian eggs as a primary food source (Dyer 1996). The breeding seasons of the avian species they prey on spread out over the entire year such that the Mole Snakes have a constant supply of avian eggs as food (Dyer 1996; Crawford & Dyer 2000). Their population on the island is therefore closely linked with the breeding population of birds (Crawford & Dyer 2000). Several of the snakes were considered to have died of hunger in 1997 when Swift Terns and Hartlaub's Gulls failed to breed (Crawford & Dyer 2000). The Robben Island

Mole Snake population is thought to have occurred naturally and has been present on the Island since at least 1610, before humans colonised the Island (Crawford & Dyer 2000).

Mole Snakes on the island may be more beneficial than detrimental and should be protected. Since the snakes have several alternative bird eggs on which they forage (Dyer 1996; Crawford & Dyer 2000) and appear to switch in a density-dependent manner, it is unlikely that a single bird species would be highly impacted by them. Mole Snakes may be an important ecological component of the biodiversity on the island, for example, they are known to 'clean-up' by feeding on abandoned eggs of African Penguins (Dyer 1996; Crawford & Dyer 2000). The current breeding population of oystercatchers on Robben Island has increased, and the annual breeding productivity is around the threshold needed to maintain a stable population, despite nest predation by Mole Snakes and other sources of nest failure (Chapter Six). Given that oystercatchers are thriving, plus the fact that Mole Snakes are indigenous to the island (Crawford & Dyer 2000) and their predation of oystercatchers' nests is already limited by natural factors such as extreme temperatures, the openness of oystercatchers' nest-sites, and the availability of nests, it is recommended that the snakes should not be controlled. However, further studies to understand the biology of the snakes, their number, and other ecological roles that they play on the island is recommended.

Overall, this study enriched our understanding of nest predator identity and highlighted important ecological factors influencing nest predation of the oystercatchers on Robben Island in a way that was not previously known. It thus provides useful information on which management decisions and further studies can be based.

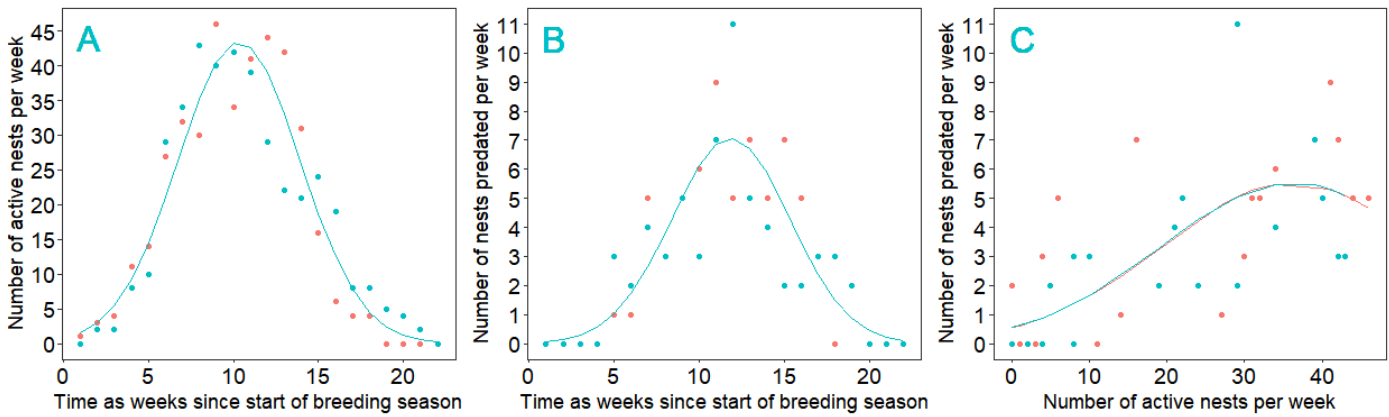
Appendix



Appendix 5.1: The yellow arrow in A point to the identity marking made on eggs using a black marker. The dark mark was very similar to the natural dark markings on the eggs and did not make the eggs more obvious and was unlikely to have increased the eggs' risk of predation. The yellow and red arrows in B point to the unique nest identity marking on a stone which was already at the nest-site.



Appendix 5.2: The yellow arrow points to the camera placement and how it is camouflaged with stones over, beside and behind such that it generally blends in with the surrounding to minimise their conspicuousness to pedestrians and potential predators. Only the front (which contains the lens, and the infrared faces the nest), is left uncovered. A pedestrian or predator must have come very close to a nest before seeing the camera. Note the inconspicuousness of the nest and egg markings too. *Please, excuse the shadow in the picture.*

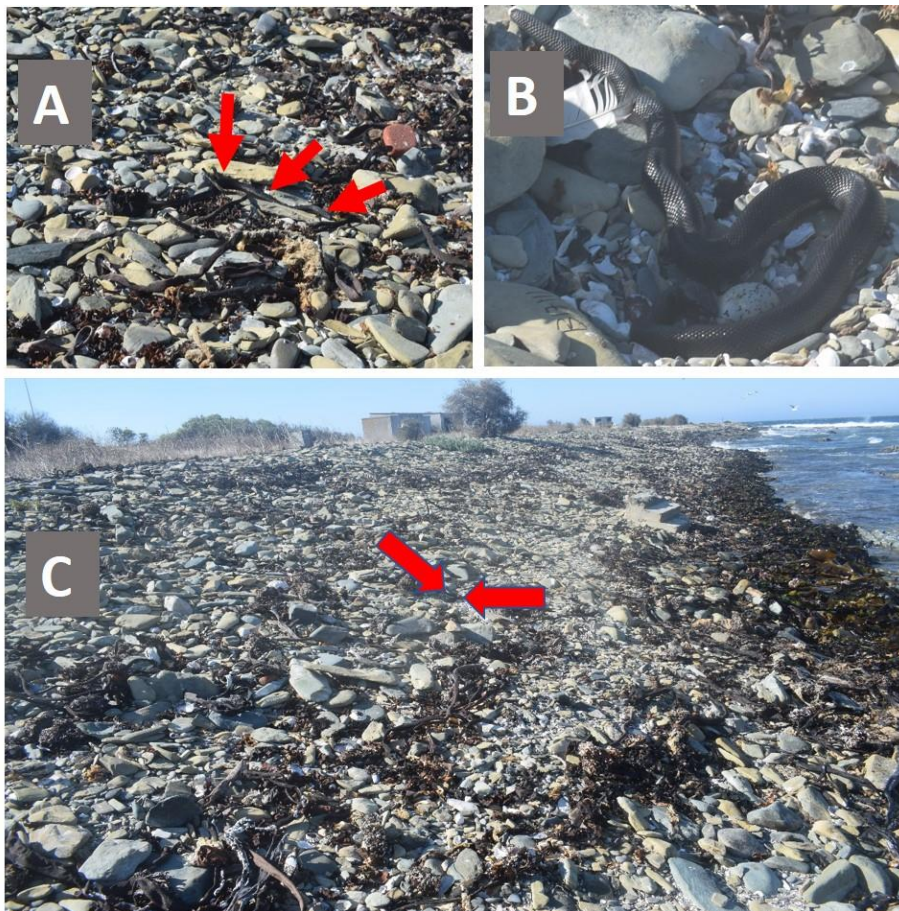


Appendix 5.3: The number of active nests per week is strongly related to the time since the start of the breeding season ($\beta = 0.80$, $SE=0.045$, $z=17.65$, $p < 0.001$; $\beta^2 = -0.039$, $SE=0.0021$, $z = -18.32$, $p < 0.001$) (panel A). The number of predated nests per week is significantly linked to the time since the start of the breeding season ($\beta = 0.98$, $SE=0.13$, $z=7.34$, $p < 0.001$; $\beta^2 = -0.041$, $SE=0.0055$, $z = -7.47$, $p < 0.001$) (panel B) and the number of active nests ($\beta = 0.12$, $SE=0.027$, $z=4.77$, $p < 0.001$; $\beta^2 = -0.0018$, $SE=0.00054$, $z = -3.29$, $p < 0.001$) (panel C). Sample size = 44 weeks from the 2017 (red) and 2018 (turquoise blue) breeding seasons of oystercatchers on Robben Island.

Appendix 5.4: Details of the oystercatchers' nests predated and the timing of nest predation by Mole Snakes during the 2017 and 2018 breeding seasons on Robben Island

Nest ID	Clutch size	Nest age	Date	Time*	Temp**	Egg1 measurements			Egg2 measurements		
						M	B	L	Mass	B	L
B17012	2	14.5	7/12/17	16:57	37.1 (35.1)	61.9	43.0	63.4	58.8	42.6	61.7
B17031	2	26	2/01/18	09:53	23.2 (16.8)	51.7	43.1	59.5	56.7	42.2	61.5
B17074	2	18	16/01/18	18:43	31.0 (23.1)	63.6	43.2	64.8	58.6	43.2	64.0
B17111	1	1	19/01/18	17:01	26.9 (24.0)	60.2	42.5	62.0			
B18014	1	1	27/11/18	10:35	21.0 (13.7)						
B18138	1	22	26/02/19	11:10	23.8 (19.8)	56.6	42.3	60.2			
B18107	2	19	28/01/19	14:38	35.9 (34.4)	56.9	41.7	61.9	56.7	41.6	62.8

*Time = the start time of the predation event (South African Time +2:00 GMT), ** Temp = the value outside the bracket represents the maximum air temperature ($^{\circ}\text{C}$) on the day the predation event occurred (the value in the bracket represents the air temperature ($^{\circ}\text{C}$) at the start of the predation event extracted from temperature logged every five minutes by SAWS). For egg measurements: m = mass of egg in grams, B= breath of egg in mm, L= length of egg in mm. The egg in B18014 got predated before it could be measured.



Appendix 5.5: One of the nests where predation by Mole Snake occurred outside of the camera monitored ones. A Mole Snake was hiding as the observer approached (panel A). A zoomed image of the Mole Snake later observed in the nest (panel B). A broad view of the nesting habitat of the oystercatchers showing the snake in the nest (panel C). The red arrow in A point to the Mole Snake while those in C point to the snake in the nest



Appendix 5.6: A Mole Snake hiding and blending in with dried kelp. This snake was observed a few meters from an active oystercatcher nest which it later predated.



Appendix 5.7: A Mole Snake observed to be escaping from a nest which was previously found to be active, which had now been predated.

Appendix 5.8: The application of the daily nest survival analysis in Program Mark to compare candidate models using the data analysed in this chapter (The same variables highlighted as important by the binomial model are present in the two top models (the ones with the highest eights, highlighted in bold below) from the nest survival analyses.)

Candidate models	k	AICc	Δ AICc	weight	Deviance
S(~Day9 + MSLD + I(MSLD^2) + Clutch + DTENV + I(DTENV^2) + Temp + I(Temp^2) + Season)	7	786.89	0.00	0.52	772.87
S(~Day9 + MSLD + I(MSLD^2) + Clutch + DHWL + I(DHWL^2) + DTENV + I(DTENV^2) + Temp + I(Temp^2) + Season)	8	787.39	0.50	0.40	771.36
S(~Day9 + MSLD + I(MSLD^2) + Clutch + DHWL + I(DHWL^2) + DTENV + I(DTENV^2) + Season)	7	791.31	4.42	0.06	777.29
S(~Day9 + MSLD + I(MSLD^2) + Clutch + DHWL + I(DHWL^2) + Temp + I(Temp^2) + Season)	7	793.14	6.25	0.02	779.12
S(~MSLD + I(MSLD^2) + Season)	3	837.03	50.15	0.00	831.03
S(~MSLD + I(MSLD^2) + DHWL + I(DHWL^2) + Season)	4	839.00	52.12	0.00	830.99
S(~Day9 + I(Day9^2) + Temp + I(Temp^2) + Season)	4	845.53	58.65	0.00	837.53
S(~Time + I(Time^2) + Season)	4	846.23	59.35	0.00	838.23
S(~Time + I(Time^2) + Season)	4	846.23	59.35	0.00	838.23
S(~Day9 + I(Day9^2) + Season)	3	854.37	67.48	0.00	848.36
S(~Temp + I(Temp^2) + Season)	3	870.86	83.98	0.00	864.86
S(~1)	1	874.31	87.43	0.00	872.31

K= number of parameters in the model, AICc = Akaike's information criterion for small samples and Δ AICc = adjusted AICc relative to the best model, weight = Akaike weight (a measure of the relative support for each model). MSLD= distance of nest to nearest Mole Snake location, Clutch= number of eggs in a clutch, DTENV=distance of nest to the vegetation above it, DHWL= distance of nests to the mean high watermark, Temperature = maximum air temperature during the exposure period of each nest. Season = breeding season, Day9= clutch incubation start date standardized as the number of days since the start of the breeding season (1 September).

Chapter Six: Population size, breeding parameters and predictors of breeding success of African Black Oystercatchers on Robben Island



Abstract

An understanding of the current breeding parameters of African Black Oystercatchers *Haematopus moquini* (oystercatchers) on Robben Island, South Africa was needed to assess and guide management decisions in relation to previous interventions and current threats. This study examined the population and breeding parameters of oystercatchers using counts of adults and breeding data from three breeding seasons (2016–2018) on the island. An average of 498 ± 12 (418–585) individuals were counted per breeding season, from which 146 (138–160) pairs attempted to breed. A total of 492 breeding attempts were discovered across the three breeding seasons from which 474 (96.3%) were monitored: 42.4% (201 of 474) hatched at least one chick while 57.6% (273 of 474) failed (predated, washed away by wave-driven storm surge, damaged, abandoned, affected by other wildlife, or destroyed by a child). The probability that a nest would produce a chick was lowest in the section of the island with the highest human use and directly proportional to the daily maximum air temperature during the exposure period of a nest and increased with increasing distance from a Mole Snake *Pseudaspis cana* location (an important nest predator of oystercatchers' nests). Nest success was highest for nests located between 10–20 m from the mean high watermark (an area which increases a nest vulnerability to being washed away by storm surges and predation). Pairs which laid larger first clutches early in the season had the highest probability of producing a juvenile in a season. Re-nesting attempts experienced low breeding success, and most pairs did not re-nest after a failed first attempt. The average number of fledgelings per pair per season was 0.38: close to the 0.35 fledgeling per pair per season required to maintain a stable population. A comparison of the findings from this study with that of previous seasons indicates an increase in the number of adults, breeding pairs and number of nests laid in a season. This study updates the knowledge of the current population size and breeding parameters of the oystercatchers on Robben Island, therefore providing helpful information to guide management decisions.



6.1 Introduction

The study of daily nest survival (the probability of a nest surviving to the next day), hatching success (defined here as the likelihood that a nest would produce at least one chick), and overall breeding success (defined here as the likelihood that a pair would produce at least one juvenile in a given season, even if it takes more than one nesting attempt) are crucial components in the breeding biology of birds (Dinsmore et al. 2002; Andes et al. 2019; Zhao et al. 2020) because they contribute to the understanding of patterns of avian population dynamics (Newton 2007). Factors that are important to the nest survival and productivity of species need to be reliably quantified because managers need to put measures in place to protect species that are vulnerable either due to their small population sizes, low fecundity, small geographical range or increased exposure to the risk of extinction (Pincheira-Donoso & Hunt 2017; Andes et al. 2019) by making effective conservation decisions (Jehle et al. 2004; Smith & Wilson 2010; Zhao et al. 2020).

Daily nest survival rates of birds can be influenced by diverse factors including predation, poor weather, human disturbance, habitat quality, amongst others, which have the potential to destroy nests at some stage before the completion of the incubation process (for precocial birds) and also nestling process (for altricial birds) (Shitikov et al. 2012, 2019; Hötter & Segebad 2017; Plaschke et al. 2019). The longer the incubation period of a bird, the longer the duration of the exposure of its nest to these potential risk factors (Martin 2002). Parent birds are thus expected to site their nests in such a way that they minimise their exposure to these risk factors (Smith et al. 2007; Mainwaring et al. 2014).

The overall breeding success of birds may be influenced by the same factors which predict daily nest survival. For example, if the predators which limit the daily survival of eggs also limit the survival of chicks, the activity of such a predator would likely influence both daily nest survival and overall breeding success (Kearns & Rodewald 2017; Mason et al. 2018). However, the ability to breed again after a failed attempt, thereby potentially increasing the overall number of eggs laid in a given season could increase the chance that a pair will fledge at least one young in a season (Griebeler et al. 2010; Morrison et al. 2019). But the success of a renesting attempt may depend on the seasonal conditions: if breeding conditions remain stable or improve as the season advances such that the probability of successfully raising a young is constant or greater later in the season, renesting attempts

should enhance the overall breeding success (Morrison et al. 2019; Jones et al. 2020). However, if breeding conditions deteriorate as the season advances, a renesting attempt may be less rewarding (Swift et al. 2020).

Until recently, modelling the predictors of nest survival was cumbersome (Jehle et al. 2004). This is because testing how nest survival varies over time and as a function of covariates required splitting the data into groups needing large sample sizes before the influence of several factors can be considered simultaneously (Wilson et al. 2007). However, current mark-recapture nest survival analysis implemented in programme MARK (White & Burnham 1999), now enables a rigorous investigation of how daily nest survival rates vary temporally within a season, nest age and with various biological explanatory variables (Dinsmore et al. 2002).

A further common problem for avian nest survival studies is that of nest detectability (Mayfield 1961) because birds conceal their nests to avoid making them conspicuous to predators (Martin 1993b; Cresswell 1997a; Wilson et al. 2007). The implication of this nest hiding behaviour for finding and monitoring avian nests is that nests which have survived for a longer period and nearing their hatch date (for precocial birds) or fledging date (for altricial birds) are more likely to be found (Mayfield 1961; Johnson 1979). On the other hand, the nests which were initiated by individuals within the same population but failed early may go undetected and unaccounted for thereby leading to an exaggerated estimation of nest success for the study population (Mayfield 1961, 1975).

However, Johnson & Shaffer (1990) noted that this detectability bias might be study-system specific as populations of birds breeding on islands or in nest boxes, for example, may have higher detectability such that most nests may be found as they are being initiated compared with populations whose nests are hidden in shrubs scattered over large mainland areas. In large areas such as mainland sites, it could be difficult to search frequently and intensively enough to find all nests as they are initiated (Johnson 1979; Johnson & Shaffer 1990). In contrast, the nests of bird populations using nest boxes and on islands may have high visibility making it highly likely that with multiple nest searches repeated at frequent intervals most nests would be found and found closer to when they were initiated. This idea seems to hold for the African Black Oystercatchers *Haematopus moquini* (hereafter oystercatchers) on Robben Island where their natural breeding habitat is the land-sea

boundary of the island. They lay their eggs in scrapes made in the bare area immediately above the mean-high watermark and before the start of vegetation. The oystercatchers, like other ground-nesting birds, rely on camouflage such that their egg-contrast matches the surroundings of the scrapes in which they are laid (Hockey 1982; Troschianko et al. 2016). However, the open nature of the nesting area (without vegetation), the conspicuousness of the incubating oystercatchers and their behaviour, coupled with multiple nest searches conducted at regular intervals makes it likely that most of their nests would be detected not long after they are initiated (Klett & Johnson 1982). This likelihood has been the explanation for the expectation that all nesting attempts by oystercatchers on Robben Island are discovered by researchers (Tjørve & Underhill 2008). The distribution of the ages of nests when first found by researchers is usually an indicator of the presence or absence of the detectability bias within a dataset (Klett & Johnson 1982; Johnson & Shaffer 1990). If the ages of most of the nests found are skewed to the right (i.e., closer to their hatch dates when first found) then the dataset has detectability bias but if the age of the nests is skewed to the left (i.e., most nests found soon after they were initiated) then the data are not biased. (Johnson & Shaffer 1990). Also, if a dataset shows a positive correlation between the ages of nests when first found and hatching success the dataset likely contains detectability bias (Johnson 1979), because long-surviving nests found closer to their hatching date would be less likely to fail as they would only need to survive for a few more days before they hatch (Klett & Johnson 1982).

The oystercatchers on Robben Island increased from 40 individuals in 1977 to 149 in 1998 (Underhill et al. 2001) and further experienced a 2.5-fold increase in population size from an average of 126 individuals in 2001 to 345 in 2012 (Spiby 2012). Since the 2004 breeding season, there has not been an estimation of the breeding population size nor the number of fledgelings per pair, and the current breeding population size and breeding success of oystercatchers on the island are unclear. Given the management intervention of controlling the cat population following a very poor breeding season in 2004 (Braby & Underhill 2007; Spiby 2012), increasing population size (Tjørve & Underhill 2006; Spiby 2012), climate change-induced summer storminess which washes nests away (Calf & Underhill 2005) and predation by Mole Snakes *Pseudaspis cana* (Chapter Five), an understanding of the current

breeding parameters of the oystercatchers on the island is needed to assess and guide management decisions.

In this chapter, I examine the following questions: how many pairs of oystercatchers currently breed on Robben Island; how many nests are there; of these how many produced at least one chick in the breeding seasons 2016 –2018? What caused the failure of the nests which did not produce at least a chick? What factors make a nest more likely to survive until hatching? Finally, how many pairs fledged at least one young and what factors make a breeding pair more likely to fledge at least a single juvenile in a breeding season? The answers to these questions were evaluated relative to previous estimates (Tjørve 2006; Braby & Underhill 2007; Spiby 2012) to assess the current size and productivity of the population of oystercatchers on the island.

Since predation is an important cause of the failure of oystercatchers' nests as other ground-nesting shorebirds (Teunissen et al. 2008), the factors which increase nest predation (proximity of nests to an area of high predator activity) were expected to decrease nest survival while those which decreased nest predation (e.g., high air temperatures) (Chapter Five) should increase daily nest survival. Since human disturbance can negatively impact avian nest survival through physiological stress to incubating adults and exposure of nests to potentially harmful solar radiation when flushed from their nests (Leseberg et al. 2000; McGowan & Simons 2006; Sabine et al. 2006), it was predicted that nests located in areas with high human use would have a decreased nest survival. Since oystercatchers' nests are vulnerable to wave-driven storm surges which could wash them away (Hockey 1983b; Calf & Underhill 2005; Schmechel & Paterson 2005), it was predicted that nest survival rate would increase with distance from the mean high watermark because the risk of a nest being washed away by storm surge should increase with proximity to the ocean (Bailey et al. 2019). Because predation of oystercatchers' nests increases temporally (Chapter Five), it was anticipated that the probability of fledging at least a juvenile in a season would decrease as the season advances, but, an increased overall number of eggs laid in a season may improve overall breeding success (Griebeler et al. 2010).

As a methodological contribution and support for the binomial analytical method used in Chapter Five, and the predictors of overall breeding success in this chapter, the predictors of daily nest survival were examined using both a binomial regression method, that does not

account for biases due to detectability, and the standard mark-recapture nest survival method in programme MARK (White & Burnham 1999; Dinsmore et al. 2002) that does. The outcomes from both analyses were compared to test whether both methods produced similar results in the absence of the bias associated with finding most nests in an advanced stage of incubation (Johnson & Shaffer 1990). It was expected that the distribution of the ages of the nests when first found would be skewed to the left (i.e., most nests found soon after they were initiated), that the ages of nests when first found would not be correlated with hatching success and that both statistical approaches (binomial regression method and Programme MARK) would yield similar outcomes. If these expectations are met, it would suggest that most nests were found soon after initiation and that the detectability bias was minimised as would be expected given the breeding habitat, size and behaviour of the oystercatchers as well as the repeated nest searches at regular intervals by the researcher (Klett & Johnson 1982; Johnson & Shaffer 1990).

6.2 Methods

6.21 Human disturbance

Robben Island is renowned for its cultural and historical heritage and was declared a World Heritage Site in 1999 (UNESCO World Heritage Committee 2003) and receives several thousand tourists annually (Robben Island Museum 2017). Although tourists' access is restricted to certain areas within the island, some of the areas used by tourists overlap with the breeding habitats of the oystercatchers and potentially cause disturbance to those incubating eggs. The area of coastline labelled Section A in Figure 6.1 experiences the largest levels of human use as the residential area and most of the stop points for tourists are in this section of the island.

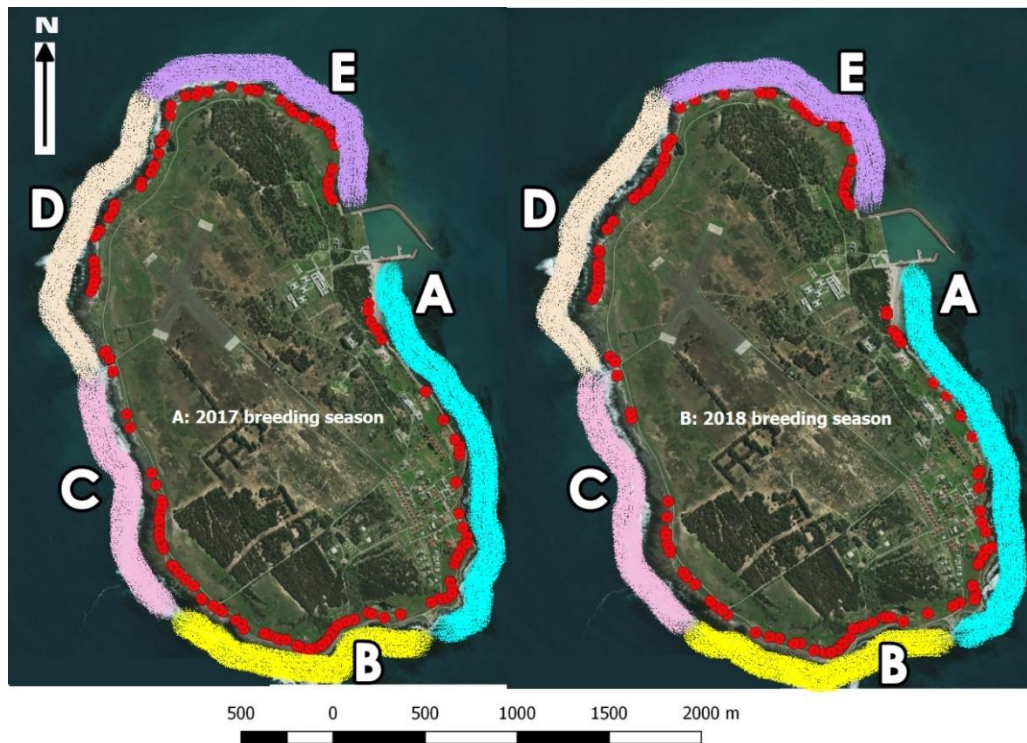


Figure 6.1: The map of Robben Island showing the nest locations of the oystercatchers in 2017 (red dots on the map to the left) and 2018 (red dots on the map on the right), as well as the different locations within the island, classed according to levels of human use from high to low A, B, C, E, D (5,4,3,1,2). The groupings were made using existing landmarks on the island and the levels of human use and presence within each section of the island.

6.22 Estimating the numbers of adult oystercatchers and breeding pairs

A monthly survey of adult oystercatchers was made in 2016 (between September 2016 and April 2017), 2017 (between November 2017 and May 2018) and 2018 (between November 2018 and April 2019) breeding seasons. The survey entailed walking the entire coastline of the island during high tide to count every adult oystercatcher observed. The count was done during high tide to maximise the chance of counting 'all' the adults present. This is because, during high tide, they are forced to come into the open and narrow area between the high tide watermark and vegetation above it. This contrasts with low tide time when many are hidden behind rocks over a wider intertidal zone. The average number of adult oystercatchers recorded during the monthly counts for each breeding season was used as the estimated number of adults (including both breeding and non-breeding birds) on the island in each season. The breeding population size per season was estimated as the total number of pairs on whose territory at least one breeding attempt was discovered either as eggs or fledgelings.

6.23 Finding nests, ageing, and monitoring them to failure or success

From the beginning of each breeding season of 2016, 2017 and 2018, the entire coastline of the island was searched to find the nests of oystercatchers. Most of the nests were observed as empty scrapes which were monitored on subsequent visits for the presence of eggs. The scrapes were recorded as active nests when they contain at least one egg. When an active nest was found the nest and its contents were uniquely marked by using a black marker pen to write an identity number on a stone nearby the nest and the nest location stored on a handheld Global Positioning System (Garmin GPSMAP 64st). The dimensions and mass of eggs were taken and based on the principle that eggs, in general, lose about 16% of their mass during incubation, due to water loss (Ar & Rahn 1980), the dimensions and mass measurements were used to estimate the incubation start date of the eggs in a nest (Green 1984). This was done by inputting the dimensions and mass measurements into the equation of the rate of weight loss derived specifically for the population of the oystercatchers on Robben Island (Underhill & Calf 2005). This method enabled the age of the nest to be determined to an accuracy of about 1–3 days, especially when found soon after nest initiation (Underhill & Calf 2005). The estimated date of start of incubation of the clutch was calculated by counting days backwards, starting from the date the nest was first observed (Underhill & Calf 2005). Nest age was determined as the difference in days between the date incubation started and the day the nest was found. The predicted number of days until hatching for each nest was calculated as the average incubation period of the oystercatchers (30 days (Hockey et al. 2005; Tjørve 2006)) – nest age when found.

New nests were searched for, and old ones monitored at intervals of 3–7 days, except a few occasions when weather interrupted a scheduled trip to the island. Nests nearing their hatching date were monitored more frequently. The fate of the clutches was recorded as hatched if chicks or eggshells were seen in and around the nests or when parents exhibited aggressive chick guarding behaviour. Nests were recorded as predated if the predation event was witnessed, captured on camera, broken eggs observed in or near a nest or when eggs disappeared before their estimated hatch date and when parents did not display any chick guarding behaviour. Nests were recorded as being washed away if the nest location were covered with freshly washed-up kelp (in some cases the eggs could be seen displaced from the nests and covered with kelp). Nests were recorded as damaged when eggs looked

dried, cracked, and inviable. Nests were scored as abandoned when eggs were cold and unattended by parents for two or more visits and failed to hatch after being monitored for about 30 days or more (the usual incubation period of oystercatchers). The nests that were scored as hatched by parent behaviour were later confirmed in subsequent visits when chicks or juveniles were seen in the territory. Nests scored as depredated were later confirmed as truly depredated (rather than hatched) when subsequent visits revealed a renesting attempt, or when no chicks were found, and the parents continued to show no sign of guarding chicks.

Clutch size was determined as the number of eggs in a nest, usually confirmed during a second monitoring visit for most nests. Nesting attempts were recorded as 'first' if the nest was the first to be observed in a territory, 'second' if a second nest is found within a territory where the first nest had failed. Nests were recorded as a 'third' attempt when it was found in a territory where the first and second nests have failed. The replacement nests are usually in the same nest scrapes or few meters from those where the previous attempts were sited. Some of the adults were ringed, which helped confirm the identity of pairs with replacement nests.

6.24 Monitoring chicks to fledging

Territories, where at least a chick was hatched, were monitored weekly. Chicks were considered active if they were seen in the territory or if their parents exhibited aggressive chick guarding behaviours (Tjørve 2006). The pairs on whose territories any juvenile capable of flying was found was considered to have fledged a juvenile (Parsons 2006). The chicks usually hide and camouflage in the washed-up kelp when they are still young and unable to fly. But when they are capable of flying, they stand by their parents in the open and fly away if they perceive any threat. Chicks were considered dead/predated if dead chicks were observed in or around the nests, or if the parents were present in the territory but were non-aggressive during at least two to three visits and if no chick or fledgeling was ever observed again (Tjørve & Underhill 2008; Tjørve & Tjørve 2016). The number of nests which produced at least a juvenile from a season was considered as the sum of the number of territories where at least a juvenile was observed at any point during the monitoring visits for that season. The total number of juveniles was the sum of the highest number (mostly 1 and sometimes 2) of the juveniles found on each territory. In the 2017 breeding season, 2%

(4 of 161) of all nesting attempts were discovered post the egg-stage and were included in the total number of fledgelings for that season.

6.25 Data collection (predictors of nest survival and overall breeding success)

Human disturbance: I categorised sections of coast according to the levels of human presence and use (Figure 6.1). The vulnerability of a nest to predation was measured as the distance of a nest to any location within the island where a Mole Snake has been observed during nest monitoring visits or where predation by a Mole Snake had occurred (Chapter Five). The temporal index was measured as the clutch incubation start date for each nest converted to Julian days starting from September 1 (the month in which the earliest nest was found). The daily maximum air temperature during the exposure period of each nest and over the hatch date to fledging or failure date of chicks were extracted from the weather data provided by the South African Weather Services (SAWS). SAWS recorded data through a weather station on the island. The distance of nests to the mean high watermark below it was measured as an index of vulnerability to destruction by wave-driven storm surges. Distance measurements were taken only in the 2017 and 2018 seasons using the FIND function on a Garmin GPSMAP 64st handheld GPS unit, a laser range finder (Nikon, LASER 550) or a 10-meter tape measure for distances less than 10 m.

6.25 Data analysis

Nest age, days until hatching and binomial regression analysis

Abandoned nests and nests with unknown fate were excluded from both the binomial and the survival analyses as most abandoned nests were not truly confirmed as abandoned nests until they had been monitored for about 30 days or more and failed to hatch. So, the 'death date' was not really known and including them in the survival analysis may bias the results because it would suggest that the nests had survived for as long as hatched nests. Hatching success (hatch =1, fail =0) was modelled as a function of nest age using a binomial model to test the assumption that detectability bias should not be a significant confounding effect because most nests could be detected soon after clutch initiation, given the open breeding habitat and conspicuousness of nesting oystercatchers as well as the repeated nest searches at repeated intervals by the researcher (Johnson & Shaffer 1990). If longer surviving nests were more likely to be found and monitored, one would expect that nest age when found would be positively correlated with hatching success (Johnson 1979). This

positive relationship should arise for nests found in their advanced incubation stage by chance because if there is a constant daily probability of failure, nests found in their advanced incubation stages would be less likely to fail because they have fewer days to survive before they hatch (Klett & Johnson 1982). The number of days until hatching was therefore included in the binomial model exploring the relationship between hatching success and all the potential predictors tested. An interaction term between the number of days until hatching and each of the explanatory variables tested (specified in the model structure below) was included in the full model. If the interactions were significant so that there was a steeper gradient for earlier nests, then this would indicate that there was a detectability bias and nests that were more likely to succeed were found. Also, the distribution of the ages of the nests when first found as well as the comparison of the results from the binomial regression method, that does not account for biases due to detectability, and the standard mark-recapture nest survival method in programme MARK that does (White & Burnham 1999; Dinsmore et al. 2002) were used to assess the vulnerability of the oystercatcher breeding data to detectability bias as explained in Section 6.1.

The full model was: Hatching success (hatch =1, fail =0) ~ the number of days until hatching (continuous) + nest attempt (factor of three levels: first, second or third attempt) + location of a nest with respect to the level of human use (factor of five levels as in figure 6.1) + daily maximum air temperature during the exposure period of each nest (continuous) + distance of a nest to a Mole Snake location (continuous) + distance of a nest to the mean high watermark (continuous) and its quadratic term + breeding season (two-level factor: 2017 or 2018) + the two-way interaction term between each of these variables and the number of days until hatching.

The quadratic term of the distance of a nest to the mean high watermark was added to the model because it was anticipated that there would be an optimum distance which would favour nest success (Benvenuti et al. 2018; Chapter Two). This is because oystercatchers may need to balance the placement of their nests away from the ocean to reduce the risk of being washed away against being closer to the vegetation which could increase nest predation risk (Ma et al. 2019; Chapters Two & Five).

The best binomial model was arrived at by removing the variables that were not significant at $p=0.05$, starting with the interaction terms. The regular Akaike's information criterion (AIC) values of all the models explored was compared, and the model with the lowest AIC was selected as the best. The full and best models are presented in Appendix 1.

Daily nest survival analyses

Daily nest survival was estimated and analysed (using the exact data set used in the binomial model above) through the nest survival approach in programme MARK (White & Burnham 1999; Dinsmore et al. 2002) using the RMark package (Laake 2013). September 26 was standardised as day one of the nesting seasons for both seasons analysed (because Programme MARK requires that the date on which the first nest of the season was found be standardized as day one (Dinsmore et al. 2002)). The fate of nests was scored as 0 = successful, 1 = failed (predated, damaged, or washed away by storm surge). The daily nest survival rate of the oystercatchers was modelled as a function of the variables in the full binomial model specified above. Multiple candidate models (Appendix 2) exploring the relationship between daily nest survival and various combinations of the explanatory variables were tested and ranked by AICc. The model with the smallest AICc was considered as the best model (Dinsmore et al. 2002). The logit-link function was used for all models. The best model from both the binomial method and the survival model from programme MARK are presented. The nest survival estimates for the different nest attempts and seasons were extracted from program Mark and raised to the power of 30 to calculate the probability that a nest would survive 30 days of incubation to produce at least one chick (Johnson 1979).

Predictors of fledging success

To determine which factors influence whether a breeding pair would fledge a young in a given season, the probability of a breeding pair producing at least a fledgeling in a season was modelled using a binomial model utilising only the data from the first clutches. This is because the probability of fledging a juvenile in a season irrespective of the number of attempts relates to breeding pairs and not nests. Using only first clutches ensured that each breeding pair was considered only once in the analysis.

The full model was: Fledging success (fledged at least a juvenile even if it took more than one attempt = 1, did not fledge any chick from all attempts = 0) ~ clutch size of first nesting

attempt (continuous) + the incubation start date of the first nesting attempt (continuous) + location of nests with respect to the levels of human use (five-level factor: A, B, C, D or E as in figure 6.1) + breeding season (two-level factor: 2017 or 2018).

The number of fledgelings per breeding pair was calculated as the total number of fledgelings found in a season divided by the total number of breeding pairs in that season (Tjørve 2006; Tjørve & Underhill 2008). This method was used by previous studies on Robben Island oystercatchers (Braby & Underhill 2007; Tjørve & Underhill 2008). Hence using the method would enable comparisons to be made with historical estimates of the number of fledgelings per pair per season. All analyses were implemented in the R statistical software (R Core Team 2019).

6.3 Results

6.31 The numbers of adult oystercatchers and breeding pairs

The average number of adults on the island from six surveys each in 2016, 2017, and 2018 breeding seasons are presented in Table 6.1. On average, the adult population size of oystercatchers on the island during the three breeding seasons studied was about 500 individuals.

6.32 How many nests were found, what were their fate and how many produced at least a chick?

A total of 492 breeding attempts were discovered across the three breeding seasons (Table 6.1) out of which 474 (96.3%) were monitored sufficiently to determine success or failure. The main outcomes of the nests monitored were: abandoned 3.6% (17 of 474), damaged 2.3% (11 of 474), washed away by wave-driven storm surge 6.5% (31 of 474), predated 44.5% (211 of 474), hatched at least one chick 42.4% (201 of 474) (Figure 6.2).

Table 6.1: The number of breeding pairs, attempts and the clutch size distribution of oystercatchers during the 2016, 2017 and 2018 breeding seasons on Robben Island

Breeding pairs	2016	2017	2018	Overall
Average number of adults on the island*	503±20 (430–573)	499±27 (439–585)	492±19 (418–547)	498±12 (418–585)
Number of breeding pairs	160	139	138	146 (138–160)
Percentage attempting to breed	63.6% (320 of 503)	55.7% (278 of 499)	56.1% (276 of 492)	58.5%
Nesting attempts				
Number of first clutches	160	135	138	433
Number of second clutches	17	20	14	51
Number of third clutches	1	2	1	4
Found as chick and monitored to fledgeling	0	1	0	1
Sum of monitored attempts	178	158	153	489
Found as fledgling	0	3	0	3
Overall total	178	161	153	492
Probability of producing at least one chick#		0.44	0.34	
Clutch size				
One-egg clutch	40	30	36	106
Two-egg clutch	128	119	111	358
Three-egg clutch	10	9	6	25
	178	158	153	489

*mean, standard error and range are presented #2016 breeding season is blank because not all the nests found in 2016 were monitored sufficiently to enable a reliable estimate of daily survival rates.

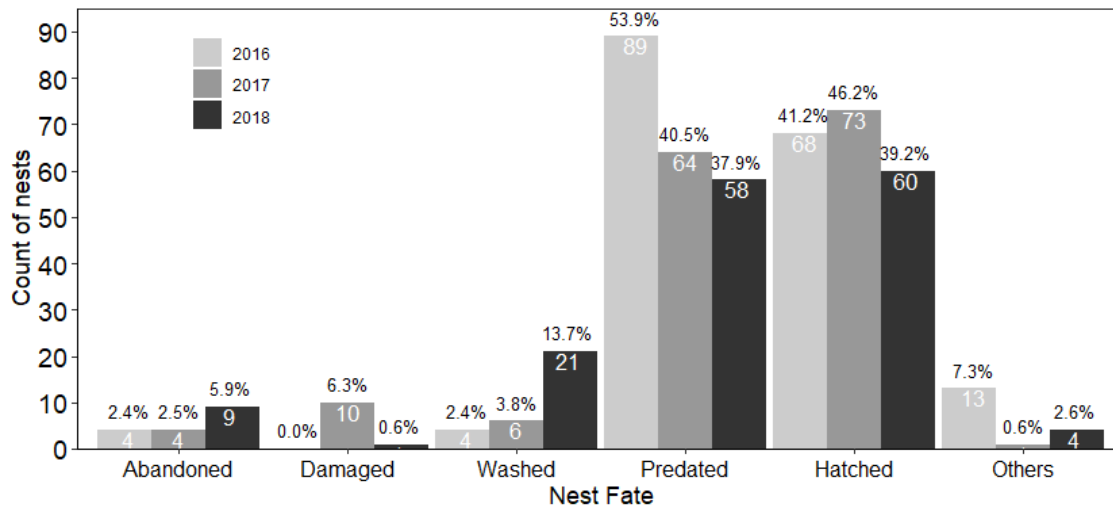


Figure 6.2: The fate of the nests found during the 2016, 2017 and 2018 breeding seasons on Robben Island. 'Damaged' represents nests where all the eggs failed because the shell looked abnormal and was glued to the embryos. 'Washed' represents nests which failed because they were displaced or completely washed away by wave-driven storm surges. 'Hatched' represents nests which produced at least one chick. 'Others' in 2016 represents 13 nests which formed 7.3% of the 178 nests found in 2016 which were not monitored to success or failure. 'Others' in 2017 represents a nest where a child was observed picking up the two eggs in the nest. 'Others' in 2018 represent 4 nests: two could not be monitored to the end to avoid disturbing other breeding birds as Swift Terns *Thalasseus bergii* later established a huge breeding colony around the nests, one was displaced by a group of Cape Cormorants *Phalacrocorax capensis*, and another appeared to have been affected by a Steenbok *Raphicerus campestris*.

6.33 Predictors of daily nest survival

Of the 311 nests found in 2017 and 2018 breeding seasons, 288 were included in the analysis of daily nest survival (the others were excluded because they were abandoned, of unknown fate or have incomplete explanatory variables). The date when the first nest was found and the date when the last nest hatched or failed for both years was 26-September and 25-March, respectively making a total of 180 days of observation per season. Daily nest survival rates were therefore estimated for 179 days. The overall exposure days of all nests included in the analysis for both years was 4987. Of the 288 nests included in the analysis 133 (46.18%) hatched at least one chick while 155 (53.82%) failed. Of the 155 nests which failed, 118 (76.13%) were due to predation, 27 (17.42%) were washed away by storm surge, and 10 (6.45%) were damaged. Of the 288 nests, 253 (87.50%) were from first nesting attempts, 33 (11.46%) were from a second attempt, and three (1.04%) were from a third attempt. Fifty-eight (20.14%) of the 288 nests included in the analysis contained one egg, 215 (74.65%) contained two eggs, and 15 (5.21%) contained three eggs.

Was nest age or days until hatching a significant predictor of nest survival probability?

Of the 288 nests included in this analysis, 155 nests (53.8%) were found when they were between 0–5 days old, 73 (25.35%) were found at ages between 6–10 days old, 31 (10.76%) were found when they were 11–15 days old, 20 (6.9 %) were found between ages 16–20, 6 (2.08%) were found when they were 21–25 days old, and 3 (1.04) were found when they were between 26–31 days old (Figure 6.3).

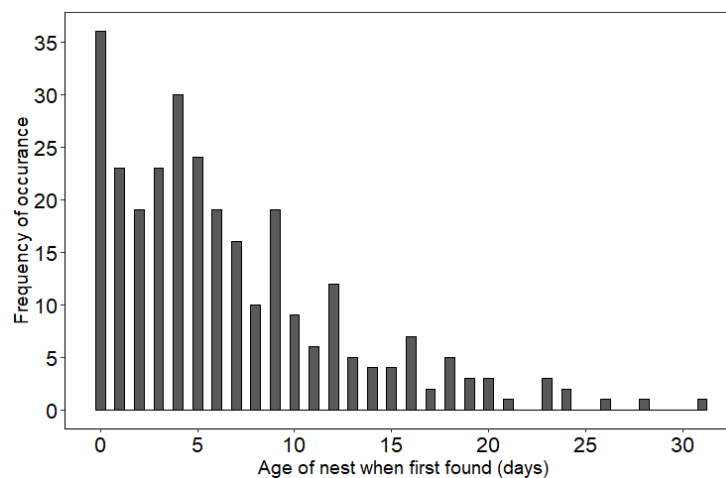


Figure 6.3: The distribution of the ages of nests when they were first found during the 2017 and 2018 breeding seasons on Robben Island.

Nest age when found was not significantly related to hatching success of the oystercatcher nests ($\beta = -0.0025$, $SE = 0.019$, $p = 0.90$). Similarly, the number of days until hatching was not significantly related to hatching success ($\beta = 0.0025$, $SE = 0.020$, $p = 0.90$). The full binomial regression model identified the interaction between the number of days until hatching and location D (the area with the least human disturbance on the island) as the only significant interaction term (Appendix 6.1).

What factors significantly predicted daily nest survival?

The best models from the two methods (binomial and nest survival model in program MARK) yielded similar outcomes and retained the same set of variables (Table 6.2). Daily nest survival increased with daily maximum air temperature and distance of nests from a Mole Snake location but had a quadratic relationship with the distance of nests to the high watermark (Table 6.2; Figure 6.4, Panels A–C). Nests that were located between 10–20 m from the mean high watermark had over 65% chance of surviving the incubation period to produce a chick compared with those closer or further away (Table 6.2; Figure 6.4, Panels A–C). The nests located in the area with the highest human use on the island (location A) had the least chance of surviving through the incubation period (Table 6.2; Figure 6.4D).

Table 6.2: Comparing the parameter estimates from the best nest survival model and the binomial model with the lowest AIC value predicting the factors influencing the nest survival probability of oystercatchers on Robben Island in the 2017 and 2018 breeding seasons. Sample size = 288 nests

A: Nest survival model with least AIC+ season			B: Binomial model with least AIC + season			
	Estimate	SE	Estimate	SE	z value	P
S: Intercept	-148.62	<0.0000001	-6.81	1.58	-4.30	<0.001
S: MSLD	0.0018	0.00041	0.0025	0.00064	3.81	<0.001
S: DHWL	0.0013	0.011	0.19	0.066	2.88	0.0039
S: I(DHWL^2)	-149.02	<0.0000001	-0.0061	0.0021	-2.91	0.0036
S: Temperature	0.17	0.027	0.13	0.045	2.90	0.0037
S: Location B	0.84	0.22	1.22	0.43	2.80	0.0051
S: Location C	0.77	0.25	0.90	0.47	1.89	0.058
S: Location D	1.04	0.26	1.24	0.43	2.86	0.0042
S: Location E	0.64	0.22	0.94	0.45	2.09	0.037
S: Season 2018	0.15	<0.0000001	0.19	0.30	0.64	0.52

Significant p-values are in bold. Location A and 2017 season take the value of the intercept. MSLD= distance of nest to nearest Mole Snake location, DHWL= distance of nests to the mean high watermark, Maximum temperature = maximum temperature during the exposure period of each nest.

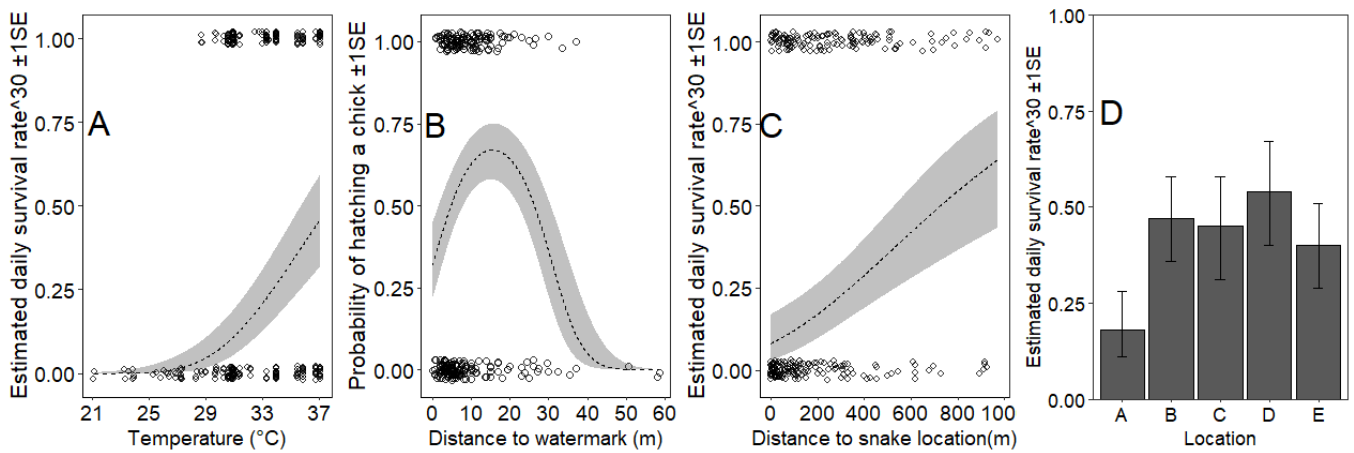


Figure 6.4: The predicted relationship between the maximum air temperature during the exposure period of a nest (Panel A), the distance of a nest to the mean high watermark (Panel B), the distance of a nest to a Mole Snake location (Panel C) and the probability that a nest would survive 30 days of incubation to produce at least one chick. The predicted differences in the probability that a nest would survive 30 days of incubation to produce at least one chick among sections of the island with different levels of human use is presented in Panel D. The predicted values in Panels A, C, and D were plotted from the daily survival estimates from the model in Table 6.2A, while B was plotted from the binomial model in Table 6.2B for 2017 and location D while mean values were set for the other variables. Panel 3B was illustrated from the binomial model and not the nest survival model like the plots in the other three panels because it was easier to illustrate the quadratic nature of the variable ‘distance to watermark’ from the binomial model than from the nest survival model. The circles in Panels A–C represent raw data points for the 2017 and 2018 breeding seasons.

6.34 Overall breeding success

How successful were renesting attempts at fledging a juvenile?

Of the number of breeding pairs observed in 2017 and 2018 breeding seasons, 14.4% (20 of 139 pairs) and 10.1% (14 of 138 pairs), respectively made a second attempt after a failed first attempt. Only 1.4% (2 of 139 pairs) and 0.7% (1 of 138 pairs) made a third attempt after a failed second attempt in 2017 and 2018, respectively. Estimates from Programme MARK indicated that the probability of surviving the entire 30 days of incubation to produce a chick was 0.41, 0.23 and 0.12 for the first, second and third nesting attempts, respectively. Of the first clutches from both seasons, 147 failed, and only 34 (23.1%) made a further attempt. Of all 37 replacement nests from both seasons, only five (13.5%) fledged a juvenile.

Of the overall nests which hatched at least one chick, how many produced at least one fledgeling?

Of the total nests which hatched at least a chick in 2017 and 2018 combined, 70% (95 of 136 nests) fledged at least one juvenile. The total number of fledgelings from both seasons were 103 individuals. The average number of fledgelings per pair per season was 0.38 over two seasons. Individual season summary and the number of fledgelings per pair are presented in Table 6.3. In 2016, not all the chicks were followed closely to fledgeling as was done in the subsequent seasons. However, the two largest counts of juveniles were 38 and 62 made on March 17, 2017, and April 21, 2017.

Table 6.3: Productivity of oystercatchers on Robben Island for the 2017 and 2018 breeding seasons

Productivity	2017	2018	Total
Number of nests which fledged at least one juvenile	50	45	95
Total fledglings	54	49	103
Fledgelings per pair (# number of fledgelings/#of breeding pairs)	0.39	0.36	
Fledglings per nest (#number of fledgling/#of nests)	0.36	0.32	

Predictors of the probability that a pair would fledge at least one juvenile in a breeding season

The probability that a pair would fledge at least one juvenile in a given season increased with the number of eggs laid in the first attempt but decreased with the incubation start date of the first nest attempt (Table 6.4; Figure 6.5, Panels A–B). The probability of a pair producing a juvenile in a season was smallest in the section of the island with the highest human use (Table 6.4; Figure 6.5, Panel C).

Table 6.4: Binomial models predicting the factors influencing the probability that an oystercatcher pair would fledge at least one juvenile on Robben Island in the 2017 and 2018 breeding seasons. Sample size = 252 nests

	Estimate	SE	z value	P
Intercept	-0.33	1.12	-0.29	0.77
Incubation start date of 1 st clutch	-0.023	0.0067	-3.50	<0.001
Size of 1 st clutch	0.79	0.34	2.35	0.019
Season 2018	0.070	0.29	0.25	0.81
Location B	0.95	0.46	2.07	0.038
Location C	0.85	0.48	1.76	0.078
Location D	1.18	0.47	2.54	0.011
Location E	0.57	0.47	1.21	0.22

Location A and 2017 season take the value of the intercept.

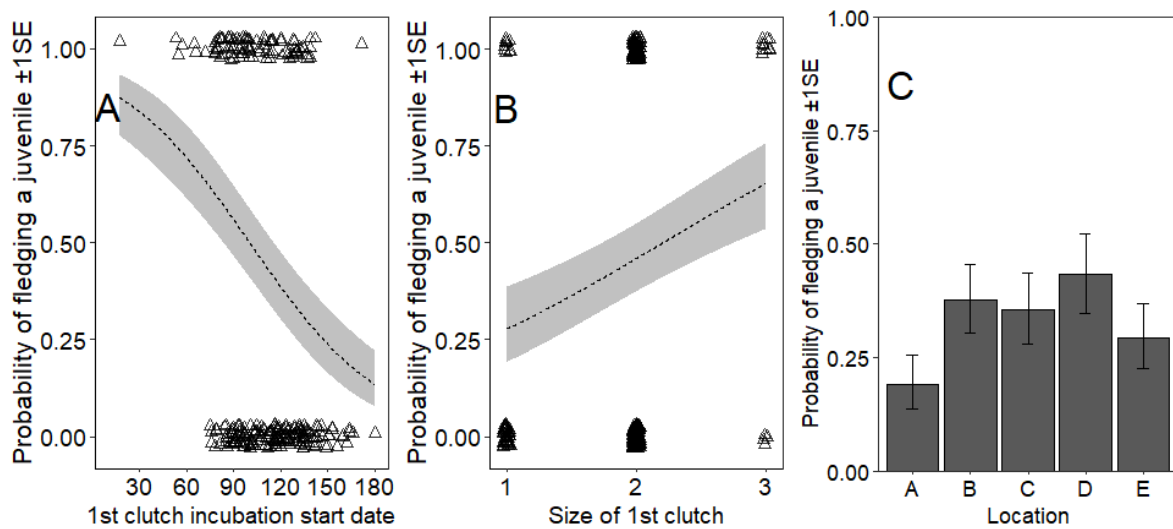


Figure 6.5: The predicted relationships between the incubation start date (as the number of days since the start of the breeding season (1 September)) of first nest attempt (panel A), size of the first clutch (panel B), and the probability that a pair would produce a juvenile in a season. The predicted differences in the probability that a pair would produce a juvenile in a season among sections of the island with different levels of human use (panel C). The predicted values in all panels are from the model in Table 6.4 for 2017. In panels A–B: location was set at D while mean values were set for the other variables in the model; triangles represent raw data points for the 2017 and 2018 breeding seasons.

6.4 Discussion

This study reports a current average of 498 ± 12 (418–585) individual oystercatchers and an average of 146 ± 8 (138–160) breeding pairs on Robben Island and shows that the causes of nest failure are predation, destruction by storm surges which wash nests away, damage of eggs, nest abandonment and the impacts of other wildlife on Robben Island. The results also show that the probability that a nest would produce a chick was influenced by human disturbance, the daily maximum temperature during the exposure period of nests, the distance of a nest to the mean high watermark, and distance to a Mole Snake location. The probability of a pair fledging at least one young in a season was predicted by human disturbance, the timing of the start of the first clutch, and the number of eggs in their first clutch. The average number of fledgelings per pair per season was 0.38.

6.41 Overall population, breeding population and number of nests found

The average (and maximum) number of adults observed for each of the three breeding seasons (Table 6.1) are the highest numbers ever reported for the species on Robben Island so far. The most recent update on the population size of the oystercatchers on the island reports an average of 345 adults between 2001 and 2012 (Spiby 2012). The breeding population size has more than doubled from 64, 68, 49, and 61 breeding pairs in 2001, 2002, 2003 and 2004 breeding seasons, respectively (Tjørve 2006; Braby & Underhill 2007) to 160, 139 and 138 in 2016, 2017 and 2018 breeding seasons. The number of nests observed in this study also represents the highest ever observed since the start of monitoring in 2001. These values indicate an increase from the mean of 74.5 ± 11.01 between 2001 and 2011 breeding seasons (Spiby 2012) and close to the 147 observed in 2013 (Joana Agudo Unpublished data).

These observations show that the population of the oystercatchers has increased significantly since the last updates in 2012. The similarity between the counts of adults and the numbers of breeding pairs for the three seasons monitored in this study suggests that they may be approaching carrying capacity and are beginning to attain stability. The increase in population size on the island has been attributed to reduced human disturbance and increased food availability in the form of Mediterranean Mussels *Mytilus galloprovincialis* (Tjørve & Underhill 2006; Spiby 2012). This population increase is not

limited to Robben Island but also occurs at the global population level (Loewenthal et al. 2015; Brown et al. 2019).

6.42 Predictors of daily nest survival

Daily nest survival and hence the probability of producing a chick, was lowest in the area of the island with the highest level of human presence (Table 6.2; Figure 6.4, Panel D) but increased with daily maximum air temperature and distance of nests from a Mole Snake location (Table 6.2; Figure 6.4, Panels A&C). Nests located between 10–20 m from the mean high watermark had over a 65% chance of producing one chick compared with those closer or further away (Table 6.2; Figure 6.4, Panels A–C). The results from the binomial regression model which did not account for potential biases due to detectability, and the standard mark-recapture nest survival method in programme MARK (White & Burnham 1999; Dinsmore et al. 2002) which did, yielded very similar outcomes (Table 6.2). Furthermore, the age of a nest when it was found was not positively correlated with hatching success and most nests were found closer to when they were initiated. Taken together, these results show that the oystercatchers' breeding data is not being confounded by a detectability bias of finding more longer surviving nests more often than shorter surviving ones (Mayfield 1961, 1975). This is perhaps not surprising given the context of the nesting habitat and the conspicuousness of nesting oystercatchers on Robben Island. This corroborates the suggestion by Johnson & Shaffer (1990) that detectability bias of finding longer surviving nests more than those in early stages of incubation (Mayfield 1961, 1975) may be study-system specific, and be further reduced under multiple visits which are repeated at regular intervals (Klett & Johnson 1982).

Section A of the island (Figure 6.1) is where most of the areas used by tourists and the residential area of the island are located. Hence, there is an increased human presence and activities, such as people sitting, walking, and sometimes children playing along the beach. Section B also experiences some level of human disturbance in the form of vehicles driving past nests and people walking or jogging on the road. Although these human activities are nonlethal, oystercatchers respond to the perceived predation risk by crouching or temporarily moving away to a place that they consider to be safe until the source of disturbance moves away. Oystercatchers located in section A may have experienced reduced probability of hatching at least one chick because of increased levels of human

disturbance which causes incubating birds to frequently flush from their nests (Mcgowan & Simons 2006; Sabine III et al. 2008; Chapter Four). The number of tourists visiting Robben Island during summer when the oystercatchers breed has increased from about 1000 visitors per day in the early 2000s to between 1800–2000 visitors in recent years (UNESCO World Heritage Committee 2003; Robben Island Museum 2017). The increasing tourist numbers mean that the number of people making use of the tourist stop points per time has increased (Robben Island Museum 2017). The number of trips made per day between the harbour and the tourist stop points within Section A of the island by the buses transporting tourists has therefore also increased (Robben Island Museum 2017). This increased disturbance may lead to the departure of incubating parents exposing the eggs to direct solar radiation which may render the eggs inviable (Amat & Masero 2007; Clauser & McRae 2017). Repeated flushing of adults may lead to physiological stress following increased vigilance and crouching to make themselves hidden (Steen et al. 1988; Derose-Wilson et al. 2015; Felton et al. 2018). It may also increase nest predation if predators use the increased activity of incubating adults as a cue to find nests (Jeffery 1987; Martin et al. 2000; Matysioková & Remeš 2018).

Birds may habituate to repeated non-lethal human activities such as the ones from tourists but may find the direct impact of human activities such as potentially trampling or outright taking of eggs (by humans walking or sitting along the shoreline) harder to manage (Mcgowan & Simons 2006). For example, video footage captured some children walking along the shoreline in the section of the island with the highest human use (Figure 6.1, Section A). While some of the children passed by the nest, almost trampling it without knowing, another child saw the nest and picked up the two eggs in the nest. The child walked away with the eggs. Another child was heard in the background, asking that the eggs be returned. However, the eggs were not returned. Section A of the island also had some of the narrowest beaches, and nests in narrow beaches were more likely to fail (Chapter Two). Hence, it is also likely that the smaller breeding success in Section A may have been due to the narrowness of the beach, or perhaps, a combined effects of human disturbance and the narrowness of the beach.

The pattern of nest survival probability observed as air temperature increased may have reflected the importance of temperature on predation rates as temperature changes (Cox et

al. 2013; Oswald et al. 2020). Predation of oystercatchers' nests was very high at moderately high air temperatures probably because of increased Mole Snake activity and the incubation behaviour of oystercatchers which potentially made their nests more obvious (Chapters Three, Four & Five). But a reduced predation probability was observed at very high air temperatures (Chapter Five). This pattern of predation fits the low likelihood of producing chicks at moderately warm temperatures in contrast to an increase at very high temperatures.

However, the pattern may also have been driven by the thermal needs of developing embryos, because, high temperatures may favour proper and prompt embryo development (Hepp & Kennamer 2012; Durant et al. 2013). A quicker incubation process under high temperatures may also reduce the period over which the eggs are vulnerable to predation and other threats (Martin et al. 2007). However, extreme temperature may have adverse post-hatching effects on the chicks (Mueller et al. 2019) and increase the thermoregulation needs of incubating parents (van de Ven et al. 2019; Chapters Three & Four). Also, extended exposure of nests at such high temperatures following disturbance by factors external to the oystercatchers may potentially expose the eggs to thermal risk (Chapter Four).

The increase in the probability of hatching at least a chick with increasing distance from a Mole Snake location signifies the importance of predation as the leading cause of oystercatchers' nest losses (Figure 6.2). It corroborates the findings from several other studies, e.g. Rönkä et al. (2006), Macdonald & Bolton (2008), Teunissen et al. (2008) and Laidlaw et al. (2020) that predation is indeed the primary cause of the nest failure of most shorebirds and therefore constitutes an important selective force on avian populations (Lima 2009).

The high percentage of predated nests in 2016 (Figure 6.2) may have been exaggerated for two reasons, which may also apply to predation estimates for other seasons before 2016. First, the use of cameras to monitor nests (Chapter Five) was implemented in the 2017 and 2018 seasons only and nests which failed for other reasons such as the impact of humans or other wildlife would have been classified as predated if camera evidence did not indicate otherwise. Secondly, some of the observations reported as likely predation by Kelp Gulls *Larus dominicanus* (broken eggs with yolk in or around the nest) may have resulted from trampling by ungulates. Observations of oystercatchers reacting to ungulates, frequent

observations of ungulates roaming the shoreline as well as the comparisons of ungulate numbers and the occurrence of broken oystercatcher eggs with yolk on the island suggest that the ungulates may have had an undetected impact on the breeding success of oystercatchers. The number of nests where broken eggs with yolk were observed on the island declined from 8.2% (12 of 147) in 2013 (Joana Agudo Unpublished data) to only 1.3% (2 of 153) in the 2018 season in a manner which matched a decline in the estimated number of ungulates on the island (Christopher Wilke Unpublished data).

The significant impact of the distance of nests to the mean high watermark may reflect the impact of the risk of losing nests to wave-driven storms (Chapter Two). The vulnerability of the nests of coastal breeding birds to destruction by storm surges and tidal flooding is projected to increase as sea-level continues to rise and the frequency of extreme storm events increases under anthropogenic climate change (van de Pol et al. 2010; Bailey et al. 2017). One of the ways coastal breeding birds could cope with this vulnerability is by choosing optimal nest-sites that minimise the risk of losing their nests to storm surges (Benvenuti et al. 2018; Bailey et al. 2019; Chapter Two). For example, by siting their nests far enough into the beach, they could be putting the nests beyond the reach of the storm surge (Virzi et al. 2016; Chapter Two). The high probability of producing at least one chick from the nests sited between 10–20 m from the mean high watermark and poor success when too close to it confirms that the risk of nests losses to wave-driven storm surges may have decreased with distance away from the mean high watermark. It also highlights an optimum threshold distance where oystercatchers could site their nests to maximise nest success.

However, the choice of an optimal nesting site may be affected by the availability of quality habitat. For the population of oystercatchers on Robben Island, the area between the mean high watermark and the vegetated boundary of the island where they breed is about 17.3 ± 0.80 (1–89) m wide (Chapter Two). This is quite narrow and in some parts of the island the oystercatchers have no chance of choosing an optimum nesting site as the available space between the mean high watermark and the vegetation is less than 10 m and sometimes even as narrow as 1 m or less. African Black Oystercatchers, unlike the European Oystercatchers which breed in more diverse habitats like coastal, inland, grassland and agricultural lands (Buxton 1961; Wilson et al. 2005), are obligate coastal breeders. The population of oystercatchers studied here also differs from European Oystercatchers in not

using the leapfrogging habit method which enables parents to breed in habitats that are further from their feeding grounds and then leapfrog between the two habitats to transport prey items to their chicks (Ens et al. 1992). The reluctance by the oystercatchers to breed in the interior of the island, despite the narrowness of the area between the mean high watermark and the vegetated part of Robben Island, may be related to the increased risks of nest predation in such habitats as well as the thermoregulatory benefits that they appear to gain by being close to the ocean (Chapters Three, Four and Five). Sea-level rise, and increased frequency and magnitude of storm events may cause increased shoreline flooding and coastal erosion thereby resulting in more habitat reduction or even complete loss for some coastal breeding species (Reynolds et al. 2015; Widlansky et al. 2015). Management interventions and further research into the continued availability of optimum habitats to support the island breeding populations of oystercatchers in the future would benefit the species.

The predictors of the chance that a pair would fledge at least one young in a season

The pairs which laid large first clutches and initiated the incubation of their first clutches earlier in the season had a higher chance of fledging one young compared to others (Table 6.4; Figure 6.5, Panel A&B). The probability of a pair producing a juvenile in a season was smallest in the section of the island with the highest human use (Table 6.4; Figure 6.5, Panel C).

These results highlight the importance of starting to breed earlier in the season, laying larger first clutches at the time of the breeding season when breeding conditions support higher success but reducing clutch investment as the condition worsens and the likelihood of success drops (Crick et al. 1993; Weiser et al. 2018; Kaliński et al. 2019). Breeding conditions may have declined as the season advanced because of increased predation as the number of available nests increases in the season (Chapter Five) or because of increased wave-driven storminess later in the season (Tjørve 2006; van de Pol et al. 2010; Plaschke et al. 2019).

The survival rates of second and third nesting attempts were very low and may explain why most of the pairs which experienced a failed first attempt did not attempt to reneest. This pattern is very similar to that of Piping Plovers *Charadrius melodus*, which also experience

lower daily nest survival of repeat clutches (Swift et al. 2020). This suggests that renesting attempts may not be generally rewarding because the probability of successfully hatching, rearing, and fledging a juvenile may be lower as the season advances, and particularly because post-fledging survival of juveniles fledged later in the season is lower than those fledged earlier (Daan et al. 1990). However, the only chance of raising a juvenile in a given season after a failed first attempt is to keep trying until repeat attempts become successful, time permitting (Morrison et al. 2019). But, given that favourable conditions decline as the season advances, smaller clutch size for repeated attempts may become more favoured (Dawson 2008).

The reduced probability of fledging a juvenile by pairs breeding in the area with the highest human disturbance may be because of a reduced likelihood of hatching chicks in that area for the reasons discussed under predictors of nest survival. A renesting attempt will likely fail if the cause of failure of the first attempt is still prevalent in the area (Benvenuti et al. 2018). Also, even if they successfully hatch a chick, disturbance generally reduces the amount of low tide time available for parents to forage and provision their young, and this may therefore still reduce the probability of fledging the chicks (Leseberg et al. 2000).

6.43 The number of fledgelings per pair per year

The number of fledgelings per pair per season observed in this study appears low (Table 6.1). However, it is still around the 0.35 which is required to maintain a stable population of the species (Hockey et al. 2005). The values reported here are similar to those of previous estimates, except for that observed in the 2001 breeding season (Tjørve & Underhill 2008) which was about double that noted in the current study (Appendix 3).

Density-dependent factors can operate to reduce reproductive success or increase adult mortality rate as the number of adult birds attains or exceeds carrying capacity (Ashmole 1963). Oystercatchers are long-lived species with high annual adult survival rates of about 96% (Loewenthal 2007), suggesting that the reduction of breeding success might be the likely route by which density-dependent factors would first act. An example of a density-dependent factor which appears to be acting on the population size of the oystercatchers studied here is nest predation (Tjørve 2006; Chapter Five). Nest predation has been a significant cause of nest losses, thus moderating the overall productivity of the oystercatchers (Tjørve 2006; Braby & Underhill 2007). Predation rates, especially by Mole

Snakes, are still widespread and increase as the number of active nests increases (Chapter Five). (Chicks were more difficult to monitor comprehensively compared to the nests, so the factors causing the loss of oystercatcher chicks were not comprehensively determined as those for the nests were. However, incidental, direct attacks observed on oystercatcher chicks were by groups of non-breeding adult oystercatchers, but the parents defended the chicks against the attack and guarded the chicks to safety on two different occasions and two different territories. Two chicks were also observed dead in the nest, with no wounds or any obvious sign to suggest predation. It may be possible that harsh weather conditions may have been responsible. It is possible that Kelp Gulls or Mole Snakes may be responsible for the loss of oystercatcher chicks before they fledge, but no clear evidence was found to suggest that Kelp Gulls or Mole Snakes predate oystercatcher chicks during the period of this study (Chapter Five)).

Also, given that no population can continue to increase beyond the resources available to it, density-dependent factors in the form of a limited amount of breeding habitat must eventually limit the continued population growth of oystercatchers on the island (Newton 2007; Barbraud et al. 2018; Southwell & Emmerson 2020). The percentage of the overall numbers of oystercatchers on the island which bred in 2001 was 100%, and an additional 5% were observed to move in to settle to breed in the course of the season and also nested (Tjørve 2006). But this percentage declined in the subsequent seasons (Tjørve 2006). During the three seasons reported here, 64%, 56% and 56% of the average number of adults on the island attempted to breed. This decline in the percentage of the adult population attempting to breed could reflect a limiting number of territories available for adult birds. Oystercatcher juveniles migrate to nurseries but return to their natal grounds to breed after attaining maturity (Hockey 2003; Loewenthal 2007; Rao et al. 2014). It is likely that as they arrive back to breed on Robben Island, they are having to wait for an extended period before being able to secure breeding territories. This situation may have been exacerbated by the potential contraction in the width of the breeding habitat available to the oystercatchers in some sections of the island due to the effects of coastal flooding (Chapter Two). Some observations suggestive of limiting habitat are captured in Appendix 4.

Both predation and limiting habitat may act individually but may also have an additive impact on the population of oystercatchers on the island, curtailing their overall productivity

and thereby reducing the number of recruitments made into the adult population. Results from Chapter Five indicate that nests located very close to vegetation are exposed to a higher risk of nest predation. The current chapter shows that nesting too close to the mean high watermark may result in nest losses probably due to storm surges and predation. Both findings suggest the optimum nesting habitat to be a wide area of shore. Yet, some sections of the island's shoreline are less than 5 meters in width, with some as narrow as a meter. Birds breeding in such narrow areas of shore may be unable to contribute substantially to the adult population because of reduced fitness (Newton 2007; Sæther et al. 2016).

Given that oystercatchers which laid large first clutches early in the season were the most likely to produce one juvenile in a season (Table 6.4, Figure 6.5) and the fact that the ability to do both is dependent on individual quality (Verhulst & Nilsson 2008), and age (van De Pol & Verhulst 2006), it is likely that good quality birds, which may be older and more experienced, are the ones occupying high-quality territories and therefore able to lay large clutches earlier in the season. These high-quality individuals may, consequently, be experiencing higher overall breeding success compared with lower quality ones (Pincheira-Donoso & Hunt 2017). This possibility may influence the composition of the overall population because it suggests that high-quality individuals would have higher fitness and contribute more to the population than others (Newton 2007).

6.5 Conclusion

This study reports an increase in the number of adults, breeding pairs and number of nests laid in a season as compared with values from earlier seasons. It highlights the causes of nest failure and shows that daily nest survival rates are influenced by predation, human disturbance, temperature, and the risk of nest losses to storm surges. It reports that individuals laying larger clutches early in the breeding season are more likely to produce at least one juvenile. The probability of success was low for renesting attempts, and most individuals did not renest after a failed first attempt. The action of density-dependent impacts such as increased nest predation and reduced availability of nesting space seems to be moderating the overall productivity in a way that minimises the number of recruitments (especially those from poor-quality individuals) into the population. Continued monitoring of the population of oystercatchers on the island is recommended. Should any management intervention be required in the future, exploration of possible ways of reducing the vegetated edge of the breeding habitat of the oystercatchers in a way that widens the area of shore available to them is recommended.

Appendix

Appendix 6.1: The results from the full binomial model (AIC=321.41) and the model with the smallest AIC (AIC = 304.89) examining the factors influencing the chance that an oystercatcher's nest would survive the incubation period to produce at least one chick on Robben Island in the 2017 and 2018 breeding seasons. Sample size = 288 nests

	Full model				Model with smallest AIC + season			
	Estimate	SE	z value	p	Estimate	SE	z value	p
Intercept	-1.67	6.66	-0.25	0.80	-6.81	1.58	-4.30	<0.001
Days until hatching	-0.22	0.28	-0.76	0.45	–	–	–	–
2nd nest attempt	0.50	1.75	0.28	0.78	–	–	–	–
3rd nest attempt	28.39	1775	0.016	0.99	–	–	–	–
MSLD	0.0033	0.0030	1.10	0.27	0.0025	0.00064	3.81	<0.001
Location B	-1.55	2.42	-0.64	0.52	1.22	0.43	2.80	0.0051
Location C	0.65	2.15	0.30	0.76	0.90	0.47	1.89	0.058
Location D	-3.45	2.26	-1.52	0.13	1.24	0.43	2.86	0.0042
Location E	-0.46	2.23	-0.21	0.84	0.94	0.45	2.09	0.037
DHWL	0.13	0.14	0.95	0.34	0.19	0.066	2.88	0.0039
I(DHWL^2)	-0.0068	0.0024	-2.80	0.0052	-0.0061	0.0021	-2.91	0.0036
Temperature	0.022	0.20	0.11	0.91	0.13	0.045	2.90	0.0037
2018 season	0.33	1.32	0.25	0.81	0.19	0.30	0.64	0.52
Days2hatch: 2nd nest attempt	-0.033	0.075	-0.43	0.66	–	–	–	–
Days2hatch: 3rd nest attempt	-1.68	87.92	-0.019	0.98	–	–	–	–
Days2hatch: MSLD	-0.000023	0.00012	-0.18	0.86	–	–	–	–
Days2hatch: Location B	0.11	0.10	1.15	0.25	–	–	–	–
Days2hatch: Location C	0.0061	0.087	0.069	0.94	–	–	–	–
Days2hatch: Location D	0.20	0.093	2.18	0.029	–	–	–	–
Days2hatch: Location E	0.059	0.090	0.65	0.52	–	–	–	–
Days2hatch: DHWL	0.0033	0.0048	0.68	0.50	–	–	–	–
Days2hatch: Temperature	0.0046	0.0084	0.54	0.59	–	–	–	–
Days2hatch: 2018 season	-0.0075	0.055	-0.14	0.89	–	–	–	–

Significant p-values are in bold. Location A, first nest attempt and 2017 season are represented by the value of the intercept. Days2hatch=number of days until hatching (calculated for each nest from the day they were found), DHWL= distance of nests to the mean high watermark, MSLD= distance of nest to nearest Mole Snake location, Temperature = maximum air temperature during the exposure period of each nest.

Appendix 6.2: The candidate models tested under the daily survival analysis

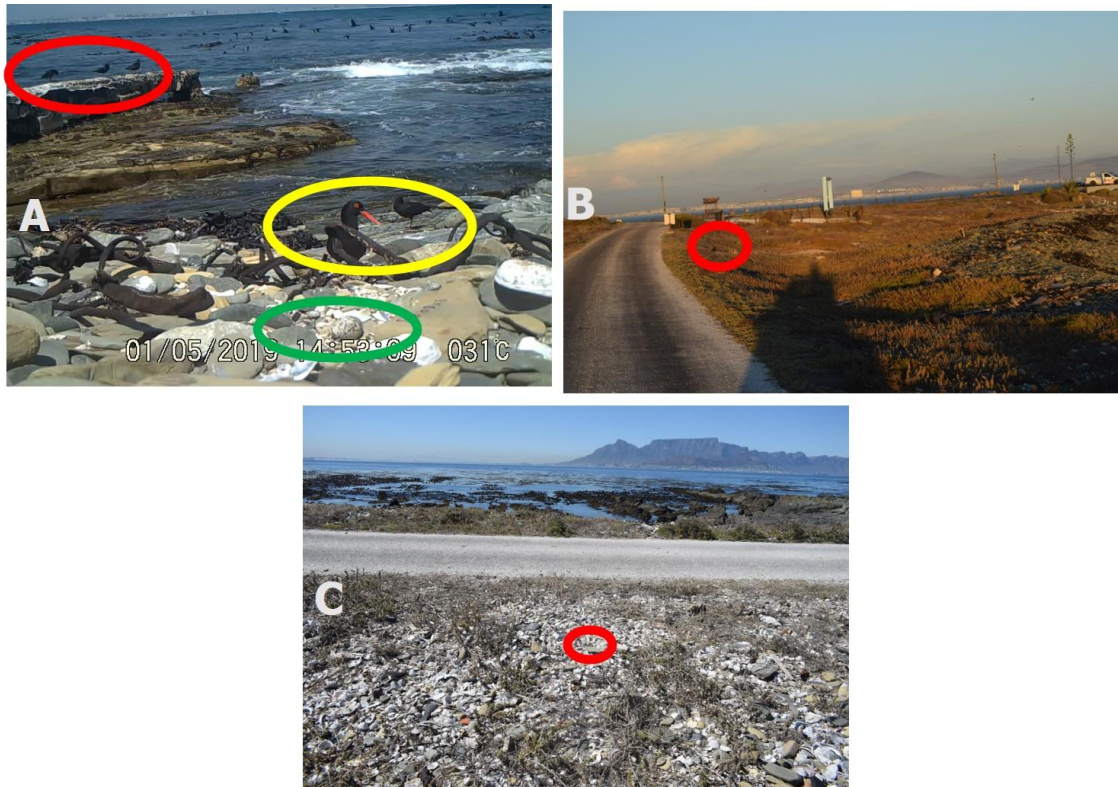
Model	K	AICc	Δ AICc	Weight	Deviance
S(~MSLD + DHWL + I(DHWL^2) + Temperature + Location + Season)	10	1024.47	0.00	0.91	1004.43
S(~MSLD + DHWL + I(DHWL^2) + Temperature + Days2hatch + Season)	6	1030.04	5.57	0.06	1018.02
S(~Time + I(Time^2) + Age of nest when Found + Season)	4	1031.10	6.64	0.03	1023.10
S(~Time + I(Time^2) + I(Time^3) + Season)	4	1040.16	15.69	0.00	1032.15
S(~MSLD + I(MSLD^2) + Days2hatch + Season)	5	1064.94	40.47	0.00	1054.93
S(~DHWL + I(DHWL^2) + Age of nest when Found + Location + Season)	9	1070.67	46.21	0.00	1052.64
S(~DHWL + I(DHWL^2) + Days2hatch + Location + Season)	9	1070.67	46.21	0.00	1052.64
S(~MSLD + I(MSLD^2) + DHWL + I(DHWL^2) + Season)	6	1077.29	52.82	0.00	1065.27
S(~Age of nest when Found + Season)	3	1083.06	58.59	0.00	1077.06
S(~Location)	5	1085.76	61.30	0.00	1075.75
S(~Season)	2	1095.71	71.24	0.00	1091.71
S(~1)	1	1096.78	72.31	0.00	1094.78
S(~DHWL + I(DHWL^2) + Season)	4	1097.05	72.58	0.00	1089.04

K= number of parameters in the model, AICc = Akaike's information criterion for small samples and Δ AICc = adjusted AICc relative to the best model, weight = Akaike weight (a measure of the relative support for each model). Days2hatch=number of days until hatching, DHWL= distance of nests to the mean high watermark, MSLD= distance of nest to nearest Mole Snake location, Temperature = maximum air temperature during the exposure period of each nest.

Appendix 6.3: Number of fledglings per pair of the oystercatchers breeding on Robben Island in the 2001—2004 and 2017—2018 breeding seasons

Season	Number of fledglings/ pair/seasons
2001*	0.74
2002*	0.41
2003*	0.35
2004**	0.098
2017***	0.39
2018***	0.36

Source: * extracted from Tjørve & Underhill (2008), ** extracted from (Braby & Underhill 2007) and *** from the current study.



Appendix 6.4: Some observations suggesting that the oystercatchers on Robben Island may be experiencing limited availability of breeding habitat. Picture A shows two pairs observed to share one territory for the three seasons monitored. The red circle highlights one of the pairs with their juvenile. This pair was always the first of the two pairs to breed, usually started to breed very early and always raised one juvenile annually. The yellow circle highlights the second pair, and the green circle highlights their nest (the nest of the first pair was less than a meter from where the second pair sited their nest). This pair did not commence egg-laying until the juvenile from the first pair had fledged in all three seasons. None of the nests from the second pair survived to produce any chick over the three seasons. The red circle in picture B shows an incubating oystercatcher in the vegetation very close to the road in one of the areas with heavy tourist use. The pair hatched a chick but could not fledge it. The red circle in picture C shows an oystercatchers' nest observed across the road in 2018 on Robben Island: this observation is unusual as oystercatchers on Robben Island are not known to breed across the road. The pair made a first attempt in the usual area of shore between the high mean watermark and the vegetation above it. But the first clutch failed. It was their second clutch that was laid across the road. The second attempt also failed. In all these cases, at least one member of the pair had colour rings for identification. In another observation of pairs with colour-rings two different pairs nested on the same territory in two seasons (one pair nested in 2017 while the other in 2018).

Chapter Seven: General discussion

7.1 Introduction

In this thesis, I examined how the biotic and abiotic components of the environment affect African Black Oystercatchers *Haematopus moquini* (oystercatchers) during the breeding season and the behavioural flexibilities used by the species to cope under current sea-level and weather conditions. Oystercatchers may be vulnerable to the impacts of the large increases and variability of weather conditions and sea-level change under the climate scenarios projected for the future because of the nature of their breeding habitat. Studying the strategies used by the species to cope with current weather conditions may be useful to assess the vulnerability of the species to future climate change and to guide management decisions. I collected habitat, breeding, behavioural and temperature data over three breeding seasons (2016—2018) on Robben Island, South Africa. I found that oystercatchers experienced constraints from biological and non-biological components of their environment. But they also showed significant flexibilities in response to these environmental conditions which enabled them to optimise breeding productivity under the habitat conditions in which they bred.

In this chapter, I synthesise and discuss the findings of this thesis considering current behaviours exhibited by the oystercatchers, the potential impacts of future climate change on the population dynamics of the species and how their current flexibilities to environmental conditions may help deal with the challenges of greater climate change in the future. Management recommendations and direction for future studies are also presented.

7.2 Evidence of adaptation to environmental variations

1. *Dealing with the risk of nest losses to storm surges without increasing vulnerability to nest predation*

Nest losses to storm surges constitute a major cause of nest failure for coastal breeding birds and strategies used by individuals to minimise this risk could be adaptive (Tjørve 2006; van de Pol et al. 2010; Field et al. 2017). The vulnerability of oystercatchers' nests to being washed away by storm surges increased with the proximity of their nest-sites to the ocean, as expected (Chapter Two), suggesting that nest-site selection away from the ocean should be adaptive (Bailey et al. 2019). But given that nest predation pressure increases with

proximity to the vegetated upper part of the breeding habitat as it could potentially conceal nest predators (Chapter Five), oystercatchers needed to trade-off the risk of nest predation with that of nest losses to storm surges (Ma et al. 2019). Oystercatchers appeared to use spatial and temporal adjustments to balance these risks.

Spatially, oystercatchers which occupied wide territories selected nest-sites that were in the lower half of their breeding habitat (decreasing vulnerability to nest predation) while still maintaining a safe distance away from the ocean (decreasing the vulnerability of nest losses to storm surges). But the pairs in narrow territories prioritised safety from storm surges over that of nest predation by choosing nest-sites in the upper half of the breeding habitat thereby minimising the risk of nest losses to storm surges while potentially increasing nest predation risk. This behaviour of prioritising safety from storm surges over that of nest predation suggests that oystercatchers perhaps considered the risk of nest losses to storm surges to be greater than that of nest predation. Prioritising safety from storm surges over that of nest predation makes sense because, a nest placed too close to the ocean will almost certainly get washed away when exposed to a stormy event. But a nest placed too high up in the beach may be exposed to high risk of predation but may still have a chance of escaping predation. The behaviour of prioritising safety from storm surges over that of nest predation also suggests that oystercatchers use nest-site selection to manage the risk posed by storm surges (Bailey et al. 2019) and nest predation (Benvenuti et al. 2018) but could be constrained by the breeding habitat width. Being constrained by habitat width in the manner observed in this study could have implications for population dynamics and the ability of oystercatchers to cope with future climate change (discussed further below in Section 7.3).

The use of nest-site selection to manage the risk of nest losses to storm surges has been confirmed in shorebird and non-shorebird species breeding in coastal areas in different geographical localities. For example, the European Oystercatchers *Haematopus ostralegus* (Haematopodidae family) breeding in the Wadden Sea (Bailey et al. 2019), Reed Parrotbills *Paradoxornis heudei* (Paradoxornithidae family) in Yongnianwa Wetland, China (Ma et al. 2019) and Seaside Sparrows *Ammodramus maritimus* (Passerellidae family) in Connecticut, USA (Gjerdrum et al. 2005) have all been observed to use nest-site selection to reduce the vulnerability of nest losses to storm surges. This suggests that storm surge is a strong

selection pressure across several coastal breeding species and the use of nest-site selection to manage the risk of nest losses to storm surges by different species across different phylogenies of birds occupying similar breeding habitats provides strong evidence that this behaviour is an adaption to the environmental condition prevailing in the habitat type in which they breed (Koenig 1984; Stearns & Koella 1986; Tetsuji 1996). Additionally, it confirms the general use of nest-site selection as behaviour which potentially maximises fitness by minimising the exposure of adults and/or their nest contents to factors which could threaten their survival (Amat & Masero 2004a; Anteau et al. 2012; de Zwaan & Martin 2018; Devries et al. 2018; Laidlaw et al. 2020).

Temporally, oystercatchers synchronised the timing of the start of incubation around the semilunar spring tide cycle (Chapter Two). They initiated incubation for more nests around a spring tide than at other times, perhaps as an adaptation to minimise the number of spring tide cycles that they experience during their nearly 30-day incubation period, thereby potentially decreasing the risk of nest losses to storm surges during the next spring tides. This is because few studies of other coastal breeding birds with incubation period below 30 days have also found evidence that birds time the onset of their nests to occur around or soon after a spring tide so that the eggs would have hatched before the timing of the next cycle of spring tides (Gjerdrum et al. 2005; Shriver et al. 2007). Parents could use increased nest attentiveness to hasten embryo development in a manner that shortens the incubation period helping the eggs to hatch before the arrival of the next spring tides (Hepp et al. 2005; Durant et al. 2013; Plaschke et al. 2019). This possibility may be further enhanced by the ongoing climate change as the incubation periods of some bird species have been observed to shorten as temperature increases (Martin et al. 2007; Mueller et al. 2019).

It has also been suggested that another reason for synchronising nest initiations with the semilunar spring tides by coastal breeding birds may be so they could use the height of the highest tides during the semilunar spring tide to determine how far into the beach the storm surges of spring high tides would reach and then use such information to guide the selection of a nest-site which is safe from subsequent spring high tides (Plaschke et al. 2019). This suggestion was tested in this study by examining nest positions relative to the midpoint of the beach for nests initiated on different days across the semilunar spring tide cycle (Chapter Two). Although oystercatchers' nests for which incubation started around a

spring tide date had a slightly higher probability of occurring higher up into the breeding habitat than those initiated further away from a spring tide date, the difference was not statistically significant. This, perhaps, might be due to the modest sample size or the use of incubation start date alone rather than actual nest initiation dates. The fact that some oystercatchers only had very narrow strips of beach on which to nest may also have contributed because how high up on the beach a nest is placed depends on the availability of sufficiently wide beach (Chapter Two).

The behaviour of using the semilunar spring tide cycle to time breeding activities has been observed in several fish species (Korringa 1957; Takemura et al. 2010; Ikegami et al. 2014; Díaz-Astudillo et al. 2017). However, while the use of moonlight by birds to synchronise nocturnal foraging and breeding activities have been widely studied (Pinet et al. 2011; Cruz et al. 2013; Hayes et al. 2018; Portugal et al. 2019), relatively fewer studies have described the use of the semilunar spring tide cycle to manage the risk of nest losses to storm surges. The only two species of birds for which such studies have been conducted include the Saltmarsh Sparrows *Ammodramus caudacutus* (Gjerdrum et al. 2005; Shriver et al. 2007) in the USA and Snowy Plovers *Charadrius nivosus* in Mexico (Plaschke et al. 2019). This study is the first to examine in detail how the African Black Oystercatchers might use nest-site selection and synchronisation of the onset of a nest with the semilunar springtide cycle to manage the risk of nest losses to storm surges. Other coastal breeding birds in Africa and other parts of the world may be using these strategies more frequently than has been realised. These results provide insights into how oystercatchers adapt to the specialised breeding habitat where they breed and add to the growing knowledge (e.g., Shriver et al. 2007; Plaschke et al. 2019) that coastal breeding birds may use the semilunar periodicity as a cue to inform breeding activities.

2. Flexible responses to environmental conditions by oystercatchers in balancing the competing needs of adults and their eggs during incubation

One of the most energy-demanding aspects of avian reproduction with fitness implications for both adult survival and reproductive output is the incubation stage (Vleck 1981; Hepp et al. 2005). Parents need to trade-off the benefits of extended nest attentiveness (increased egg viability) with its costs (decreased body maintenance activity by parents) (Prescott 1964; Williams 1966). The ability of incubating adults to balance their needs with the

thermoregulatory needs of their eggs can be adaptive under dynamic environmental conditions (Conway & Martin 2000a; Delia et al. 2013). In this thesis, I show that oystercatchers used the biparental incubation strategy to increase the chance of meeting their somatic needs without compromising the thermal needs of their eggs (Hall 1959; Chapter Two). Male and female oystercatchers contributed equally to incubation duties and maintained high overall nest attentiveness (Chapter Two). In addition to using the biparental strategy, oystercatchers showed high flexibility under changing environmental conditions which potentially influenced their energetic needs and the thermal needs of their eggs (Chapter Two). They scheduled their incubation bout length around the tidal cycle: shorter bout lengths at low tide and longer ones at high tide, enabling both parents to forage within a single low-high tide cycle to meet their energetic and hydration needs. Also, in cold environmental conditions (low temperature, high windspeed and at night) oystercatchers had longer incubation bouts in contrast to warm conditions (increasing temperature during the day) when they had shorter incubation bouts.

These flexibilities exhibited by the oystercatchers in this study make sense in terms of balancing the costs and benefits related to adult survival and proper development of eggs (Williams 1966). This is because an extended incubation effort under cold environmental conditions could ensure that the eggs are not exposed to periodic cooling. Periodic cooling is known to delay embryonic development (Olson et al. 2006; Carter et al. 2014) and the energetic costs incurred by adults to rewarm eggs after a temperature drop is higher than that needed to maintain the temperature of already warm eggs (Vleck 1981; Cresswell et al. 2004). When ambient temperatures are high, energetic costs, hydration and thermoregulatory needs of adults increase, and shorter incubation bouts become more beneficial for adults than extended ones (Amat & Masero 2004b; Bourne 2020). The risk of egg cooling or overheating during the frequent exchanges between parents under warm conditions may have been low because both parents are incubating (AlRashidi et al. 2011). One nest during this study was abandoned by the female when the male failed to return, probably because the female could not cope alone or that the eggs became inviable because of repeated prolonged exposures when it took recesses (it remains unclear what happened to the male as it was never seen again even in the subsequent breeding season) (Chapter Four).

These results provide evidence in support of the idea that biparental incubation increases the possibility of maintaining very high nest attentiveness at a relatively reduced energetic cost to the adults compared with the uniparental incubation system (Cresswell et al. 2003; Bulla et al. 2014). Because in a biparental system when one parent is on recess foraging or thermoregulating the other is usually on incubation duty ensuring that the nest is rarely left unattended (AlRashidi et al. 2011; Ospina et al. 2015; Hoppe et al. 2019), except when external sources of disturbances make both parents leave the nest unattended as discussed below in Section 7.3. The biparental system, therefore, allows parents to meet their needs while still tending their eggs most of the time (attaining nearly 100% attentiveness) thereby potentially maximising reproductive success at a reduced cost of incubation (Cresswell et al. 2003; Bulla et al. 2015a). This is in contrast with the uniparental system where eggs are left unattended (exposed to harsh ambient conditions and potential predators) when the sole incubator goes on a recess (Cantar & Montgomerie 1985; Tulp et al. 2009). Biparental incubation systems are even more essential in harsh environmental conditions, for example, in extremely cold (e.g., in the arctic) or hot environments (e.g., deserts) where leaving eggs unattended for few minutes could render the eggs inviable (under extremely hot conditions which can overheat the eggs) or halt embryo development (if egg temperature falls below the physiological zero under cold environmental conditions) (Carey 1980; AlRashidi et al. 2010; Clauser & McRae 2017; Bourne 2020). Biparental incubation systems may perhaps also be important for birds like oystercatchers that feed their chicks for months post-hatching (Hockey 1983a, 1997): if they can maintain their body condition during the incubation phase, they may potentially dedicate more food resources to their growing chicks.

The results are consistent with the idea that varying environmental conditions should influence the energetic costs of incubation in birds. Incubating individuals will therefore usually trade-off the costs of incubation with the benefits of maintaining viable eggs by varying their incubation schedules in response to the environmental factors which could potentially influence their energy demands and the viability of their eggs (Tulp & Schekkerman 2006; Klimczuk et al. 2015; Hoppe et al. 2019). This flexibility could help birds adapt to different environmental conditions and deal with their projected changes under climate change, maximise adult and egg survival and increase population resilience and

survival. Additionally, these results build on the work of Hall (1959) and Adams et al. (1999). They confirm the use of the biparental incubation system by oystercatchers, detailing how both parents relieve each other under varying environmental conditions and showing that they continue incubation into the night, having nearly double-length incubation bouts at night compared to the day, in keeping with similar incubation patterns in American Black Oystercatchers *Haematopus bachmani* Spiegel et al. (2012).

3. Dealing with heat stress during incubation

Temperature is an important environmental factor that significantly impacts the cost and outcome of avian reproduction (Ghalambor & Martin 2002). Given the daily variability in air temperature, the nature of the breeding habitat of the oystercatchers (open, ground-nests with little to no lining) and exposure to high heat loads during the time of day with high solar radiation, oystercatchers may need to deal with the challenges imposed by the range of temperatures that they experience during incubation (Adams et al. 1999). Besides the adjustments of incubation schedules to changes in temperature during incubation (Chapter Four), I examined the set of on-bout thermoregulation behaviours used by oystercatchers to deal with high heat loads and low temperatures during incubation (Chapter Three).

Oystercatchers used a suite of on-bout thermoregulation behaviours to cope with the range of temperatures that they experienced during incubation. They used the back-rest posture to cope with low temperatures at night, shading behaviour, increased egg-turning frequency and panting to cope with increased heat loads during the day. Some of the costs associated with the use of these thermoregulation behaviours may have been reduced given the context of the breeding habitat of the oystercatchers. For example, the use of the backrest posture is known to increase the risk of predation because of the potential inability to detect an approaching predator early enough to enable a swift escape (Ryeland et al. 2017; Tattersall et al. 2017). But there are currently no known predators of adult oystercatchers on Robben Island and the nest predator identified, Mole Snake *Pseudaspis cana*, are mostly active during the time of day (Branch 2002) when oystercatchers rarely use the backrest posture. It is, however, not clear whether the predominant use of the backrest posture by oystercatchers in the night is strictly temperature-driven or whether it also includes a response by the oystercatchers to the activity patterns of the Mole Snake which is generally low at night (Branch 2002). This is because, it might be expected that vigilance (increased

head up and scanning for potential predators which goes parallel with the use of backrest posture) would be highest during the time of day when nest predator activity is highest and vice versa (Felton et al. 2018), and the behaviour of the oystercatchers fits well into this pattern.

Also, the increased risk of dangerous levels of dehydration known to be associated with heavy panting (Jacobs 2017; Sharpe et al. 2019) as exhibited by the oystercatchers may have been reduced by the proximity of their nesting site to the ocean. During the frequent trips of oystercatchers off the nests under conditions of high temperature (short incubation bouts) as noted in Chapter Four, some were seen foraging, wading, belly-soaking, and bathing. These behaviours are known to facilitate prompt heat loss from birds to water and foraging on the wet and fleshy mussels and limpets, as oystercatchers do, may have contributed to replenish some of the water that they may have lost during panting, despite not being able to drink sea-water directly because of high salt content (Battley et al. 2003; Amat & Masero 2009; Marchi et al. 2015). These results perhaps highlight how important the breeding habitat (proximity to food and water for thermoregulation) of the oystercatchers is to their capability to effectively thermoregulate during the energetically demanding period of incubation and this seems likely to be true for many other coastal birds breeding in a warm climate.

The thermoregulation advantages derived by oystercatchers by being close to the ocean support the idea that the proximity to water could significantly improve the ability of endothermic organisms to cope with increased heat loads in warm climates (Angilletta Jr. et al. 2010). For example, in Southern Spain Amat & Masero (2004b) compared the fate of the nests of Kentish Plovers *Charadrius alexandrinus* in proximity to water (Fuente de Piedra lake, Malaga province) with those further away from water and found that pairs incubating closer to water were less likely to abandon their nests under increased heat loads because they could use belly-soaking to thermoregulate. Also, in the arid regions of Australia, Cooper et al. (2020) investigated the physiological state and responses of wild Zebra Finches *Taeniopygia guttata* to heatwaves and found that as long as drinking water was available, the finches were not significantly heat-stressed on hot days, even with mean maximum air temperature as high as 42.7°C. Whereas in the absence of drinking water, some species may derive water from the food they eat (Bartholomew & Cade 1963), some retreat into

thermally buffered microhabitats while forgoing other profiting activities (Cunningham et al. 2015; van de Ven et al. 2019) or delay the use of evaporative cooling which might expose them to lethal dehydration by allowing their body temperature to rise above normal levels (facultative hyperthermia) (Cain III et al. 2006; Angilletta Jr. et al. 2010; Gerson et al. 2019).

However, under conditions of poor food and water availability, mass bird mortalities from lethal dehydration have been predicted in the near future in extremely hot climates of the world facing climate change-induced rise in temperature and decreased rainfall (Albright et al. 2017; Conradie et al. 2020). Water availability is extremely important in enhancing adaptation to extreme temperatures and may remain very essential to the ability of living organisms to cope with projected increases in temperature under future climate change (Angilletta Jr. et al. 2010). Availability of water is so important for survival, growth, and reproduction for many species that it generally influences the distribution of biodiversity both geographically and temporally with water availability resulting in high species abundance and diversity (Leeuw et al. 2001; Prenda et al. 2001; Rich et al. 2019; Naidoo et al. 2020). As climate change results in decreased rainfall, disappearances of wetland habitats and increased droughts, the resilience of living organisms in dealing with increased heatwaves in the future may decline without some form of management intervention (Finkler 1999; Albright et al. 2017).

The use of heat-dissipating behaviours may make the nest position more obvious and could attract nest predators (Martin et al. 2000). For example, shading is likely to increase the visibility of the nest position because a standing bird may be more conspicuous than a sitting one. Also, the frequent trips to and from the nest and the body movements associated with panting and frequent egg-turning done by oystercatchers as temperature increases may collectively make their nests more obvious to predators thereby increasing the costs associated with the use of these heat-dissipating behaviours (Ghalambor & Martin 2002; Matysioková & Remeš 2018). However, the heavy use of these behaviours by oystercatchers despite the potential increase in nest predation risk suggests that the benefits they gain from these behaviours may outweigh the associated increased risk of nest predation (Williams 1966; Ghalambor & Martin 2002). For example, by successfully thermoregulating under increased heat loads, oystercatchers, which are typically long-lived, could benefit from reduced adult mortality risk and stay alive to nest again in the future

should the current nest get predated. Also, behaviours such as egg-turning and shading are known to benefit the eggs by contributing to the continued viability and hatchability of the eggs (New 1957).

The costs and benefits associated with the trade-offs between predation risk and thermoregulation may have taken a different form in a different context to that of the oystercatchers in my study. For example, if adult predation risk were to be higher than nest predation pressure, the cost of getting preyed upon, which outrightly prevents all future breeding opportunities, may outweigh the benefits of thermoregulation and may be reflected in the behaviour and decisions of individuals (Radzio & O'Connor 2017). For example, Pitt (2000) found that grasshoppers exposed to high predation risk from avian, mammalian and reptilian predators, selected foraging habitats in thermally disadvantaged habitats thus trading the increased thermoregulatory costs in such habitats with the benefits of avoiding death from predators. Also, Kentish Plovers, *Charadrius alexandrinus* incubating in a site where adults are exposed to high risk of predation from mammalian predators minimised the risk of getting predated by choosing nest-sites which increased their cost of thermoregulation and potentially risked the survival of their eggs (Amat & Masero 2004a). These examples show that the environmental context in which organisms occur play significant roles in determining the nature and directions of the trade-offs between predation and thermoregulation. The results concerning the on-bout thermoregulation behaviour of the oystercatchers collectively provide insight into the suite of behaviours used by oystercatchers on their nests to thermoregulate and tend their eggs and show that even within short hour-long incubation bouts, birds were actively assessing the costs and exhibiting trade-offs in balancing the costs and benefits of reproduction.

4. Other adaptations for dealing with nest predation

Nest predation is a major selective pressure acting on the breeding ecology and behaviour of avian species because it directly influences their ability to produce offspring (Slagsvold 1982; Bellamy et al. 2018). Hence species may exhibit diverse strategies to minimise the risk of nest predation and maximise breeding success. For species requiring conservation management, the true identity of the specific predator acting as the main nest predator in an area is crucial to informing management decisions as the pattern of nest predation can

vary by whether the main agents are mammalian, avian or reptilian predators or a combination of these (Weatherhead & Blouin-Demers 2004; Lahti 2009; Raine et al. 2020).

I found that the primary nest predator of oystercatchers' nests on Robben Island is the Mole Snake, contrary to previous suspicions (Underhill 2014) that it was the Kelp Gull (Chapter Five). While tropical nesting birds are generally subject to a diverse array of nest predators, snakes play important biological roles in influencing the breeding ecology and demography of birds in the tropics (Robinson et al. 2005b; Roper et al. 2010; Oswald et al. 2020). But the selective effects of predatory snakes in shaping the behaviour of birds are largely underappreciated, probably because most behavioural ecological studies on the cost of incubation have been conducted in temperate regions (Weatherhead & Blouin-Demers 2004; Griebeler et al. 2010). For example, Kubelka et al. (2018) noted, while investigating the impact of climate change on shorebirds' nest predation globally, that the knowledge of shorebird nest predators in the tropics was primarily based on incidental observations or assumptions. The study highlighted the generally low numbers of empirical studies focusing on nest predators of shorebirds from tropical regions and the need to fill such gaps.

Chapter Five of this thesis is the first empirical study that was designed primarily to investigate the predictors of nest predation and predator identity of the oystercatchers using digital cameras to provide direct and unmistakable evidence of nest predator identity. Earlier studies have used the footprints of potential predators (Parsons 2006) and the likely time of occurrence of nest predation events (Braby & Underhill 2007) as well as incidental observations (Calf 2004) to identify potential avian, reptilian and mammalian predators of oystercatchers' nests. Likely, other populations of oystercatchers, other shorebirds, seabirds, and birds, in general, could be impacted by other predatory snake species in similar ways as the Robben Island population of oystercatchers are by Mole Snakes. For example, predatory snakes such as Common Egg-eater snake *Dasypeltis scabra* and Boomslangs *Dispholidus typus* have been identified as nest predators of many birds species in some South African Island and mainland sites (Dyer 1996; Bates & Little 2013; Oswald et al. 2020). Largely, the activities of snakes are less conspicuous compared to avian and mammalian nest predators because they are generally shy organisms which avoid humans and some hardly leave reliable evidence behind after nest predation events (as in the case of the Mole Snakes in this study) (Weatherhead & Blouin-Demers 2004; Robinson et al.

2005b; Chapter Five). These characteristics may explain why the impacts of predatory snakes are often underestimated.

I observed that several factors, including temperature, influenced the nest predation probability of oystercatchers, with temperature having a quadratic relationship with nest predation risk (nest predation was highest when the maximum air temperature was between 21–27°C and declined at 30°C and was lowest from 33.4°C). This result suggests that while nest predation by Mole Snakes could increase with moderate increases in temperature, extreme increases will reduce the activity of the snake thereby reduce nest predation. Interestingly, while oystercatchers panted for 50% of the time from 22.6°C they only used shading behaviour for 50% of the time when the temperature was 34.0°C and above (Chapter Three). Oystercatchers perhaps delayed the substantial use of shading behaviour until a temperature range with lower predation pressure to minimise the risk of nest predation, given that a shading adult might be more obvious than a sitting adult. Given the impact of temperature on the activity of snakes generally (Cox et al. 2013; Putman & Clark 2017), and the increasing awareness of snakes constituting main nest predators of many tropical birds (Robinson et al. 2005b; Oswald et al. 2020), the selective effects of predatory snakes may increase as temperature increases under future climate change with possible implications for nest predation patterns, avian species productivity and overall demography. However, it should be noted that the temperature used to examine the effects of temperature on nest predation and the behaviour of the oystercatchers was the air temperature at a temporal scale which may not have accurately match the operative temperatures that the snakes and the birds were experiencing.

I also found that nest predation pressure increased as more nests became available as the season progressed: nests which were initiated earlier in the season had the least chance of being predated compared to those initiated later (Chapter Five). This pattern of nest predation agrees with the predictions of the predator search image hypothesis which predicts mobile predators foraging on prey items that occur in different relative proportions in time and space to have a flexible learned search image of their prey items and switch from a low-density prey to a higher density prey as availability changes (Cornell 1976). The impact of nest predation in decreasing nest survival as the season advanced is similar to the findings of several avian studies reporting a within-season variation in optimal breeding

conditions, with favourable conditions for successful reproduction generally deteriorating as the season advances (Dawson 2008; Verhulst & Nilsson 2008; Smith & Wilson 2010). This pattern of increasing nest predation with time also caused the optimal clutch size in oystercatchers to vary across the season with larger clutches being more favoured at the start of the season with low predation pressure, while smaller clutches became optimal under increased nest predation pressure as the season advanced (Chapter Five). This pattern agrees generally with the predictions of life-history theory that individuals should decrease reproductive investments as the cost of reproduction increases (Williams 1966; Drent & Daan 1980; Hogstedt 1980; Tinbergen & Daan 1990).

Also, the position of oystercatchers' nests relative to the vegetation influenced their risk of predation with the nests located away from the vegetation having reduced probability of getting predated (Chapter Five). The higher probability of nest predation in proximity to vegetation might be because the vegetated area of the island could provide a hiding place for snakes, preventing their being detected by potential prey or predators (Lima & Valone 1991; Lima 2009; Cresswell et al. 2010). It could also provide cooler micro-habitat in which reptilian predators like Mole Snakes could hide during the heat of the day to reduce their cost of thermoregulation (Weatherhead & Blouin-Demers 2004). Oystercatchers' nests placed sufficiently away from predator-concealing vegetation, therefore, had a higher chance of survival, highlighting the importance of habitat openness. In narrow territories, the area where predators need to search would be small thereby making it easier for predators to locate nests faster compared to those located in larger territories on broader stretches of beach. Also, snakes may be reluctant to forage in territories with a large open area which is generally rocky or shelly and without vegetation because it may increase their thermoregulatory costs and makes them more visible (Weatherhead & Blouin-Demers 2004). However, with poor availability of sufficiently wide territories, some oystercatcher pairs selected narrower habitats and nested closer to the vegetation as shown in Chapter Two that nests were more likely to be placed closer to the vegetation in narrow beaches compared to wider ones. The dynamics between nest predators, vegetation, and breeding birds, in general, may be influenced by climate change, as increases in temperature may influence the pattern of vegetation growth as well as the thermoregulatory needs of both nest predators and breeding birds leading to changes in overall ecological communities

(discussed further in Section 7.3 below). Together, these results on the nest predation of oystercatchers (Chapter Five) enrich our understanding of the nest predator identity of the species, highlighting many important ecological factors that collectively influence nest predation risk and show why research into the predation pressure on organisms should consider these factors together.

5. Overall breeding outcomes and current population size

Overall breeding success is a key component of reproductive fitness and influences population dynamics directly (Snapp 1976; Brown et al. 1993). In Chapter Six, I examined the overall breeding success of oystercatchers and its predictors on Robben Island. I found that pairs which started breeding earlier in the season, had larger first clutches, experienced high air temperature during incubation, located their nests away from the sources of human disturbance, the mean high watermark, predator concealing vegetation, and nest predator locations (where Mole Snakes had been observed or where predation by Mole Snake had occurred) were more likely to hatch and fledge at least one juvenile in a breeding season. These results show that diverse biotic and abiotic components of the environment could act together in a complex manner to influence the likelihood that a breeding pair would produce an offspring in each breeding season (Smith et al. 2007; Shitikov et al. 2012; Mainwaring et al. 2014; Hötter & Segebade 2017). Breeding pairs, therefore, need to exhibit several trade-offs in balancing breeding timing, placement, and the number of eggs in their nests with the many constraints (human disturbance, predation, storm surges, poor weather) in their breeding habitat to reproduce successfully.

Some pairs with failed first attempts made a second and sometimes a third attempt, but re-nesting attempts experienced low breeding success, and most pairs did not re-nest after a failed first attempt. The average number of fledgelings per pair per season was 0.38 and close to the 0.35 fledgeling per pair per season required to maintain a stable population (Hockey et al. 2005) and in keeping with other research suggesting that oystercatchers generally experience a low, but adequate, reproductive output per breeding pair per year (Summers & Cooper 1977; Hockey 1983b; Tjørve 2006; Loewenthal et al. 2016). This is probably related to the high demands of successfully hatching and raising offspring that are completely dependent on adults for provisioning even after being able to fly (Hockey 1997; Parsons 2006; Tjørve 2006). The low annual productivity of oystercatchers is also in line with

what might be expected given that they are generally long-lived (Leseberg 2001) and should spread reproductive effort over several years to optimise overall lifetime reproductive success (Williams 1966; Ricklefs 2000; Brosset et al. 2016).

I also found that the average number of oystercatchers on Robben Island has increased to 498 ± 12 (418–585) between 2016 and 2019 compared with an average of 345 individuals reported between 2001 and 2012 (Spiby 2012). The breeding population of oystercatchers on Robben Island increased to an average of 146 ± 8 (range: 138–160) pairs between 2016 and 2018 breeding seasons compared to the 64, 68, 49, and 61 breeding pairs in 2001, 2002, 2003 and 2004 breeding seasons, respectively (Tjørve 2006; Braby & Underhill 2007). These results show that despite nest losses to predation by Mole Snakes and other sources of nest failure (weather, storm surges, human disturbances, and the activities of other wildlife), the oystercatcher population on Robben Island has increased.

The increases in population size of African Black Oystercatchers generally across their geographical range has been attributed in part to the increased availability of food brought about by the successful invasion of the Southern African coastlines by the Mediterranean Mussel *Mytilus galloprovincialis* (Coleman & Hockey 2008). Increased availability of food has resulted in increased breeding productivity in many populations which has in turn positively impacted the population of the oystercatchers (Coleman & Hockey 2008; Kohler et al. 2011; Assis et al. 2015). For example, Loewenthal et al. (2016) found that oystercatcher populations with low levels of human disturbance and high abundance of Mediterranean Mussels had the highest breeding success. Although the Robben Island coastline has also been invaded by the Mediterranean Mussels (Tjørve 2006), no data exist for the extent and rate of increase of the invasion over time to enable a quantitative comparison of the abundance of the mussel with actual population size and breeding productivity of oystercatchers on the island. But the mussel has likely contributed significantly to the population increase of the oystercatchers on Robben Island as it has in other sites for which mussel data exist (Loewenthal et al. 2016).

The mussel is resistant to the parasites that are prevalent in indigenous mussels, makes dense beds in the intertidal zone, and grows and reproduces very fast almost throughout the year (Schurink & Griffiths 1991; Calvo-Ugarteburu & McQuaid 1998; Branch & Steffani 2004; Sadchatheeswaran et al. 2015). Estimated as reaching a total intertidal biomass of

about 50 000 tons in South Africa (Griffiths et al. 1992), the mussel is the most successful alien species on the South African coastline, becoming the most dominant intertidal organism and out-competing most of the indigenous mussel and limpet species (Griffiths et al. 1992; Robinson & Griffiths 2002; Branch & Steffani 2004; Robinson et al. 2005a; Assis et al. 2015). But despite being the most dominant mussel species in the intertidal zone, the Mediterranean Mussel is outperformed in the subtidal zone by native mussel species (Skein et al. 2018). It is also limited by temperature preferring the cooler sections of the southern Africa coastlines to the warmer sections (Assis et al. 2015).

While oystercatchers and the aquaculture industries have benefited from the invasion of the Mediterranean mussel through increased food biomass, one of the losers has been a native predatory crab *Ovalipes trimaculatus* which occupies the surf zone of sandy beaches (Branch & Steffani 2004; Coleman & Hockey 2008). The recruits of the Mediterranean Mussel settle on the eyestalks and mouthparts of the crab causing mass mortality of the crab (Branch & Steffani 2004). The extensive foraging activity of the oystercatchers in the intertidal zone may then contribute significantly to the moderation of local assemblages of intertidal flora and fauna and so community structure because the species may be a significant mussel predator (Hockey 1997; Coleman & Hockey 2008).

Another factor considered to have contributed significantly to the population increase of the oystercatchers is conservation management intervention (Williams et al. 2004; Loewenthal 2007). Human disturbance in the form of chick predation by dogs, pedestrians and off-road vehicles accidentally crushing eggs and the inability of adults to forage and provision their chicks adequately in proximity to human activities, has inhibited the growth of the population of oystercatchers, particularly on mainland sites across their range (Jeffery 1987; Leseberg et al. 2000; Jeffery & Scott 2005). Increased protection for otherwise unprotected mainland breeding sites of oystercatchers and the banning of off-road vehicles from the South African beaches since 2001 have contributed significantly to the recovery of the species (Williams et al. 2004; Loewenthal et al. 2016; Brown et al. 2019).

On Robben Island specifically, the closure of the prison in 1996, which caused the human population size and associated human activities like angling to decrease, as well as the culling of the feral cat population on the island, have resulted in improved breeding success of oystercatchers on the island (Tjørve 2006; Spiby 2012). However, the declaration of the

island as a World Heritage Site because of its cultural value has made Robben Island a choice destination site for thousands of tourists. The number of tourists visiting the island during summer (the period when the oystercatchers breed) increased from about 1000 visitors per day in the early 2000s to about 1800–2000 visitors in recent years (UNESCO World Heritage Committee 2003; Robben Island Museum 2017). The activities of the tourists are restricted to the portion of the island that coincides largely with the settlement area where the remaining resident population resides on the island. The oystercatchers occupying this portion of the island experienced the lowest breeding success. This was also the section of the island where I observed a nest where eggs were almost trampled and eventually removed by a child. The low breeding success experienced by oystercatchers in the section of the island with the highest human presence and the removal of eggs by a child suggest some level of impact of human disturbance on the Robben Island population of oystercatchers, despite the island being a protected and managed site. Oystercatchers generally are vulnerable to disturbances when nesting in proximity to human settlements (Van de Voorde et al. 2015; Loewenthal et al. 2016).

The increases in oystercatcher population size, at least for the Robben Island population, could also have resulted from increases in temperature because nest survival increased with the maximum temperature experienced by eggs during the exposure period of the nest (Chapter Six). Temperature increases could potentially decrease predation if it reduces the activity patterns of predatory snakes or even other types of predators. For example, although nest predation probability increased with moderate increases in temperature, it declined drastically at extreme air temperatures (Chapter Five), suggesting that high-temperature increases could improve breeding success through its effect on nest predators. Also, temperature increases could improve embryo development, and so shorten the incubation period, thereby reducing the period over which the nest is exposed to potential threats (Martin et al. 2007; Mueller et al. 2019), provided that the eggs are actively tended by adults most of the time to prevent direct exposure to solar radiation. The impact of temperature increases on species is likely to vary by locality and according to the baseline temperatures in the region, and the extent to which other populations of oystercatchers are being influenced by rising temperature generally is yet to be determined.

Upon fledging, juvenile oystercatchers are believed to disperse from their natal grounds to nurseries in the northern part of the species range (southern Angola, central and northern Namibia) and aggregate there until maturity before returning to their natal grounds to find territories on which to settle (Leseberg 2001; Hockey 2003; Rao et al. 2014). Because the reproductive output in many unprotected mainland sites is usually below that required to maintain a stable population, immigration into less favourable mainland sites (which could be considered as sink populations) from island sites (which could be considered as source populations) are speculated to occur at regional levels (Vernon 2004; Jeffery & Scott 2005). It seems likely that returning birds which are unable to find territories in their natal grounds on which to settle may move to other sites in the search for territories. It remains unclear to what extent the ongoing increases in the population size of the species across its global range represents effects of actual reproductive success across most sites or whether the increases are due to local movements between sites (Brown et al. 2019).

Under the current increases in population size and the potential of a further narrowing of the shore due to projected sea-level rise and increased storminess (as discussed further in Section 7.3), the carrying capacity of Robben Island, and likely other island sites, may reduce. If that happens, high-quality pairs may take up the wider territories while lower-quality individuals might be forced to occupy poorer territories which increases nest vulnerability to predation and being washed away by storm surges or they could forgo breeding altogether (Burger 1984; Ens et al. 1992; Ariew & Lewontin 2004; Flemming et al. 2019; Southwell & Emmerson 2020). It is also possible for oystercatchers to adopt new breeding strategies which allow multiple pairs to share a territory as the observations at some territories suggest that two oystercatcher pairs could use some form of temporal tactics to share the same territory (Appendix of Chapter Six). Oystercatchers may also be expected to colonise other mainland habitats like their European counterpart, however, the reliance on the ocean for food and thermoregulation opportunities may limit the possibility of oystercatchers' colonising inland habitats. However, they may eventually need to trade-off the foraging and thermoregulation benefits of the proximity of their nests to the ocean with that of increased nest losses to storm surges under future climate change. All these possibilities could have significant implications for the population dynamics and persistence of the species in the future.

7.3 Potential impacts of future climate change

1. Sea-level rise, increases in frequency and severity of extreme storm events

One of the effects of global warming is sea-level rise (Rahmstorf 2007). Global mean sea-level rose by an estimated 1.8 ± 0.3 mm (0.18 cm) annually between 1950 and 2000 (Church et al. 2004). It has continued to increase more rapidly in the 20th century and larger increases are projected for the 21st century (IPCC 2007b; Rahmstorf et al. 2007). For example, there is a prediction of 0.5–2 m (50–200 cm) for a temperature rise of 4 °C by 2100 (Nicholls et al. 2011) and 27–112 cm by 2100 for a conservative temperature rise of 1.5–2 °C, over the same period (Jevrejeva et al. 2018). The interaction of sea-level rise, changes in storm intensities and dynamic wind patterns are predicted to cause severe weather events with high impacts on shoreline ecosystem and infrastructure (Theron & Rossouw 2008; Mather & Stretch 2012; Idier et al. 2019; Li et al. 2020). The impact of current levels of sea-level rise and increased severity of storm surges on shore-breeding species include severe nest losses in some breeding seasons in the Chatham Islands Oystercatcher *Haematopus chathamensis* (Schmechel & Paterson 2005), European Oystercatchers *Haematopus ostralegus* (van de Pol et al. 2010), African Black Oystercatchers (Calf & Underhill 2005), Saltmarsh Sparrow *Ammodramus caudacutus* in the USA (Bayard & Elphick 2011; Field et al. 2017), Snowy Plovers *Charadrius nivosus* in Mexico (Plaschke et al. 2019) and Black-winged Stilt *Himantopus himantopus* in Ghana (Taye 2019).

This study showed that oystercatchers currently exhibit two forms of adaptation to reduce vulnerability to current sea-levels and the predictable patterns of storm surges: nest-site selection and synchronising nest initiations with the semilunar spring tide cycle (Chapter Two). One of the key findings of this study with an implication for future climate change is the fact that oystercatchers could be constrained by the narrowness of the shore (Chapter Two). Given that more habitat would be lost under future climate change, oystercatchers may face even more difficulties securing territories that are wide enough for successful breeding. This is because habitat losses due to increased sediment transport and coastal erosion are some of the projected characteristics of increases in sea-level rise, and the frequency and severity of storm surges in the future (Reynolds et al. 2015; Widlansky et al. 2015). It has been suggested that the most severe losses are likely to occur in sites where the current coastline is unable to move inland because of steep topography or coastal

defence structures such as sea walls (Galbraith et al. 2002). For example, a 39–55% reduction in the size of the group of islands on which American Oystercatchers *Haematopus palliatus* breed along Florida's Gulf Coast due to climate change-induced sea-level rise and increased magnitude of storms have been observed (Vitale et al. 2020). In South Africa, 80% of sandy shores are susceptible to a large variability in storm intensity and increases in wave heights resulting in increased coastal sediment transport and erosion (Theron & Rossouw 2008). No study has been conducted to estimate the specific rate or amount of loss of the shoreline on Robben Island, yet. However, some parts of the beach show obvious signs of gradual erosion and since infrastructures such as roads and in some areas, buildings restrict the expansion of the shore, the breeding space of the oystercatchers in such areas is shrinking and likely to continue to shrink into the future.

Significant impacts of future increases in sea-level rise, and frequency, and severity of storm surges on the fitness and persistence of coastal dwelling or breeding species may occur through two means in the future: an indirect path which involves increased vulnerability because of the narrowness of shorelines and a direct impact involving direct nest losses to increased variability, frequency, and severity of storm events. The use of the semilunar spring tide cycle by oystercatchers and other coastal breeding birds to time the onset of a nest in an adaptive manner (Shriver et al. 2007; Plaschke et al. 2019) may become less effective in protecting their nests if high variability of wind patterns and other local conditions interact with increased frequency of storm surges to cause surges that are equally or even more severe than those associated with spring high tides. These likelihoods may decrease the carrying capacity of offshore islands, decrease breeding productivity and even adult body condition (if it affects their feeding opportunities (Galbraith et al. 2002; Burger et al. 2018)) thereby impacting population dynamics (van de Pol et al. 2010). Given that the offshore islands of southern Africa support the healthiest populations of oystercatchers across its global range (Hockey 1983b, 1983a; Loewenthal et al. 2015), the effects of climate change on island breeding populations may have implications for the global population of the species.

2. Temperature increases

Current increases in mean and extreme temperature are examples of environmental constraints faced by living organisms especially during the energetically demanding period

of reproduction (AlRashidi et al. 2010; DuRant et al. 2012; AlRashidi 2016; van de Ven et al. 2019; Cook et al. 2020). Future climate change is projected to be characterised by a larger increase in mean global temperature, frequency, and severity of heatwaves (IPCC 2007a; Coffel et al. 2018). Understanding the current adaptations employed by species to deal with ongoing climate change could be useful in predicting vulnerability to future projected climate change (Theron & Rossouw 2008; Durant et al. 2019).

The impacts of increases in temperature due to climate change on the fitness, population dynamics and persistence of avian species have been both positive and negative. For example, Weiser et al. (2018) investigated the impact of rising temperature on the reproductive output and other life-history traits of 17 species of Arctic-breeding shorebirds at multiple sites for 7 years and found that rising temperature resulted in early breeding, longer breeding season, shorter incubation length, a higher probability of full clutches and high breeding success in most of the 17 species. Similarly, due to increases in spring temperatures, historically single-brooded Pied Flycatchers *Ficedula hypoleuca* in Netherlands and Switzerland have been observed to commence breeding earlier than usual and to take advantage of the extended favourable condition to lay a second clutch within a single season (Both et al. 2019). Raising two successful broods per season significantly enhanced the reproductive success of the species thereby having positive population impacts (Both et al. 2019).

However, several species face increasing challenges in dealing with excessive heat loads especially during incubation (Conradie et al. 2019; Durant et al. 2019). The challenge of dealing with increased heat loads during incubation is the increased risk of being unable to forage sufficiently to maintain optimal body mass and exposure to lethal dehydration especially in habitats where water sources are scarce (Bartholomew & Cade 1963; McKechnie & Wolf 2010; Conradie et al. 2020). In dealing with increased heat loads some species prioritise adult survival over egg viability by abandoning their nests, leaving them exposed to threatening temperatures thereby reducing hatching success. For example, incubating Pied Babblers *Turdoides bicolor* in the Kalahari desert of South Africa (Bourne 2020) and Jacky Winters *Microeca fascinans* in Australia (Sharpe et al. 2019) leave their nests on hot days exposing their eggs to temperatures that lead to poor hatching success.

On Robben Island where this study was conducted air temperature rose as high as 37°C while the ground level temperature was as high as 58°C (Chapter Three). The mean daily air temperature has not increased significantly over the nearly two decades of data examined, probably because of the short period examined. However, the number of days in the breeding season when temperatures exceeded those at which oystercatchers pant heavily has increased significantly (Chapter Three). I examined the impacts of temperature on the incubation bout schedules and on-bout thermoregulation behaviours of oystercatchers (Chapters Three and Four). Oystercatchers used several behavioural flexibilities to cope with the current levels of heat loads (discussed above). These behavioural adaptations and the thermoregulation advantage of the proximity of their nesting sites to the ocean appear to enable oystercatchers to meet their energy and water needs without compromising the viability of their eggs under current climate conditions (Chapters Three and Four). This may continue into the near future and may help the oystercatchers to cope with larger temperature increases in the distant future.

However, the impact of rising temperature on breeding oystercatchers may be exacerbated by anthropogenic disturbances (and sometimes other wildlife) which cause incubating adults to leave their nests exposed during the heat of the day (Chapter Four). This is because, as noted above, both parents incubated in a manner that maintained a very high overall nest attentiveness and rarely left their nests unattended unless disturbed by external factors (Chapter Four). Such forced exposure during the warmest hours of the day (usually between 10h00 to 16h00) may have exposed some eggs to high temperatures causing the inability of some to hatch properly (as observed in some nests) (Chapter Four). Anthropogenic disturbances causing prolonged exposure of eggs during the heat of the day could be one mechanism through which the impact of climate change-induced rising temperature would act to reduce breeding productivity of oystercatchers. This highlights the potential of anthropogenic disturbances to make most of the existing constraints experienced by oystercatchers, and indeed other wildlife in general, harder for them to deal with. Conservation management efforts which reduce human disturbances significantly could assist organisms to cope with these pressures under future climate change.

Another impact of climate change on avian species is dealing with the biotic components of the environment which are themselves influenced by climate change. For example, climate

change may lead to ecological mismatches between the timing of maximum food demand during key breeding events of a species and that of the peak availability of its invertebrate prey item, causing poor breeding outcomes (Visser & Gienapp 2019). Increased temperature may also influence vegetation growth rate in a manner that provides nest concealment for birds breeding early in the season thereby reducing predation rate and increasing breeding success (Laidlaw et al. 2020). But an overall negative ecological impact may occur if some species benefit extremely from increased vegetation either for protection from predators or as food and experience a disproportionate increase in population size relative to other species in the community. For example, the population of Ross' Geese *Chen rossii* in North America increased significantly over time and exerted negative impacts on cover-nesting shorebirds that breed in the same areas as them (Flemming et al. 2019). The burgeoning population of the goose usually forages on the vegetation that is used as nest concealment by shorebirds and also attracts predators making the breeding habitat less favourable for the shorebirds, thereby causing their population to decline (Flemming et al. 2019). Another example involves the effect of temperature on the activities of potential nest predators as observed in the Cape Rockjumper *Chaetops frenatus* breeding in South Africa (Oswald et al. 2020). As climate change caused temperature increases, the activity of a predatory snake, the Boomslangs *Dispholidus typus*, increased, causing increased nest predation as temperature increased, thereby decreasing the overall nest survival of Cape Rockjumper (Oswald et al. 2020). As temperature continues to increase into the future, the demography of bird species which are significantly impacted by predatory snakes may be influenced either positively or negatively depending on the responses of the various snake species to increases in temperature and vegetation structure under future climate change. This emphasises the need for more research into the biology of nest predators of birds in general and particularly those involving predatory snakes (Weatherhead & Blouin-Demers 2004). Temperature increases may also impact the distribution of the Mediterranean Mussel in the future because the species' current distribution along the southern African coastline is limited by temperature, with the species preferring the cooler regions (Assis et al. 2015). If the preferred cooler parts of the coastline experience significant temperature increase in the future, the mussel may be impacted with likely significant implications for the oystercatchers in terms of reduced food biomass which could have negative impacts on the recent global population recovery of the species.

7.4 Prospectus

7.41 Management recommendations for African Black Oystercatchers

1. Given that there is no evidence to show that Kelp Gulls negatively influence the productivity of oystercatchers on Robben Island, it is recommended that the Robben Island Kelp Gull population should not be controlled on the account of oystercatchers.
2. Given that Mole Snakes are indigenous to Robben Island and constrained by environmental factors such as temperature, the increases in oystercatcher population size, the fact that the number of fledgelings per pair per season appears around that needed to maintain a stable population, it is recommended that no management intervention should be taken to control the population of Mole Snakes on the island.
3. However, the influence of Kelp Gulls and Mole Snakes on other wildlife may differ from that observed for oystercatchers in this study. Hence, research into the ecological relationships between these two species on other wildlife on the island is recommended.
4. Given the importance of habitat width to minimising the risk of predation and that of nest losses to storm surges, it is recommended that habitat management interventions which seek to broaden the narrow breeding areas of the oystercatchers should be considered in the future to increase the resilience of oystercatchers to the impacts of future climate change. As this is likely to be expensive and perhaps unachievable with human development along the top edge of vulnerable beaches, attempts at further minimising human disturbance on breeding beaches should be made. Continued efforts in creating awareness for the need to protect breeding birds should be made.
5. Since it takes about four to five years for juvenile oystercatchers to recruit into their natal population, the effects of potential poor breeding outputs which may occur in the future may not be immediately noticed. Hence continued monitoring of the breeding productivity of the species in key island breeding sites is recommended. The monitoring should watch out for the density-dependent effects that would eventually kick in to control the species population growth. For Robben Island, a gap exists in breeding productivity data as the number of fledgelings per pair per year

and the breeding population size exist only for 2001 to 2004 breeding seasons alone and now also 2017 to 2018 (from this study). Monitoring either did not occur at all or was not completed to enable such estimates to be made for subsequent years. Continued monitoring which endeavours to collect such key data annually will be useful.

6. It is recommended that a central study system which evaluates the vulnerability of oystercatchers to future climate change in the key island and mainland breeding sites across its range be implemented. Examination of changes to habitat extents of these sites under increased sea-level rise and storminess may provide information on the rate of habitat loss.

7.42 Future research

1. The current study did not evaluate the vulnerability of juvenile oystercatchers to climate change. It is recommended that young oystercatchers should be studied in the sites to which they disperse and stay before eventually returning to their natal site to breed, to examine their vulnerability to climate change during that stage of their life-history.
2. It is recommended that research be made into the movement of individuals between localities to foster the understanding of sink and source dynamics of the species across its range. New technologies which enable insight into the spatial use and tracking of the movement of individuals between sites could be employed.
3. It is recommended that further research be made into understanding the interaction between anthropogenic disturbances and the challenges posed by future climate change to determine how best to channel management in improving the resilience of species to future climate change.
4. During this research at least two ringed breeding adults (known identity), disappeared and were never observed again even in subsequent breeding years. It is unclear whether they emigrated or died. Also, two dead adults were observed during this study, one without a ring and the other with an old metal ring which could not be read because the numbers were already wiped out from being worn by the bird for several years. The nature of the ring indicates that the bird would have been ringed during 2001, 2002 or 2003 breeding seasons and should be not younger than

16 years. It is recommended that research be made into the adult survival rates to track changes that may be occurring in adult survival rates under current constraints and population increase.

5. It is recommended that research be made into the biology of the Mole Snake population on Robben Island to provide insight into the behaviour and demography of the snake, particularly how temperature and increased vegetation may influence the species.
6. Future studies using more samples and the exact nest initiation dates (rather than the onset of incubation alone) could be used to detect a stronger effect of the use of spring tide water levels by coastal birds to inform nest-sites which are beyond the reach of subsequent high tides.
7. It is recommended that research be carried out to determine the upper thermal tolerance threshold of oystercatchers' eggs and the physiological heat tolerance of adult oystercatchers to further provide insight into the impacts of repeated exposure to high temperatures on adults and eggs especially when exposed for an extended period during the heat of the day.
8. The increasing risk of lethal dehydration faced by birds as temperature increases may also be true for other bird species on Robben Island. Research into how impactful the installation of freshwater holes in strategic parts of the island would be for the bird species on the island might help future management to increase the resilience of those birds to increased heat loads especially during the day.
9. Future research could explore the extent and rate of beach habitat loss to increased erosion due to increasing sea-level rise and increased storminess as well as estimate the current size of the breeding habitat available to the oystercatchers using digitized historic satellite images.
10. The estimates of the available breeding habitat together with key demography data could be used to make a population model considering habitat availability and reduction due to sea-level rise and increased (or decreased) human disturbance. This would allow predictions of productivity to be made in terms of beach width which would then allow modelling of how oystercatcher population growth rate would change as sea-level rises with a topographical map of Robben Island to predict future beach width.

Overall, the results from this thesis show that oystercatchers possess several behavioural adaptations that help them to cope with the many challenges that characterise their breeding habitats in a manner consistent with the predictions of life-history theories. These findings improve our understanding of the breeding ecology and behavioural adaptations of the oystercatchers which might help them to cope with climate change in the near and distant future. The results also improve our knowledge of how birds in general and coastal breeding birds may be vulnerable to future climate change and the likely flexibilities that species might use to cope. These results provide new insights on which oystercatcher management decisions and further studies can be based.



References

- Adams N, Kerley Z G, Watson J. 1999. Disturbance of incubating African Black Oystercatchers: is heating of exposed eggs a problem? *Ostrich* **70**:225–228.
- Afton AD. 1980. Factors affecting incubation rhythms of Northern Shovelers. *Condor* **82**:132–137.
- Akresh ME, Ardia DR, King DI. 2017. Effect of nest characteristics on thermal properties, clutch size, and reproductive performance for an open-cup nesting songbird. *Avian Biology Research* **10**:107–118.
- Albright TP, Mutiibwa D, Gerson AR, Smith EK, Talbot WA, O'Neill JJ, McKechnie AE, Wolf BO. 2017. Mapping evaporative water loss in desert passerines reveals an expanding threat of lethal dehydration. *Proceedings of the National Academy of Sciences of the United States of America* **114**:2283–2288.
- Allan JB, Hockey PAR. 1984. Behavioral and vocal affinities of the African Black Oystercatcher (*Haematopus moquini*). *The Wilson Bulletin* **96**:656–671.
- Allen WL, Street SE, Capellini I. 2017. Fast life history traits promote invasion success in amphibians and reptiles. *Ecology Letters* **20**:222–230.
- AlRashidi M. 2016. The challenge of coping in an extremely hot environment: a case study of the incubation of Lesser Crested Terns (*Thalasseus bengalensis*). *Waterbirds* **39**:215–221.
- AlRashidi M, Kosztolányi A, Küpper C, Cuthill IC, Javed S, Székely T. 2010. The influence of extreme hot environment on biparental incubation of a ground-nesting shorebird, the Kentish Plover *Charadrius alexandrinus*. *Frontiers in Zoology* **7**:1–10.
- AlRashidi M, Kosztolányi A, Shobrak M, Küpper C, Székely T. 2011. Parental cooperation in an extreme hot environment: Natural behaviour and experimental evidence. *Animal Behaviour* **82**:235–243.
- Amat JA, Masero JA. 2004a. Predation risk on incubating adults constrains the choice of thermally favourable nest sites in a plover. *Animal Behaviour* **67**:293–300.
- Amat JA, Masero JA. 2004b. How Kentish Plovers, *Charadrius alexandrinus*, cope with heat stress during incubation. *Behavioral Ecology and Sociobiology* **56**:26–33.
- Amat JA, Masero JA. 2007. The functions of belly-soaking in Kentish Plovers *Charadrius alexandrinus*. *Ibis* **149**:91–97.
- Amat JA, Masero JA. 2009. Belly-soaking: A behavioural solution to reduce excess body heat in the Kentish Plover *Charadrius alexandrinus*. *Journal of Ethology* **27**:507–510.
- Amininasab SM, Kingma SA, Birker M, Hildenbrandt H, Komdeur J. 2016. The effect of ambient temperature, habitat quality and individual age on incubation behaviour and incubation feeding in a socially monogamous songbird. *Behavioral Ecology and Sociobiology* **70**:1591–1600.
- Andes AK, Shaffer TL, Sherfy MH, Hofer CM, Dovichin CM, Ellis-Felege SN. 2019. Accuracy of nest fate classification and predator identification from evidence at nests of Least Terns and Piping Plovers. *Ibis* **161**:286–300.

- Andes AK, Sherfy MH, Shaffer TL, Ellis-Felege SN. 2020. Plasticity of Least Tern and Piping Plover nesting behaviors in response to sand temperature. *Journal of Thermal Biology*:102579.
- Angilletta Jr. MJ, Cooper BS, Schuler MS, Boyles JG. 2010. The evolution of thermal physiology in endotherms. *Frontiers in Bioscience* **E2**:861–881.
- Anteau MJ, Sherfy MH, Wiltermuth MT. 2012. Selection indicates preference in diverse habitats: A Ground-Nesting bird (*Charadrius melodus*) using reservoir shoreline. *PLoS ONE* **7**:1–9.
- Ar A, Rahn H. 1980. Water in the avian egg: Overall budget of incubation. *American Zoologist* **20**:373–384.
- Ariew A, Lewontin RC. 2004. The confusions of fitness. *The British Journal for the Philosophy of Science* **55**:347–363.
- Ashmole NP. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* **103 b**:458–473.
- Assis J, Zupan M, Nicastro KR, Zardi GI, McQuaid CD, Serrão EA. 2015. Oceanographic conditions limit the spread of a marine invader along southern African shores. *PLoS ONE* **10**:e0128124.
- Auer SK, Bassar RD, Martin TE. 2007. Biparental incubation in the Chestnut-vented Tit-babbler *Parisoma subcaeruleum*: Mates devote equal time, but males keep eggs warmer. *Journal of Avian Biology* **38**:278–283.
- Badyaev A V, Ghalambor CK. 2001. Evolution of life histories along elevational gradients: trade-off between parental Care and fecundity. *Ecology* **82**:2948–2960.
- Bailey LD, Ens BJ, Both C, Heg D, Oosterbeek K, van de Pol M. 2019. Habitat selection can reduce effects of extreme climatic events in a long-lived shorebird. *Journal of Animal Ecology* **00**:1–12.
- Bailey LD, Ens BJ, Both C, Heg D, Oosterbeek K, van De Pol M. 2017. No phenotypic plasticity in nest-site selection in response to extreme flooding events. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**:20160139.
- Bakken GS, Santee WR, Erskine DJ. 1985. Operative and standard operative temperature: Tools for thermal energetics studies. *Integrative and Comparative Biology* **25**:933–943.
- Barbraud C et al. 2018. Density dependence, prey accessibility and prey depletion by fisheries drive Peruvian seabird population dynamics. *Ecography* **41**:1092–1102.
- Barbraud C, Rolland V, Jenouvrier S, Nevoux M, Delord K, Weimerskirch H. 2012. Effects of climate change and fisheries bycatch on southern ocean seabirds: A review. *Marine Ecology Progress Series* **454**:285–307.
- Barrientos R, Barbosa A, Valera F, Moreno E. 2007. Temperature but not rainfall influences timing of breeding in a desert bird, the trumpeter finch (*Bucanetes githagineus*). *Journal of Ornithology* **148**:411–416.
- Bartholomew GA., Cade TJ. 1963. The water economy of land birds. *The Auk* **80**:504–539.
- Bartholomew GA, Dawson WR. 1979. Thermoregulatory behavior during incubation in Heermann's Gulls. *Physiological Zoology* **52**:422–437.

- Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**:1–48.
- Bates MF, Little IT. 2013. Predation on the eggs of ground-nesting birds by *Dasypeltis scabra* (Linnaeus, 1758) in the moist highland grasslands of South Africa. *African Journal of Herpetology* **62**:125–134. Taylor & Francis.
- Battley PF, Rogers DI, Piersma T, Koolhaas A. 2003. Behavioural evidence for heat-load problems in Great Knots in tropical Australia fuelling for long-distance flight. *Emu* **103**:97–103.
- Bayard TS, Elphick CS. 2011. Planning for sea-level rise: quantifying patterns of Saltmarsh Sparrow (*Ammodramus Caudacutus*) nest flooding under current sea-level conditions. *The Auk* **128**:393–403.
- Beever EA, Hall LE, Varner J, Loosen AE, Dunham JB, Gahl MK, Smith FA, Lawler JJ. 2017. Behavioral flexibility as a mechanism for coping with climate change. *Frontiers in Ecology and the Environment* **15**:299–308.
- Beintema AJ, Muskens GJDM. 1987. Nesting success of birds breeding in Dutch agricultural grasslands. *Journal of Applied Ecology* **24**:743–758.
- Bell M. 2017. Population size, breeding success and predators of Black-fronted Tern (*Chlidonias albobristatus*) in the Upper Clarence River catchment, New Zealand. *The Ornithological Society of New Zealand* **64**:154–161.
- Bellamy PE, Burgess MD, Mallord JW, Cristinacce A, Orsman CJ, Davis T, Grice P V., Charman EC. 2018. Nest predation and the influence of habitat structure on nest predation of Wood Warbler *Phylloscopus sibilatrix*, a ground-nesting forest passerine. *Journal of Ornithology* **159**:493–506.
- Benvenuti B, Walsh J, O'Brien KM, Kovach AI. 2018. Plasticity in nesting adaptations of a tidal marsh endemic bird. *Ecology and Evolution* **8**:10780–10793.
- Berven KA, Gill DE. 1983. Interpreting geographic variation in life-history traits. *American Zoologist* **23**:85–97.
- Bhatnagar T, Tolstoy M, Waldhauser F. 2016. Influence of fortnightly tides on earthquake triggering at the East Pacific Rise at 9°50'N. *Journal of Geophysical Research: Solid Earth* **121**:1262–1279.
- Birdlife International. 2019. Species factsheet: African Oystercatcher (*Haematopus moquini*) - BirdLife species factsheet. Available from <http://datazone.birdlife.org/species/factsheet/22693627> (accessed June 6, 2019).
- Birkhead T. 1991. *The Magpies: The ecology and behaviour of Black-billed and Yellow-billed Magpies*, 1st edition. T & AD Poyser, London.
- Blévin P, Shaffer SA, Bustamante P, Angelier F, Picard B, Herzke D, Moe B, Gabrielsen GW, Bustnes JO, Chastel O. 2020. Contaminants, prolactin and parental care in an Arctic seabird: Contrasted associations of perfluoroalkyl substances and organochlorine compounds with egg-turning behavior. *General and Comparative Endocrinology* **291**:113420.
- Bodrati A, Cockle KL. 2017. Nest predation and interspecific nesting associations involving

- Plumbeous Kite (*ictinia plumbea*) and Becards (*pachyramphus spp.*). *Ornitologia Neotropical* **28**:201–207.
- Booty JM, Underwood GJC, Parris A, Davies RG, Tolhurst TJ. 2020. Shorebirds affect ecosystem functioning on an intertidal mudflat. *Frontiers in Marine Science* **7**:685.
- Both C, Ubels R, Ravussin PA. 2019. Life-history innovation to climate change: can single-brooded migrant birds become multiple breeders? *Journal of Avian Biology* **50**:e01951.
- Both C, van Asch M, Bijlsma RG, van den Burg AB, Visser ME. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *The Journal of animal ecology* **78**:73–83.
- Boulton RL, Cassey P. 2012. How avian incubation behaviour influences egg surface temperatures: Relationships with egg position, development and clutch size. *Journal of Avian Biology* **43**:289–296.
- Bourne AR. 2020. Can sociality buffer the impacts of climate change on a cooperatively-breeding bird, the Southern Pied Babbler *Turdoides bicolor*?
- Bourne AR, Ridley AR, McKechnie AE, Spottiswoode CN, Cunningham SJ. 2021. Dehydration risk is associated with reduced nest attendance and hatching success in a cooperatively breeding bird, the Southern Pied babbler *Turdoides bicolor*. *Conservation Physiology* **9**:1–16.
- Boyles JG, Seebacher F, Smit B, McKechnie AE. 2011. Adaptive thermoregulation in endotherms may alter responses to climate change. *Integrative and Comparative Biology* **51**:676–690.
- Braby J, Underhill LG. 2007. Was poor breeding productivity of African Black Oystercatchers on Robben Island in 2004/05 caused by Feral Cats, Kelp Gulls, Mole Snakes or the Sumatra tsunami? *Wader Study Group Bulletin* **113**:66–70.
- Brambilla M, Scridel D, Sangalli B, Capelli F, Pedrini P, Bogliani G, Rubolini D. 2019. Ecological factors affecting foraging behaviour during nestling rearing in a high-elevation species, the White-winged Snowfinch (*Montifringilla nivalis*). *Ornis Fennica* **96**:142–151.
- Branch B. 2002. A photographic guide to snakes and other reptiles of Southern Africa. Struik Publishers, Cape Town, South Africa.
- Branch GM, Steffani NC. 2004. Can we predict the effects of alien species? A case-history of the invasion of South Africa by *Mytilus galloprovincialis* (Lamarck). *Journal of Experimental Marine Biology and Ecology* **300**:189–215.
- Brightsmith DJ, Hobson EA, Martinez G. 2018. Food availability and breeding season as predictors of geophagy in Amazonian Parrots. *Ibis* **160**:112–129.
- Brooke MDL. 2019. Extreme rainfall-related clutch size variation in the Critically Endangered Raso Lark *Alauda razae* of the arid Cape Verde islands. *Bird Conservation International* **29**:321–326.
- Brosset P, Lloret J, Muñoz M, Fauvel C, Van Beveren E, Marques V, Fromentin JM, Ménard F, Saraux C. 2016. Body reserves mediate trade-offs between life-history traits: New insights from small pelagic fish reproduction. *Royal Society Open Science* **3**:160202.
- Brown JH, Marquet PA, Taper ML. 1993. Evolution of body size: Consequences of an

- energetic definition of fitness. *The American Naturalist* **142**:573–584.
- Brown M, Arendse B, Mels B, Lee ATK. 2019. Bucking the trend: the African Black Oystercatcher as a recent conservation success story. *Ostrich* **90**:327–333.
- Brown M, Downs CT. 2003. The role of shading behaviour in the thermoregulation of breeding Crowned Plovers (*Vanellus coronatus*). *Journal of Thermal Biology* **28**:51–58.
- Brown M, Downs CT. 2004. Daily and seasonal differences in body and egg temperature in free-ranging Crowned Lapwings (*Vanellus coronatus*). *African Zoology* **39**:115–122.
- Brua RB, Nuechterlein GL, Buitron D. 1996. Vocal response of Eared Grebe embryos to egg cooling and egg turning. *The Auk* **113**:525–533.
- Bueno-Enciso J, Barrientos R, Ferrer ES, Sanz JJ. 2017. Do extended incubation recesses carry fitness costs in two cavity-nesting birds? *Journal of Field Ornithology* **88**:146–155.
- Bulla M et al. 2016. Unexpected diversity in socially synchronized rhythms of shorebirds. *Nature* **540**:109–113.
- Bulla M. 2016. Behavioural rhythms and parental cooperation in biparentally incubating shorebirds. Max-Planck-Institut für Ornithologie, Ludwig-Maximilians-Universität München.
- Bulla M, Cresswell W, Rutten AL, Valcu M, Kempenaers B. 2015a. Biparental incubation-scheduling: no experimental evidence for major energetic constraints. *Behavioral Ecology* **26**:30–37.
- Bulla M, Oudman T, Bijleveld AI, Piersma T, Kyriacou CP. 2017. Marine biorhythms: Bridging chronobiology and ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**:20160253.
- Bulla M, Stich E, Valcu M, Kempenaers B. 2015b. Off-nest behaviour in a biparentally incubating shorebird varies with sex, time of day and weather. *Ibis* **157**:575–589.
- Bulla M, Valcu M, Rutten AL, Kempenaers B. 2014. Biparental incubation patterns in a high-arctic breeding shorebird: how do pairs divide their duties? *Behavioral Ecology* **25**:152–164.
- Burger J. 1984. Pattern, mechanism, and adaptive significance of territoriality in Herring Gulls (*Larus argentatus*). *Ornithological Monographs* **34**:1–92.
- Burger J. 2018. Use of intertidal habitat by four species of shorebirds in an experimental array of oyster racks, reefs and controls on Delaware Bay, New Jersey: Avoidance of oyster racks. *Science of the Total Environment* **624**:1234–1243.
- Burger J, Niles L, Jeitner C, Gochfeld M. 2018. Habitat risk: Use of intertidal flats by foraging Red Knots (*Calidris canutus rufa*), Ruddy Turnstones, (*Arenaria interpres*), Semipalmated Sandpipers (*Calidris pusilla*), and Sanderling (*Calidris alba*) on Delaware Bay beaches. *Environmental Research* **165**:237–246.
- Buxton EJM. 1961. The inland breeding of the oystercatcher in Great Britain, 1958-59. *Bird Study* **8**:198–209.
- Cain III JW, Krausman PR, Rosenstock SS, Turner JC. 2006. Mechanisms of thermoregulation and water balance in desert ungulates. *Wildlife Society Bulletin* **34**:570–581.

- Calf K. 2004. Mole Snake *Pseudaspis cana* predation of African Black Oystercatcher *Haematopus moquini* eggs. Wader Study Group Bulletin **104**:103–104.
- Calf K, Cooper J, Underhill L. 2003. First breeding records of Kelp Gulls *Larus dominicanus vetula* at Robben Island, Western Cape, South Africa. African Journal of Marine Science **25**:391–393.
- Calf KM, Underhill LG. 2002. Productivity of African Black Oystercatchers *Haematopus moquini* on Robben Island, South Africa, in the 2001–2002 breeding season. Wader Study Bulletin **99**:45–49.
- Calf KM, Underhill LG. 2005. Tidal impact on breeding African Black Oystercatchers on Robben Island, Western Cape, South Africa. Ostrich **76**:219–221.
- Calvo-Ugarteburu G, McQuaid CD. 1998. Parasitism and introduced species: Epidemiology of trematodes in the intertidal mussels *Perna perna* and *Mytilus galloprovincialis*. Journal of Experimental Marine Biology and Ecology **220**:47–65.
- Campobello D, Lindström M J, Di Maggio R, Sarà M. 2017. An integrated analysis of micro-and macro- habitat features as a tool to detect weather-driven constraints: A case study with cavity nesters. PLoS ONE **12**:e0174090.
- Cantar RV., Montgomerie RD. 1985. The influence of weather on incubation scheduling of the White-rumped Sandpiper (*Calidris fuscicollis*): A uniparental incubator in a cold environment. Behaviour **95**:261–289.
- Capstick LA, Sage RB, Madden JR. 2019. Predation of artificial nests in UK farmland by magpies (*Pica pica*): Interacting environmental, temporal, and social factors influence a nest's risk. European Journal of Wildlife Research **65**:1–11.
- Carey C. 1980. The ecology of avian incubation. BioScience **30**:819–824.
- Carlzon L, Karlsson A, Falk K, Lliess A, Møller S. 2018. Extreme weather affects Peregrine Falcon (*Falco peregrinus tundrius*) breeding success in South Greenland. Ornis Hungarica **26**:38–50.
- Carneiro C, Gunnarsson TG, Alves JA. 2020. Linking weather and phenology to stopover dynamics of a long-distance migrant. Frontiers in Ecology and Evolution **8**:1–10.
- Carnicer J, Brotons L, Stefanescu C, Peñuelas J. 2012. Biogeography of species richness gradients: Linking adaptive traits, demography and diversification. Biological Reviews **87**:457–479.
- Carr JM, Lima SL. 2012. Heat-conserving postures hinder escape: A thermoregulation-predation trade-off in wintering birds. Behavioral Ecology **23**:434–441.
- Carroll RL, Davis CA, Fuhlendorf SD, Elmore RD, DuRant SE, Carroll JM. 2018. Avian parental behavior and nest success influenced by temperature fluctuations. Journal of Thermal Biology **74**:140–148.
- Carter AW, Hopkins WA, Moore IT, Durant SE. 2014. Influence of incubation recess patterns on incubation period and hatchling traits in wood ducks *Aix sponsa*. Journal of Avian Biology **45**:273–279.
- Castro M, Masero JA, Pérez-Hurtado A, Amat JA, Megina C. 2009. Sex-related seasonal differences in the foraging strategy of the Kentish Plover. The Condor **111**:624–632.

- Chakraborty U. 2018. Effects of different phases of the lunar month on living organisms. *Biological Rhythm Research* **00**:1–29.
- Chambers LE et al. 2013. Phenological changes in the southern hemisphere. *PLoS ONE* **8**:e75514.
- Chaurand T, Weimerskirch H. 1994. Incubation routine, body mass regulation and egg neglect in the Blue Petrel *Halobaena caerulea*. *Ibis* **136**:285–290.
- Christians JK, Evanson M, Aiken JJ. 2001. Seasonal decline in clutch size in European starlings: A novel randomization test to distinguish between the timing and quality hypotheses. *Journal of Animal Ecology* **70**:1080–1087.
- Church JA, White NJ, Coleman R, Lambeck K, Mitrovica JX. 2004. Estimates of the regional distribution of sea level rise over the 1950–2000 period. *Journal of Climate* **17**:2609–2625.
- Clarke GM. 1995. Relationships between developmental stability and fitness: Application for Conservation Biology. *Conservation Biology* **9**:18–24.
- Clatterbuck CA, Young LC, VanderWerf EA, Naiman AD, Bower GC, Shaffer SA. 2017. Data loggers in artificial eggs reveal that egg-turning behavior varies on multiple ecological scales in seabirds. *The Auk* **134**:432–442.
- Clauser AJ, McRae SB. 2017. Plasticity in incubation behavior and shading by King Rails *Rallus elegans* in response to temperature. *Journal of Avian Biology* **48**:479–488.
- Coates SE, Wright BW, Carlisle JD. 2019. Long-billed Curlew nest site selection and success in the intermountain west. *Journal of Wildlife Management* **83**:1197–1213.
- Cockrem JF. 1995. Timing of seasonal breeding in birds, with particular reference to New Zealand birds. *Reproduction, Fertility and Development* **7**:1–19.
- Coe BH, Beck ML, Chin SY, Jachowski CMB, Hopkins WA. 2015. Local variation in weather conditions influences incubation behavior and temperature in a passerine bird. *Journal of Avian Biology* **46**:385–394.
- Coffel ED, Horton RM, Sherbinin A De. 2018. Temperature and humidity based projections of a rapid rise in global heat stress exposure during the 21st century. *Environmental Research Letters* **13**:014001.
- Coleman RA, Hockey PAR. 2008. Effects of an alien invertebrate species and wave action on prey selection by African black oystercatchers (*Haematopus moquini*). *Austral Ecology* **33**:232–240.
- Collins PM, Halsey LG, Arnould JPY, Shaw PJA, Dodd S, Green JA. 2016. Energetic consequences of time-activity budgets for a breeding seabird. *Journal of Zoology* **300**:153–162.
- Conradie SR, Woodborne SM, Cunningham SJ, McKechnie AE. 2019. Chronic, sublethal effects of high temperatures will cause severe declines in southern African arid-zone birds during the 21st century. *Proceedings of the National Academy of Sciences of the United States of America* **116**:14065–14070.
- Conradie SR, Woodborne SM, Wolf BO, Pessato A, Mariette MM, McKechnie AE. 2020. Avian mortality risk during heat waves will increase greatly in arid Australia during the 21st

- Century. Conservation Physiology **8**:1–14.
- Conway CJ, Martin TE. 2000a. Evolution of passerine incubation behavior: Influence of food, temperature, and nest predation. *Evolution* **54**:670–685.
- Conway CJ, Martin TE. 2000b. Effects of ambient temperature on avian incubation behavior. *Behavioral Ecology* **11**:178–188.
- Cook TR, Martin R, Roberts J, Häkkinen H, Botha P, Meyer C, Sparks E, Underhill LG, Ryan PG, Sherley RB. 2020. Parenting in a warming world: thermoregulatory responses to heat stress in an endangered seabird. *Conservation Physiology* **8**:1–13.
- Cooper CE, Hurley LL, Deviche P, Griffith SC. 2020. Physiological responses of wild Zebra Finches (*Taeniopygia guttata*) to heatwaves. *The Journal of Experimental Biology*:1–31.
- Cornell H. 1976. Search strategies and the adaptive significance of switching in some general predators. *American Naturalist* **110**:317–320.
- Cox WA, Pruett MS, Benson TJ, Chiavacci SJ, Frank III R. 2012. Development of camera technology for monitoring nests. Chapter 15. In: Ribic, CA; Thompson, FR, III; Pietz, PJ, eds. Video surveillance of nesting birds. *Studies in Avian Biology* (no. 43). Berkeley, CA: University of California Press:185–210.
- Cox WA, Thompson FR, Reidy JL. 2013. The effects of temperature on nest predation by mammals, birds and snakes. *The Auk* **130**:784–790.
- Crawford R, Dyer B. 2000. Wildlife of Robben Island, Bright Continent Guide. Avian Demography Unit, Cape Town.
- Crawford RJ, Underhill LG, Altwegg R, Dyer BM, Upfold L. 2009. Trends in numbers of Kelp Gulls *Larus dominicanus* off western South Africa, 1978 – 2007. *Ostrich* **80**:139–143.
- Crawley MJ. 2005. *Statistics: an introduction using R*. John Wiley and Sons, Ltd, Chichester, England.
- Cresswell W. 1997a. Nest predation: The relative effects of nest characteristics, clutch size and parental behaviour. *Animal Behaviour* **53**:93–103.
- Cresswell W. 1997b. Nest predation rates and nest detectability in different stages of breeding in Blackbirds *Turdus merula*. *Journal of Avian Biology* **28**:296–302.
- Cresswell W, Holt S, Reid JM, Whitfield DP, Mellanby RJ. 2003. Do energetic demands constrain incubation scheduling in a biparental species? *Behavioral Ecology* **14**:97–102.
- Cresswell W, Holt S, Reid JM, Whitfield DP, Mellanby RJ, Norton D, Waldron S. 2004. The energetic costs of egg heating constrain incubation attendance but do not determine daily energy expenditure in the Pectoral Sandpiper. *Behavioral Ecology* **15**:498–507.
- Cresswell W, Lind J, Quinn JL. 2010. Predator-hunting success and prey vulnerability: Quantifying the spatial scale over which lethal and non-lethal effects of predation occur. *Journal of Animal Ecology* **79**:556–562.
- Crick HQP, Gibbons DW, Magrath RD. 1993. Seasonal changes in clutch size in British birds. *Journal of Animal Ecology* **62**:263–273.
- Crick HQP, Sparks TH. 1999. Climate change related to egg-laying trends. *Nature* **399**:423–424.

- Cruz SM, Hooten M, Huyvaert KP, Proaño CB, Anderson DJ, Afanasyev V, Wikelski M. 2013. At-sea behavior varies with lunar phase in a nocturnal pelagic seabird, the Swallow-tailed Gull. *PLoS ONE* **8**:e56889.
- Cunningham SJ, Martin RO, Hockey PAR. 2015. Can behaviour buffer the impacts of climate change on an arid-zone bird? *Ostrich* **86**:119–126.
- Daan S, Dijkstra C, Tinbergen JM. 1990. Family planning in the Kestrel (*Falco tinnunculus*): The ultimate control of covariation of laying date and clutch size. *Behaviour* **114**:83–116.
- Dalziel AC, Rogers SM, Schulte PM. 2009. Linking genotypes to phenotypes and fitness: How mechanistic biology can inform molecular ecology. *Molecular Ecology* **18**:4997–5017.
- Dawson RD. 2008. Timing of breeding and environmental factors as determinants of reproductive performance of Tree Swallows. *Canadian Journal of Zoology* **86**:843–850.
- Dawson WR. 1982. Evaporative losses of water by birds. *Comparative Biochemistry and Physiology* **71A**:495–509.
- de Heij ME, van den Hout PJ, Tinbergen JM. 2006. Fitness cost of incubation in Great Tits (*Parus major*) is related to clutch size. *Proceedings: Biological Sciences Proc. R. Soc. B* **273**:2353–2361.
- De Marchi G, Chiozzi G, Fasola M. 2017. Predatory risk favours intermittent incubation of a colonial burrowing shorebird, the Crab Plover *Dromas ardeola*. *Journal of Ornithology* **158**:1081–1090.
- de Zwaan DR, Martin K. 2018. Substrate and structure of ground nests have fitness consequences for an alpine songbird. *Ibis* **160**:790–804.
- DeClerck FAJ, Chazdon R, Holl KD, Milder JC, Finegan B, Martinez-Salinas A, Imbach P, Canet L, Ramos Z. 2010. Biodiversity conservation in human-modified landscapes of Mesoamerica: Past, present and future. *Biological Conservation* **143**:2301–2313.
- Delia JRJ, Ramírez-Bautista A, Summers K. 2013. Parents adjust care in response to weather conditions and egg dehydration in a Neotropical glassfrog. *Behavioral Ecology and Sociobiology* **67**:557–569.
- Deroose-Wilson A, Fraser DJ, Karpanty MS, Hillman MD. 2015. Effects of overflights on incubating Wilson's Plover behavior and heart rate. *The Journal of Wildlife Management* **79**:1246–1254.
- Devries JH, Clark RG, Armstrong LM. 2018. Dynamics of habitat selection in birds: Adaptive response to nest predation depends on multiple factors. *Oecologia* **187**:305–318.
- DeWitt CB. 1967. Precision of thermoregulation and its relation to environmental factors in the Desert Iguana, *Dipsosaurus dorsalis*,. Source: *Physiological Zoology* **40**:49–66.
- Díaz-Astudillo M, Castillo MI, Cáceres MA, Plaza G, Landaeta MF. 2017. Oceanographic and lunar forcing affects nearshore larval fish assemblages from temperate rocky reefs. *Marine Biology Research* **13**:1015–1026.
- Dickinson AM, Goodman AM, Deeming DC. 2019. Air movement affects insulatory values of nests constructed by Old World Warblers. *Journal of Thermal Biology* **81**:194–200.
- Dillon KG, Conway CJ. 2018. Nest predation risk explains variation in avian clutch size.

- Behavioral Ecology **29**:301–311.
- Dinsmore SJ, White GC, Knopf FL. 2002. Advanced techniques for modeling avian nest survival. *Ecology* **83**:3476.
- Dixit AS, Singh NS. 2011. Photoperiod as a proximate factor in control of seasonality in the subtropical male Tree Sparrow, *Passer montanus*. *Frontiers in Zoology* **8**:1–12.
- Dolenec Z, Dolenec P. 2011. Influence of the local spring warming on the breeding phenology in Blackcap (*Sylvia atricapilla*) in Croatia. *Journal of Environmental Biology* **32**:625–627.
- Doligez B, Jean Clobert. 2003. Clutch size reduction as a response to increased nest predation rate in the Collared Flycatcher. *Ecology* **84**:2582–2588.
- Downs CT, Ward D. 1997. Does shading behaviour of incubating shorebirds in hot environments cool the eggs or the adults? *The Auk* **114**:717–724.
- Drent R, Daan S. 1980. The prudent parent. *Ardea* **68**:225–252.
- Du WG, Shine R. 2015. The behavioural and physiological strategies of bird and reptile embryos in response to unpredictable variation in nest temperature. *Biological Reviews* **90**:19–30.
- Duca C, Brunelli WA, Doherty PF. 2019. Predator search image and the dilution effect: When is the best time to nest? *Auk* **136**:1–7.
- Dunn PO, Winkler DW. 1999. Climate change has affected the breeding date of Tree Swallows. *Proceedings of the Royal Society of London* **266**:2487–2490.
- Dunn PO, Winkler DW. 2010. Effects of climate change on timing of breeding and reproductive success in birds. Pages 113–320 in A. P. Møller, W. Fiedler, and P. Berthold, editors. *Effects of Climate Change on Birds*. Oxford University Press, London, UK.
- Durant SE, Hopkins WA, Hepp GR, Walters JR. 2013. Ecological, evolutionary, and conservation implications of incubation temperature-dependent phenotypes in birds. *Biological Reviews* **88**:499–509.
- DuRant SE, Hopkins WA, Wilson AF, Hepp GR. 2012. Incubation temperature affects the metabolic cost of thermoregulation in a young precocial bird. *Functional Ecology* **26**:416 – 422.
- Durant SE, Willson JD, Carroll RB. 2019. Parental effects and climate change: Will avian incubation behavior shield embryos from increasing environmental temperatures? *Integrative and Comparative Biology* **59**:1068–1080.
- Dwyer RG, Bearhop S, Campbell HA, Bryant DM. 2013. Shedding light on light: Benefits of anthropogenic illumination to a nocturnally foraging shorebird. *Journal of Animal Ecology* **82**:478–485.
- Dyer BM. 1996. Predation by snakes on seabirds at three South African Islands. *South African Journal of Marine Science* **17**:309–313.
- Ehmke G, Maguire GS, Bird T, Ierodiaconou D, Weston MA. 2016. An obligate beach bird selects sub-, inter- and supra-tidal habitat elements. *Estuarine, Coastal and Shelf Science* **181**:266–276.

- Ekanayake KB, Weston MA, Nimmo DG, Maguire GS, Endler JA, Küpper C. 2015. The bright incubate at night: Sexual dichromatism and adaptive incubation division in an open-nesting shorebird. *Proceedings of the Royal Society B: Biological Sciences* **282**:20143026.
- Ens BJ., Kersten M, Brenninkmeijer A, Hulscher JB. 1992. Territory quality, parental effort and reproductive success of oystercatchers (*Haematopus ostralegus*). *Journal of Animal Ecology* **61**:703–715.
- Ens BJ, Underhill LG. 2014. Synthesis of oystercatcher conservation assessments: general lessons and recommendations. *International Wader Studies* **20**:5–22.
- Etienne S. 2006. Social information, antipredatory vigilance and flight in bird flocks. *Animal Behaviour* **72**:373–382.
- Evans PR. 1976. Energy balance and optimal foraging strategies in shorebirds some implications for their distributions and movements in the non-breeding season. *Ardea* **64**:117–139.
- Evans RM. 1995. Incubation temperature in the Australasian Gannet *Moms senator*. *Ibis* **137**:340–344.
- Ezcurra P, Rivera-Collazo IC. 2018. An assessment of the impacts of climate change on Puerto Rico's Cultural Heritage with a case study on sea-level rise. *Journal of Cultural Heritage* **32**:198–209.
- Felton SK, Pollock KH, Simons TR. 2018. Response of beach-nesting American Oystercatchers to off-road vehicles: An experimental approach reveals physiological nuances and decreased nest attendance. *The Auk* **120**:47–62.
- Field CR, Bayard TS, Gjerdrum C, Hill JM, Meiman S, Elphick CS. 2017. High-resolution tide projections reveal extinction threshold in response to sea-level rise. *Global Change Biology* **23**:2058–2070.
- Finkler MS. 1999. Influence of water availability during incubation on hatchling size, body composition, desiccation tolerance, and terrestrial locomotor performance in the Snapping Turtle *Chelydra serpentina*. *Physiological and Biochemical Zoology* **72**:714–722.
- Flatt T, Heyland A. 2011. Mechanisms of life history evolution: The genetics and physiology of life history traits and trade-offs. Oxford University Press, Oxford, UK.
- Flemming SA, Nol E, Kennedy L V., Smith PA. 2019. Hyperabundant herbivores limit habitat availability and influence nest site selection of Arctic-breeding birds. *Journal of Applied Ecology* **56**:976–987.
- Folk TH, Hepp GR. 2003. Effects of habitat use and movement patterns on incubation behavior of female Wood Ducks (*Aix sponsa*) in Southeast Alabama. *The Auk* **120**:1159–1167.
- Fonseca J, Basso E, Serrano D, Navedo JG. 2017. Effects of tidal cycles on shorebird distribution and foraging behaviour in a coastal tropical wetland: Insights for carrying capacity assessment. *Estuarine, Coastal and Shelf Science* **198**:279–287.
- Fowler GS. 1995. Stages of age-related reproductive success in birds: Simultaneous effects

- of age, pair-bond duration and reproductive experience. *American Zoologist* **35**:318–328.
- Funghi C, McCowan LSC, Schuett W, Griffith SC. 2019. High air temperatures induce temporal, spatial and social changes in the foraging behaviour of wild zebra finches. *Animal Behaviour* **149**:33–43.
- Galbraith H, Jones R, Park R, Clough J, Herrod-Julius S, Harrington B, Page G. 2002. Global climate change and sea level rise: potential losses of intertidal habitat for shorebirds. *Waterbirds* **25**:173–183.
- Galgano FA. 2019. Abrupt Climate Change. *Advances in Military Geosciences* **299**:59–72.
- Gardali T, Seavy NE, DiGaudio RT, Comrack LA. 2012. A climate change vulnerability assessment of California's at-risk birds. *PLoS ONE* **7**:e29507.
- George AD, Thompson III FR, Faaborg J. 2015. Isolating weather effects from seasonal activity patterns of a temperate North American Colubrid. *Ocean Dynamics* **178**:1251–1259.
- Gerson AR, McKechnie AE, Smit B, Whitfield MC, Smith EK, Talbot WA, McWhorter TJ, Wolf BO. 2019. The functional significance of facultative hyperthermia varies with body size and phylogeny in birds. *Functional Ecology* **33**:597–607.
- Ghalambor CK, Martin TE. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. *Science* **292**:494–497.
- Ghalambor CK, Martin TE. 2002. Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses. *Behavioral Ecology* **13**:101–108.
- Gill RA, Cox WA, Thompson III FR. 2016. Timing of songbird nest predation as revealed by video surveillance. *The Wilson Journal of Ornithology* **128**:200–203.
- Gjerdrum C, Elphick CS, Rubega M. 2005. Nest site selection and nesting success in saltmarsh breeding sparrows: The importance of nest habitat, timing, and study site differences. *The Condor* **107**:849–862.
- Gómez-Serrano MA, López-López P. 2014. Nest site selection by Kentish Plover suggests a trade-off between nest-crypsis and predator detection strategies. *PLoS ONE* **9**:e107121.
- Gómez J, Ramo C, Troscianko J, Stevens M, Castro M, Pérez-Hurtado A, Liñán-Cembrano G, Amat JA. 2018. Individual egg camouflage is influenced by microhabitat selection and use of nest materials in ground-nesting birds. *Behavioral Ecology and Sociobiology* **72**:142.
- Göransson G, Karlsson J, Nilsson SG, Ulfstrand S, Gdransson G. 1975. Predation on birds' nests in relation to antipredator aggression and nest density: an experimental study. *Oikos* **26**:117–120.
- Götmark F. 1992. The effects of investigator disturbance on nesting birds. *Current Ornithology* **9**:63–104.
- Götmark F. 2002. Predation by Sparrowhawks favours early breeding and small broods in Great Tits. *Oecologia* **130**:25–32.
- Grant DM, Cohen JB, Stantial ML, Linhart RC. 2019. Substrate-level nest site selection of sympatric Piping Plovers (*Charadrius melodus*) and American Oystercatchers

- (*Haematopus palliatus*) in New Jersey, USA. *Waterbirds* **42**:272–281.
- Grant GS. 1982. Avian incubation: Egg temperature, nest humidity, and behavioural thermoregulation in a hot environment. *Ornithological Monographs* **30**:1–75.
- Grant RA, Chadwick EA, Halliday T. 2009. The lunar cycle: a cue for amphibian reproductive phenology? *Animal Behaviour* **78**:349–357.
- Gray LA, Deeming DC. 2017. Effect of air movement on the thermal insulation of avian nests. *Bird Study* **64**:492–501.
- Green R. 1984. Nomograms for estimating the stage of incubation of wader eggs in the field. *Wader Study Group Bulletin* **42**:36–39.
- Greenberg R, Cadena V, Danner RM, Tattersall G. 2012. Heat loss may explain bill size differences between birds occupying different habitats. *PLoS ONE* **7**:e40933.
- Grémillet D. 1997. Catch per unit effort, foraging efficiency, and parental investment in breeding Great Cormorants (*Phalacrocorax carbo carbo*). *ICES Journal of Marine Science* **54**:635–644.
- Griebeler EM, Caprano T, Böhning-Gaese K. 2010. Evolution of avian clutch size along latitudinal gradients: Do seasonality, nest predation or breeding season length matter? *Journal of Evolutionary Biology* **23**:888–901.
- Griffiths CL, Hockey PA, Van Erkom Schurink C, Le Roux PJ. 1992. Marine invasive aliens on South African shores: implications for community structure and trophic functioning. *South African Journal of Marine Science* **12**:713–722.
- Hadley W. 2017. Tidyverse: Easily Install and Load the “Tidyverse.” Available from <https://cran.r-project.org/package=tidyverse>.
- Hahn TP, MacDougall-Shackleton SA. 2008. Adaptive specialization, conditional plasticity and phylogenetic history in the reproductive cue response systems of birds. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363**:267–286.
- Hall KRL. 1959. Observations on the nest-sites and nesting behaviour of the Black Oystercatcher *Haematopus moquini* in the Cape Peninsula. *Ostrich* **30**:143–154.
- Hällfors MH, Antão LH, Itter M, Lehikoinen A, Lindholm T. 2020. Shifts in timing and duration of breeding for 73 boreal bird species over four decades. *Ecology* **117**:18557–18565.
- Hannah L, Flint L, Syphard AD, Moritz MA, Buckley LB, McCullough IM. 2014. Fine-grain modeling of species’ response to climate change: Holdouts, stepping-stones, and microrefugia. *Trends in Ecology and Evolution* **29**:390–397.
- Hanson HC. 1959. The incubation patch of Wild Geese: Its recognition and significance. *Arctic* **12**:139–150.
- Hayes FE, Turner DG, Zimmerly ND, Peralta MB. 2018. Nocturnal courtship, copulation, and egg-laying in the Western Grebe (*Aechmophorus occidentalis*) and Clark’s Grebe (*Aechmophorus clarkii*). *Journal of Ethology* **36**:65–75.
- Heenan CB, Seymour RS. 2012. The effect of wind on the rate of heat loss from avian cup-shaped nests. *PLoS ONE* **7**:e32252.
- Henderson RW. 1982. Thermoregulation in an Hispaniolan Tree Snake, *Uromacer catesbyi*.

- Journal of Herpetology **16**:89–91.
- Hepp GR, Folk TH, Manlove CA. 2005. Nest temperature, incubation period, and investment decisions of incubating Wood Ducks *Aix sponsa*. Journal of Avian Biology **36**:523–530.
- Hepp GR, Kennamer RA. 2012. Warm is better: Incubation temperature influences apparent survival and recruitment of Wood Ducks (*Aix sponsa*). PLoS One **7**:e47777.
- Hepp GR, Kennamer RA, Johnson MH. 2006. Maternal effects in Wood Ducks: Incubation temperature influences incubation period and neonate phenotype. Functional Ecology **20**:307–314.
- Herczeg G, Gonda A, Saarikivi J, Merilä J. 2006. Experimental support for the cost-benefit model of lizard thermoregulation. Behavioral Ecology and Sociobiology **60**:405–414.
- Herczeg G, Herrero A, Saarikivi J, Gonda A, Jäntti M, Merilä J. 2008. Experimental support for the cost-benefit model of lizard thermoregulation: The effects of predation risk and food supply. Oecologia **155**:1–10.
- Hilde HC, Pélabon C, Guéry L, Gabrielsen GW, Descamps S. 2016. Mind the wind: Microclimate effects on incubation effort of an arctic seabird. Ecology and Evolution **6**:1914–1921.
- Hilton GM, Ruxton GD, Reid JM, Monaghan P. 2004. Using artificial nests to test importance of nesting material and nest shelter for incubation energetics. The Auk **121**:777–787.
- Hochscheid S, Gremillet D, Wanless S, du Plessis M. 2002. Black and white under the South African sun: are juvenile Cape Gannets heat stressed? Journal of Thermal Biology **27**:325–332.
- Hockey P. 1997. Between the tides. Africa Birds & Birding **2**:28–34.
- Hockey PAR. 1981. Morphometrics and sexing of the African Black Oystercatcher. Ostrich **52**:244–247.
- Hockey PAR. 1982. Adaptiveness of nest site selection and egg coloration in the African Black Oystercatcher *Haematopus moquini*. Behavioral Ecology and Sociobiology **11**:117–123.
- Hockey PAR. 1983a. Ecology of the African Black Oystercatcher *Haematopus moquini*. University of Cape Town.
- Hockey PAR. 1983b. Aspects of the breeding biology of the African Black Oystercatcher. Ostrich **54**:26–35.
- Hockey PAR. 2003. Dispersal and migration of juvenile African Black Oystercatchers *Haematopus moquini*. Ibis **145**:114–123.
- Hockey PAR, Dean WRJ, Ryan PG. 2005. Roberts birds of Southern Africa, 7th edition. The Trustees of the John Voelcker Bird Book Fund, Cape Town, South Africa.
- Hockey PAR, Underhill L. 1984. Diet of the African Black Oystercatcher *Haematopus moquini* on rocky shores: spatial, temporal and sex- related variation. African Zoology **19**:1–11.
- Hogstedt G. 1980. Evolution of clutch size in birds: Adaptive variation in relation to territory quality. Science **210**:1148–1150.
- Hoppe IR, Harrison JO, Raynor EJ, Brown MB, Powell LA, Tyre AJ. 2019. Temperature, wind,

- vegetation, and roads influence incubation patterns of Greater Prairie-Chickens (*Tympanuchus cupido pinnatus*) in the Nebraska Sandhills, USA. *Canadian Journal of Zoology* **97**:91–99.
- Hötter H, Segebad A. 2017. Effects of predation and weather on the breeding success of Avocets *Recurvirostra avosetta*. *Bird Study* **47**:91–101.
- Huey RB, Slatkin M. 1976. Cost and benefits of lizard thermoregulation. *The Quarterly Review of Biology* **51**:363–384.
- Hussell DJT. 1985. Clutch size, daylength, and seasonality of resources: Comments on Ashmole's hypothesis. *The American Naturalist* **102**:632–634.
- Idier D, Bertin X, Thompson P, Pickering MD. 2019. Interactions between mean sea level, tide, surge, waves and flooding: Mechanisms and contributions to sea level variations at the coast. *Surveys in Geophysics* **40**:1603–1630.
- Ikegami T, Takeuchi Y, Hur SP, Takemura A. 2014. Impacts of moonlight on fish reproduction. *Marine Genomics* **14**:59–66.
- Ims RA. 1990. On the adaptive value of reproductive synchrony as a predator-swamping strategy. *The American Naturalist* **136**:485–498.
- IPCC. 2007a. Summary for Policymakers - Working Group II Contribution to the Intergovernmental Panel on Climate Change Fourth Assessment Report. Geneva, Switzerland.
- IPCC. 2007b. Summary for policymakers - Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland.
- Irons RD, Scurr AH, Rose AP, Hagelin JC, Blake T, Doak DF. 2017. Wind and rain are the primary climate factors driving changing phenology of an aerial insectivore. *Proceedings of the Royal Society B: Biological Sciences* **284**:20170412.
- Jackson DB. 1988. Habitat selection and breeding ecology of three species of waders in the western isles of Scotland. Durham University.
- Jacobs DL. 2017. Extreme heat: Assessing impacts of heat and microclimate on birds of the Sonoran Desert. University of Nevada.
- Janiszewski T, Minias P, Lesner B, Kaczmarek K. 2017. Age effects on reproductive success, nest-site location, and offspring condition in the Great Cormorant *Phalacrocorax carbo sinensis*. *Journal of Ornithology* **158**:193–202.
- Jeffery RG. 1987. Influence of human disturbance on the nesting success of African Black Oystercatchers. *South African Journal of Wildlife Research* **17**:71–72.
- Jeffery RG, Scott HA. 2005. Breeding success of African Black Oystercatchers *Haematopus moquini* at Cape Agulhas, Western Cape, from 1978/79 to 2001/02. *Ostrich* **76**:8–13.
- Jehle G, Adams AAY, Savidge JA, Skagen SK. 2004. Nest survival estimation: A review of alternatives to the Mayfield estimator. *The Condor* **106**:472–484.
- Jevrejeva S, Jackson LP, Grinsted A, Lincke D, Marzeion B. 2018. Flood damage costs under the sea level rise with warming of 1.5°C and 2°C. *Environmental Research Letters* **13**:074014.

- Johnson D. 1979. Estimating nest success: The Mayfield method and an alternative. *The Auk* **96**:651–661.
- Johnson D, Shaffer T. 1990. Estimating nest success: When Mayfield wins. *The Auk* **107**:595–600.
- Jones CW et al. 2020. Abundance, distribution and breeding success of the endemic Gough Island Finch *Rowettia goughensis* between 2009 and 2018. *Emu* **00**:1–9.
- Kaliński A, Bańbura M, Gładalski M, Markowski M, Skwarska J, Wawrzyniak J, Zieliński P, Bańbura J. 2019. Physiological condition of nestling Great Tits (*Parus major*) declines with the date of brood initiation: A long term study of first clutches. *Scientific Reports* **9**:9843.
- Kearns LJ, Rodewald AD. 2017. Does nest predator activity predict the location and survival of songbird nests in urbanizing landscapes? *The Condor* **119**:745–760.
- Kemper J, Underhill LG, Crawford RJM, Kirkman SP. 2007. Revision of the conservation status of seabirds and seals breeding in the Benguela Ecosystem. Pages 325–342 in S. Kirkman, editor. Final Report of the BCLME (Benguela Current Large Marine Ecosystem) Project on Top Predators as Biological Indicators of Ecosystem Change in the BCLME. Avian Demography Unit, Cape Town.
- Kimbrough SO. 1980. The concepts of fitness and selection in evolutionary biology. *Journal of Social and Biological Structures* **3**:149–170.
- Kingsolver JG, Huey RB. 2003. Introduction: The evolution of morphology, performance, and Fitness. *Integrative and Comparative Biology* **43**:361–366.
- Kirshen P, Watson C, Douglas E, Gontz A, Lee J, Tian Y. 2008. Coastal flooding in the Northeastern United States due to climate change. *Mitigation and Adaptation Strategies for Global Change* **13**:437–451.
- Klett AT, Johnson DH. 1982. Variability in nest survival rates and implications to nesting studies. *The Auk* **99**:77–87.
- Klimczuk E, Halupka L, Czyż B, Borowiec M, Nowakowski JJ, Sztwiertnia H. 2015. Factors driving variation in biparental incubation behaviour in the Reed Warbler *Acrocephalus scirpaceus*. *Ardea* **103**:51–59.
- Koenig WD. 1984. Geographic variation in clutch size in the Northern Flicker (*Colaptes auratus*): Support for Ashmole's hypothesis. *The Auk* **101**:698–706.
- Kohler S, Bonnevie B, Dano S. 2009. Can eyeflecks be used to sex African Black Oystercatchers *Haematopus moquini* in the field? *Ostrich* **80**:109–110.
- Kohler SA et al. 2011. Geographic variation in the trophic ecology of an avian rocky shore predator, the African Black Oystercatcher, along the southern African coastline. *Marine Ecology Progress Series* **435**:235–249.
- Korringa P. 1957. Lunar Periodicity. *Geological Society of America* **1**:917–934.
- Krimbas CB. 2004. On fitness. *Biology and Philosophy* **19**:185–203.
- Kubelka V, Šálek M, Tomkovich P, Végvári Z, Freckleton RP, Székely T. 2018. Global pattern of nest predation is disrupted by climate change in shorebirds. *Science* **362**:680–683.

- Kubelka V, Sládeček M, Šálek M. 2019. Great variability in nest lining size: Support for thermoregulation but not for anti-predatory adaptation hypothesis. *Journal of Ornithology* **160**:993–1002.
- Kumar V. 1997. Photoperiodism in higher vertebrates. *Indian Journal of Experimental Biology* **35**:427–437.
- Kumar V, Wingfield JC, Dawson A, Ramenofsky M, Rani S, Bartell P. 2010. Biological clocks and regulation of seasonal reproduction and migration in birds. *Physiological and Biochemical Zoology* **83**:827–835.
- Kushlan JA. 1981. Resource use strategies of wading birds. *The Wilson Bulletin* **93**:145–163.
- Laake JL. 2013. RMark: An R interface for analysis of capture-recapture data with MARK. AFSC Processed Rep 2013-01, 25p., Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.
- Lack DL. 1968. *Ecological adaptations for breeding in birds*. Methuen, London, Uk.
- Lahti DC. 2009. Why we have been unable to generalize about bird nest predation. *Animal Conservation* **12**:279–281.
- Laidlaw RA, Gunnarsson TG, Méndez V, Carneiro C, Pórisson B, Wentworth A, Gill JA, Alves JA. 2020. Vegetation structure influences predation rates of early nests in subarctic breeding waders. *Ibis* **162**:1225–1236.
- Laidlaw RA, Smart J, Smart MA, Bodey TW, Coledale T, Gill JA. 2019. Foxes, voles, and waders: drivers of predator activity in wet grassland landscapes. *Avian Conservation and Ecology* **14**:4.
- Laidlaw RA, Smart J, Smart MA, Gill JA. 2015. The influence of landscape features on nest predation rates of grassland-breeding waders. *Ibis* **157**:700–712.
- Lany NK, Ayres MP, Stange EE, Sillett TS, Rodenhouse NL, Holmes RT. 2016. Breeding timed to maximize reproductive success for a migratory songbird: The importance of phenological asynchrony. *Oikos* **125**:656–666.
- Larsen T, Sordahl T a., Byrkjedal I. 1996. Factors related to aggressive nest protection behaviour: a comparative study of Holarctic waders. *Biological Journal of the Linnean Society* **58**:409–439.
- Le Corre M. 2001. Breeding seasons of seabirds at Europa Island (southern Mozambique Channel) in relation to seasonal changes in the marine environment. *Journal of Zoology* **254**:239–249.
- Lee WS, Kwon YS, Yoo JC. 2010. Egg survival is related to the colour matching of eggs to nest background in Black-tailed Gulls. *Journal of Ornithology* **151**:765–770.
- Leeuw J de, Waweru MN, Okello OO, Maloba M, Nguru P, Said MY, Aligula HM, Heitkönig IMA, Reid RS. 2001. Distribution and diversity of wildlife in northern Kenya in relation to livestock and permanent water points. *Biological Conservation* **100**:297–306.
- Leseberg A. 2001. *The foraging ecology, demographics and conservation of African Black Oystercatchers *Haematopus moquini* in Namibian nursery areas*. University of Cape Town.
- Leseberg A, Hockey PAR, Loewenthal D. 2000. Human disturbance and the chick-rearing

- ability of African Black Oystercatchers (*Haematopus moquini*): A geographical perspective. *Biological Conservation* **96**:379–385.
- Li H, Goodale E, Quan R. 2019. Nest predation on an abundant generalist bird in tropic China. *The Wilson Journal of Ornithology* **131**:514–523.
- Li Y, Feng H, Vigouroux G, Yuan D, Zhang G, Ma X, Lei K. 2020. Storm surges in the Bohai Sea: The role of waves and tides. *Water (Switzerland)* **12**:1–20.
- Lima SL. 2009. Predators and the breeding bird: Behavioral and reproductive flexibility under the risk of predation. *Biological Reviews* **84**:485–513.
- Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**:619–640.
- Lima SL, Valone TJ. 1991. Predators and avian community organization: an experiment in a semi-desert grassland. *Oecologia* **86**:105–112.
- Lislevand T, Thomas GH. 2006. Limited male incubation ability and the evolution of egg size in shorebirds. *Biology Letters* **2**:206–208.
- Livezey BC. 2010. Phylogenetics of modern shorebirds (Charadriiformes) based on phenotypic evidence: Analysis and discussion. *Zoological Journal of the Linnean Society* **160**:567–618.
- Loewenthal D. 2007. The population dynamics and conservation of the African Black Oystercatcher *Haematopus moquini*. University of Cape Town.
- Loewenthal D, Paijmans DM, Haupt PW, Hockey PA. 2015. Trends in African Black Oystercatcher *Haematopus moquini* populations between the early 1980s and early 2000s, with consideration of the influence of protected habitats and food availability. *Ostrich* **86**:9–21.
- Loewenthal D, Paijmans DM, Hockey PA. 2016. Factors affecting the breeding success of the African Black Oystercatcher (*Haematopus moquini*): A Perspective on protection and food availability. *African Zoology* **51**:193–202.
- Lopes KGD, Bicca-Marques JC. 2017. Ambient temperature and humidity modulate the behavioural thermoregulation of a small arboreal mammal (*Callicebus bernhardi*). *Journal of Thermal Biology* **69**:104–109.
- Lourens A, Molenaar R, Van Den Brand H, Heetkamp MJW, Meijerhof R, Kemp B. 2006. Effect of egg size on heat production and the transition of energy from egg to hatchling. *Poultry Science* **85**:770–776.
- Ludynia K, Waller LJ, Sherley RB, Abadi F, Galada Y, Geldenhuys D, Crawford RJM, Shannon LJ, Jarre A. 2014. Processes influencing the population dynamics and conservation of African Penguins on Dyer Island, South Africa. *African Journal of Marine Science* **36**:253–267.
- Lustick S, Adam M, Alexander Hinko. 1980. Interaction between posture, color, and the radiative heat load in birds. *Science* **208**:1052–1053.
- Ma L, Zhang J, Liu J, Yang C, Liang W, Møller AP. 2019. Adaptation or ecological trap? Altered nest-site selection by Reed Parrotbills after an extreme flood. *Avian Research* **10**:4–11.
- MacArthur RH, Pianka ER. 1966. On optimal use of a patchy environment. *The American*

- Naturalist **100**:603–609.
- MacDonald EC, Camfield AF, Jankowski JE, Martin K. 2013. Extended incubation recesses by alpine-breeding Horned Larks: a strategy for dealing with inclement weather? *Journal of Field Ornithology* **84**:58–68.
- Macdonald MA, Bolton M. 2008. Predation on wader nests in Europe. *Ibis* **150**:54–73.
- MacCivor LH, Melvin SM, Curtice R, Griffin. 1990. Effects of research activity on Piping Plover nest predation. *The Journal of Wildlife Management* **54**:443–447.
- Mainwaring MC, Hartley IR, Lambrechts MM, Deeming DC. 2014. The design and function of birds' nests. *Ecology and Evolution* **4**:3909–3928.
- Malan L, Malan F, Williams AJ. 2004. Kelp Gulls as predators of large African Penguin chicks: observations at Possession Island, Namibia. *Bird Numbers* **13**:14.
- Manier E. 1969. "Fitness" and some explanatory patterns in Biology. *Methodological Problems in Biology* **20**:206–218.
- Manlove CA, Hepp GR. 2000. Patterns of nest attendance in female Wood Ducks. *Condor* **102**:286–291.
- Marchi G De, Chiozzi G, Dell'Omo G, Fasola M. 2015. Low incubation investment in the burrow-nesting Crab Plover *Dromas ardeola* permits extended foraging on a tidal food resource. *Ibis* **157**:31–43.
- Mares R, Doutrelant C, Paquet M, Spottiswoode CN, Covas R. 2017. Breeding decisions and output are correlated with both temperature and rainfall in an arid-region passerine, the Sociable Weaver. *Royal Society Open Science* **4**:170835.
- Marine Conservation Institute. 2020. Robben Island Marine Protected Area. Available from <https://mpatlas.org/zones/68808153/> (accessed January 13, 2020).
- Markert JA, Champlin DM, Gutjahr-gobell R, Grear JS, Kuhn A, Jr TJM, Roth A, Bagley MJ, Nacci DE. 2010. Population genetic diversity and fitness in multiple environments. *Evolutionary Biology* **10**:205.
- Martin TE. 1987. Food as a limit on breeding birds: a life-history perspective. *Annual Review of Ecology and Systematics* **18**:453–487.
- Martin TE. 1993a. Nest predation among vegetation layers and habitat types: Revising the dogmas. *The American Naturalist* **141**:897–913.
- Martin TE. 1993b. Nest predation and nest sites: new perspectives on old patterns. *BioScience* **43**:523–532.
- Martin TE. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* **65**:101–127.
- Martin TE. 1996. Life history evolution in tropical and south temperate birds: What do we really know? *Journal of Avian Biology* **27**:263–272.
- Martin TE. 2002. A new view of avian life-history evolution tested on an incubation paradox. *Proceedings of the Royal Society B: Biological Sciences* **269**:309–316.
- Martin TE, Auer SK, Bassar RD, Niklison AM, Lloyd P. 2007. Geographic variation in avian incubation periods and parental influences on embryonic temperature. *Evolution*

- 61:2558–2569.
- Martin TE, Scott J, Menge C. 2000. Nest predation increases with parental activity: Separating nest site and parental activity effects. *Proceedings of the Royal Society B: Biological Sciences* **267**:2287–2293.
- Mason LR, Smart J, Drewitt AL. 2018. Tracking day and night provides insights into the relative importance of different wader chick predators. *Ibis* **160**:71–88.
- Massimino D, Beale CM, Suggitt AJ, Crick HQP, Macgregor NA, Carroll MJ, Maclean IMD, Pearce-Higgins JW. 2020. Can microclimate offer refuge to an upland bird species under climate change? *Landscape Ecology* **35**:1907–1922.
- Mather AA, Stretch DD. 2012. A Perspective on sea level rise and coastal storm surge from southern and eastern Africa: A case study near Durban, south Africa. *Water (Switzerland)* **4**:237–259.
- Matysioková B, Remeš V. 2018. Evolution of parental activity at the nest is shaped by the risk of nest predation and ambient temperature across bird species. *Evolution* **72**:2214–2224.
- Mayfield H. 1961. Nesting success calculated from exposure. *The Wilson Bulletin* **73**:255–261.
- Mayfield HF. 1975. Suggestions for calculating nest success. *The Wilson Bulletin* **87**:456–466.
- Mcgowan CP, Simons TR. 2006. Effects of human recreation on the incubation behavior of American Black Oystercatcher. *The Wilson Journal of Ornithology* **118**:485–493.
- McKechnie AE et al. 2016. Erratum: Avian thermoregulation in the heat: Evaporative cooling capacity in an archetypal desert specialist, Burchell's Sandgrouse (*Pterocles burchelli*). *Journal of Experimental Biology* **219**:2137–2144.
- McKechnie AE, Wolf BO. 2010. Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biology Letters* **6**:253–256.
- McKinnon L, Berteaux D, Bêty J. 2014. Predator-mediated interactions between lemmings and shorebirds: A test of the alternative prey hypothesis. *The Auk* **131**:619–628.
- McKinnon L, Bêty J. 2009. Effect of camera monitoring on survival rates of High-Arctic shorebird nests. *Journal of Field Ornithology* **80**:280–288.
- Melville DS, Chen Y, Ma Z. 2016. Shorebirds along the Yellow Sea coast of China face an uncertain future - A review of threats. *Emu* **116**:100–110.
- Méndez V, Alves JA, Gill JA, Gunnarsson TG. 2018. Patterns and processes in shorebird survival rates: a global review. *Ibis* **160**:723–741.
- Menezes CT, Angelo M. 2017. Predators of bird nests in the Neotropics: A review. *Journal of Field Ornithology* **88**:99–114.
- Merrill L, Ospina EA, Santymire RM, Benson TJ. 2020. Egg incubation temperature affects development of innate immune function in nestling American Robins (*Turdus migratorius*). *Physiological and Biochemical Zoology* **93**:1–12.
- Millones A, Frere E. 2017. How nest site characteristics influence breeding success in Red-legged Cormorants *Phalacrocorax gaimardi*. *Acta Ornithologica* **52**:239–244.

- Mills SK, Beatty JH. 1979. The propensity interpretation of fitness. *Philosophy of Science* **46**:263–286.
- Mitchell D, Snelling EP, Hetem RS, Maloney SK, Strauss WM, Fuller A. 2018. Revisiting concepts of thermal physiology: Predicting responses of mammals to climate change. *Journal of Animal Ecology* **87**:956–973.
- Monk JD, Kwon E, Deroose-Wilson A, Robinson SG, Bellman HA, Karpanty SM, Catlin DH, Fraser JD. 2020. Extensive use of intertidal habitat by shorebirds outside protected nesting areas. *Journal of Wildlife Management* **84**:1338–1347.
- Moreau RE. 2008. The breeding season of African birds. *Ibis* **92**:223–267.
- Moreiras S, Lisboa MS, Mastrantonio L. 2012. The role of snow melting upon landslides in the central Argentinean Andes. *Earth Surface Processes and Landforms* **37**:1106–1119.
- Moreno J. 1989. Strategies of mass change in breeding birds. *Biological Journal of the Linnean Society* **37**:297–310.
- Morosinotto C, Thomson RL, Hänninen M, Korpimäki E. 2012. Higher nest predation risk in association with a top predator: mesopredator attraction? *Oecologia* **170**:507–515.
- Morrison CA, Alves JA, Gunnarsson TG, Pórisson B, Gill JA. 2019. Why do earlier-arriving migratory birds have better breeding success? *Ecology and Evolution* **9**:8856–8864.
- Mueller AJ, Miller KD, Bowers EK. 2019. Nest microclimate during incubation affects posthatching development and parental care in wild birds. *Scientific Reports* **9**:5161.
- Muir JJ, Colwell MA. 2010. Snowy Plovers select open habitats for courtship scrapes and nests. *Condor* **112**:507–510.
- Muis S, Apecechea MI, Dullaart J, de Lima Rego J, Madsen KS, Su J, Yan K, Verlaan M. 2020. A high-resolution global dataset of extreme sea levels, tides, and storm surges, including future projections. *Frontiers in Marine Science* **7**:263.
- Mullin SJ, Cooper RJ. 1998. The foraging ecology of the Gray Rat Snake (*Elaphe obsoleta spiloides*) -visual stimuli facilitate location of arboreal prey. *The American Naturalist* **140**:397–401.
- Munro BYM. 2017. What’s killing the world’s shorebirds? *Nature* **541**:16–20.
- Nagy LR, Holmes RT. 2005. To double-brood or not? Individual variation in the reproductive effort in Black-Throated Blue Warblers (*Dendroica caerulescens*). *The Auk* **122**:902–914.
- Naidoo R, Brennan A, Shapiro AC, Beytell P, Aschenborn O, Du Preez P, Kilian JW, Stuart-Hill G, Taylor RD. 2020. Mapping and assessing the impact of small-scale ephemeral water sources on wildlife in an African seasonal savannah. *Ecological Applications* **30**:e02203.
- Nams VO. 1997. Density-dependent predation by skunks using olfactory search images. *Oecologia* **110**:440–448.
- New DAT. 1956. The formation of sub-blastodermic fluid in hens’ eggs. *Development* **4**:221–227.
- New DAT. 1957. A critical period for the turning of hens’ eggs. *Journal of Embryology and Experimental Morphology* **5**:293–299.
- Newton I. 2007. Population limitation in birds: The last 100 years. *British Birds* **100**:518–539.

- Nicholls RJ, Marinova N, Lowe JA, Brown S, Vellinga P, De Gusmão D, Hinkel J, Tol RSJ. 2011. Sea-level rise and its possible impacts given a “beyond 4°C world” in the twenty-first century. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* **369**:161–181.
- Nisbet ICT, Winchell JM, Heise AE. 1984. Influence of age on the breeding biology of Common Terns. *Colonial Waterbirds* **7**:117–126.
- Norrdahl K, Suhonen J, Hemminki O, Korpimäki E. 1995. Predator presence may benefit: kestrels protect curlew nests against nest predators. *Oecologia* **101**:105–109.
- Ntiamoa-Baidu Y, Piersma T, Wiersma P, Poot M, Battley P, Gordon C. 1998. Water depth selection, daily feeding routines and diets of waterbirds in coastal lagoons in Ghana. *Ibis* **140**:89–103.
- Nylin S, Gotthard K. 1998. Plasticity in life-history traits. *Annual Review of Entomology* **43**:63–83.
- Oja R, Pass E, Soe E, Ligi K, Anijalg P, Laurimaa L, Saarma U, Lõhmus A, Valdmann H. 2018. Increased nest predation near protected capercaillie leks: a caveat against small reserves. *European Journal of Wildlife Research* **64**:1–8.
- Ollason JC, Dunnet GM. 1978. Age, experience and other factors affecting the breeding success of the Fulmar, *Fulmarus glacialis*, in Orkney. *Journal of Animal Ecology* **47**:961–976.
- Olson CR, Vleck CM, Vleck D. 2006. Periodic cooling of bird eggs reduces embryonic growth efficiency. *Physiological and Biochemical Zoology* **79**:927–936.
- Olsson O. 1996. Seasonal effects of timing and reproduction in the King Penguin: A unique breeding cycle. *Journal of Avian Biology* **27**:7–14.
- Orr HA. 2009. Fitness and its role in evolutionary genetics. *Nature Reviews Genetics* **10**:531–539.
- Ospina E, Cooper C, Winkler D, Ospina EA, Cooper CB, Liljesthröm M, Ardia DR, Winkler DW. 2015. Biparental nest-attendance in Chilean Swallows (*Tachycineta meyeni*) breeding in Ushuaia, Argentina. *Emu* **115**:76–79.
- Ospina EA. 2017. Incubation temperature impacts growth, physiology and survival in nestlings of an open-cup nesting passerine. University of Illinois at Urbana-Champaign. Available from <https://www.ideals.illinois.edu/bitstream/handle/2142/97488/OSPINA-THESIS-2017.pdf?sequence=1&isAllowed=y>.
- Oswald KN, Diener EF, Diener JP, Cunningham SJ, Smit B, Lee ATK. 2020. Increasing temperatures increase the risk of reproductive failure in a near threatened alpine ground-nesting bird, the Cape Rockjumper *Chaetops frenatus*. *Ibis* **162**:1363–1369.
- Oswald SA, Bearhop S, Furness RW, Huntley B, Hamer KC. 2008. Heat stress in a high-latitude seabird: Effects of temperature and food supply on bathing and nest attendance of Great Skuas *Catharacta skua*. *Journal of Avian Biology* **39**:163–169.
- Ottvall R, Larsson K, Smith HG. 2005. Nesting success in Redshank *Tringa totanus* breeding on coastal meadows and the importance of habitat features used as perches by avian predators. *Bird Study* **52**:289–296.

- Paijmans DM, Loewenthal D, Ryan PG, Philip AH. 2015. Temporal and spatial differences in three-egg clutch frequency of the African Black Oystercatcher. *Ostrich* **86**:35–41.
- Parsons N. 2006. Quantifying abundance, breeding and behaviour of the African Black Oystercatcher. University of Cape Town.
- Pärt T, Doligez B. 2003. Gathering public information for habitat selection: Prospecting birds cue on parental activity. *Proceedings of the Royal Society B: Biological Sciences* **270**:1809–1813.
- Paterson JD. 1981. Postural-positional thermoregulatory behaviour and ecological factors in primates. *Canadian Review of Physical Anthropology* **3**:3–11.
- Patrick AM, Colwell MA. 2014. Snowy Plovers select wide beaches for nesting. *Wader Study Group Bulletin* **121**:17–20.
- Pavlovic G, Weston MA, Symonds MRE. 2019. Morphology and geography predict the use of heat conservation behaviours across birds. *Functional Ecology* **33**:286–296.
- Pedler RD, Weston MA, Bennett ATD. 2016. Long incubation bouts and biparental incubation in the nomadic Banded Stilt. *Emu* **116**:75–80.
- Pence CH, Ramsey G. 2013. A New foundation for the propensity interpretation of fitness. *The British Journal for the Philosophy of Science* **64**:851–881.
- Perrella DF, Zima PVQ, Ribeiro-silva L, Biagolini CHJ, Carmignotto AP, Galetti PMJ, Francisco MR. 2020. Bats as predators at the nests of tropical birds. *Journal of Avian Biology* **00**:e02277.
- Perrins CM, McCleery RH. 1989. Laying dates and clutch size in the Great Tit. *The Wilson Bulletin* **101**:236–253.
- Pincheira-Donoso D, Hunt J. 2017. Fecundity selection theory: concepts and evidence. *Biological Reviews* **92**:341–356.
- Pinet P, Jaeger A, Cordier E, Potin G, Le Corre M. 2011. Celestial moderation of tropical seabird behavior. *PLoS ONE* **6**:e27663.
- Pinheiro J, Bates D, DebRoy S, Sarkar D, Team RC. 2019. *_nlme: Linear and Nonlinear Mixed Effects Models_*.
- Pisingan RS, Harnadi L, Takemura A. 2006. Semilunar spawning periodicity in Brackish Damsel *Pomacentrus taeniometopon*. *Fisheries Science* **72**:1256–1260.
- Pitt WC. 2000. Effects of multiple vertebrate predators on grasshopper habitat selection: Trade-offs due to predation risk, foraging, and thermoregulation. *Evolutionary Ecology* **13**:499–515.
- Plaschke S, Bulla M, Cruz-López M, Gómez Del Ángel S, Küpper C. 2019. Nest initiation and flooding in response to season and semi-lunar spring tides in a ground-nesting shorebird. *Frontiers in Zoology* **16**:1–11.
- Portugal SJ, White CR, Frappell PB, Green JA, Butler PJ. 2019. Impacts of “supermoon” events on the physiology of a wild bird. *Ecology and Evolution* **00**:1–11.
- Pratte I, Davis SE, Maftei M, Mallory ML. 2016. Aggressive neighbors and dense nesting: nest site choice and success in high-Arctic Common Eiders. *Polar Biology* **39**:1597–1604.

- Prenda J, Lpez-Nieves P, Bravo R. 2001. Conservation of otter (*Lutra lutra*) in a Mediterranean area: The importance of habitat quality and temporal variation in water availability. *Aquatic Conservation: Marine and Freshwater Ecosystems* **11**:343–355.
- Prescott KW. 1964. Constancy of incubation for the Scarlet Tanager. *The Wilson Bulletin* **76**:37–42.
- Price T, Schluter D. 1991. On the low heritability of life-history traits. *Evolution* **45**:853–861.
- Primack RB. 2010. *Essentials of conservation biology* Fifth. Sinauer Associates, Inc, Sutherland, USA.
- Purdue JR. 1976. Thermal environment of the nest and related behaviour in Snowy Plovers, *Charadrius alexandrinus*. *The Condor* **78**:180–185.
- Putman BJ, Clark RW. 2017. Behavioral thermal tolerances of free-ranging rattlesnakes (*Crotalus oreganus*) during the summer foraging season. *Journal of Thermal Biology* **65**:8–15.
- Que P, Chang Y, Eberhart-Phillips L, Liu Y, Székely T, Zhang Z. 2014. Low nest survival of a breeding shorebird in Bohai Bay, China. *Journal of Ornithology* **156**:297–307.
- R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from www.R-project.org/.
- Radzio TA, O'Connor MP. 2017. Behavior and temperature modulate a thermoregulation–predation risk trade-off in juvenile Gopher Tortoises. *Ethology* **123**:957–965.
- Rahmstorf S. 2007. A semi-empirical approach to projecting future sea-level rise. *Science* **315**:368–371.
- Rahmstorf S, Cazenave A, Church JA, Hansen JE, Keeling RF, Parker DE, Somerville RCJ. 2007. Recent climate observations compared to projections. *Science* **316**:709.
- Raine AF, Driskill S, Vynne M, Harvey D, Kyle Pias. 2020. Managing the effects of introduced predators on Hawaiian endangered seabirds. *The Journal of Wildlife Management* **84**:425–435.
- Ramírez F, Rodríguez C, Seoane J, Figuerola J, Bustamante J. 2018. How will climate change affect endangered Mediterranean waterbirds? *PLoS ONE* **13**:e0192702.
- Ramli R, Norazlimi NA. 2016. Effects of tidal states and time of day on the abundance and behavior of shorebirds utilizing tropical intertidal environment. *Journal of Animal and Plant Sciences* **26**:1164–1171.
- Rao AS, Hockey PAR, Montevecchi WA. 2014. Coastal dispersal by pre-breeding African Black Oystercatchers *Haematopus moquini*. *Marine Ornithology* **42**:105–112.
- Reed DH. 2005. Relationship between population size and fitness. *Conservation Biology* **19**:563–568.
- Reed DH, Frankham R. 2003. Correlation between fitness and genetic diversity. *Conservation Biology* **17**:230–237.
- Reid JM, Monaghan P, Ruxton GD. 2000a. The consequences of clutch size for incubation conditions and hatching success in starlings. *Functional Ecology* **14**:560–565.
- Reid JM, Monaghan P, Ruxton GD. 2000b. Resource allocation between reproductive

- phases: The importance of thermal conditions in determining the cost of incubation. *Proceedings of the Royal Society B: Biological Sciences* **267**:37–41.
- Reidy JL, Thompson FR. 2018. Songbird nest survival in managed oak savannas and woodlands in the Missouri Ozarks. *The American Midland Naturalist* **180**:189–206.
- Reidy JL, Thompson III FR. 2013. Predatory identity can explain nest predation patterns. *USGS Northern Prairie Wildlife Research Center* **256**:135–148.
- Renfrew RB, Ribic CA. 2003. Grassland passerine nest predators near pasture edges identified on videotape. *The Auk* **120**:371–383.
- Reynolds MH, Courtot KN, Berkowitz P, Storlazzi CD, Moore J, Flint E. 2015. Will the effects of sea-level rise create ecological traps for Pacific Island seabirds? *PLoS One* **10**:e0136773.
- Ribeiro-Silva L, Perrella DF, Biagolini-Jr CH, Zima PVQ, Piratelli AJ, Schlindwein MN, Galetti Junior PM, Francisco MR. 2018. Testing camera traps as a potential tool for detecting nest predation of birds in a tropical rainforest environment. *Zoologia* **35**:e14678.
- Rich LN, Beissinger SR, Brashares JS, Furnas BJ. 2019. Artificial water catchments influence wildlife distribution in the Mojave Desert. *Journal of Wildlife Management* **83**:855–865.
- Richardson TW, Gardali T, Jenkins SH. 2009. Review and meta-analysis of camera effects on avian nest success. *The Journal of Wildlife Management* **73**:287–293.
- Ricklefs RE. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* **9**:1–48.
- Ricklefs RE. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. *The Auk* **97**:38–49.
- Ricklefs RE. 1990. Seabird life histories and the marine environment: Some speculations. *Colonial Waterbirds* **13**:1–6.
- Ricklefs RE. 2000. Density dependence, evolutionary optimization, and the diversification of avian life histories. *The Condor* **102**:9–22.
- Ricklefs RE, Travis J. 1980. A morphological approach to the study of avian community organization. *The Auk* **97**:321–338.
- Robben Island Museum. 2017. Integrated carrying capacity study 2018 - 2022. Robben Island Museum, Cape Town, South Africa.
- Robinson TB, Griffiths CL. 2002. Invasion of Langebaan Lagoon, South Africa, by *Mytilus galloprovincialis* - Effects on natural communities. *African Zoology* **37**:151–158.
- Robinson TB, Griffiths CL, McQuaid CD, Rius M. 2005a. Marine alien species of South Africa - Status and impacts. *African Journal of Marine Science* **27**:297–306.
- Robinson WD, Rompré G, Robinson TR. 2005b. Videography of Panama bird nests shows snakes are principal predators. *Ornitologia Neotropical* **16**:187–195.
- Rompré G, McNeil R. 1996. Variability in day and night feeding habitat use in the Willet *Catoptrophorus semipalmatus* during the non-breeding season in the northeastern Venezuela. *Wader Study Group Bull.* **81**:82–87.
- Rönkä A, Koivula K, Ojanen M, Pakanen V, Pohjoismäki M, Rannikko K, Rauhala P. 2006.

- Increased nest predation in a declining and threatened Temminck's Stint *Calidris temminckii* population. *Ibis* **148**:55–65.
- Roper JJ. 2005. Try and try again: Nest predation favors persistence in a neotropical bird. *Ornitologia Neotropical* **16**:253–262.
- Roper JJ, Sullivan KA, Ricklefs RE. 2010. Avoid nest predation when predation rates are low, and other lessons: testing the tropical-temperate nest predation paradigm. *Oikos* **119**:719–729.
- Rosenberg A. 1983. Fitness. *Journal of Philosophy* **80**:457–473.
- Ryeland J, Weston MA, Symonds MRE. 2017. Bill size mediates behavioural thermoregulation in birds. *Functional Ecology* **31**:885–893.
- Sabine III JB, Meyers JM, Moore CT, Schweitzer SH. 2008. Effects of human activity on behavior of breeding American Oystercatcher, Cumberland Island National Seashore, Georgia, USA. *Waterbirds: The International Journal of Waterbird Biology* **31**:70–82.
- Sabine JB, Schweitzer SH, Meyers MJ. 2006. Nest fate and productivity of American Oystercatchers, Cumberland Island National Seashore, Georgia. *Waterbirds* **29**:308–314.
- Sadchatheeswaran S, Branch GM, Robinson TB. 2015. Changes in habitat complexity resulting from sequential invasions of a rocky shore: implications for community structure. *Biological Invasions* **17**:1799–1816.
- Sæther BE et al. 2016. Demographic routes to variability and regulation in bird populations. *Nature Communications* **7**:1–8.
- Sæther BE, Bakke O. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**:642–653.
- Sandoval L, Barrantes G. 2019. Is black plumage an adaptation to high elevations in a cosmopolitan bird genus? *Journal of Avian Biology* **50**:1–8.
- Saviola AJ, McKenzie VJ, Chiszar D. 2012. Chemosensory responses to chemical and visual stimuli in five species of colubrid snakes. *Acta Herpetologica* **7**:91–103.
- Schmechel FA, Paterson AM. 2005. Habitat selection and breeding ecology of the endangered Chatham Island Oystercatcher (*Haematopus chathamensis*). Department of Conservation, Wellington, New Zealand.
- Schurink CVE, Griffiths CL. 1991. A comparison of reproductive cycles and reproductive output in four southern African mussel species. *Marine Ecology Progress Series* **76**:123–134.
- Senfeld T, Shannon TJ, Pajmans DM, Tavares ES, Baker AJ, Lees AC, Collinson MJ. 2020. Taxonomic status of the extinct Canary Islands Oystercatcher *Haematopus meadewaldoi*. *Ibis* **162**:1068–1074.
- Sharpe L, Cale B, Gardner JL. 2019. Weighing the cost: the impact of serial heatwaves on body mass in a small Australian passerine. *Journal of Avian Biology* **50**:1–9.
- Sherley R, Dyer B, Underhill L, Leshoro T. 2011. Birds occurring or breeding at Robben Island, South Africa, since 2000. *Ornithological Observations* **2**:69–100.

- Sherley RB. 2010. Factors influencing the demography of endangered seabirds at Robben Island, South Africa. University of Bristol.
- Shi M, Fang Y, Zhao JM, Klaus S, Jiang Y, Swenson JE, Sun YH. 2019. Egg laying and incubation rhythm of the Chinese Grouse (*Tetrastes sewerzowi*) at Lianhuashan, Gansu, China. *Avian Research* **10**:1–9.
- Shitikov D, Samsonov S, Makarova T. 2019. Cold weather events provoke egg ejection behaviour in open-nesting passerines. *Ibis* **161**:441–446.
- Shitikov D, Vaytina T, Makarova T, Fedotova S, Volkova V, Samsonov S. 2018. Species-specific nest predation depends on the total passerine nest density in open-nesting passerines. *Journal of Ornithology* **159**:483–491.
- Shitikov DA, Fedotova SE, Gagieva VA. 2012. Nest survival, predators and breeding performance of Booted Warblers *Iduna caligata* in the abandoned fields of the north of European Russia. *Acta Ornithologica* **47**:137–146.
- Shriver WG, Vickery PD, Hodgman TP, Gibbs JP, Sandercock BK. 2007. Flood tides affect breeding ecology of two sympatric Sharp-tailed Sparrows. *The American Naturalist* **124**:552–560.
- Simeone A, Luna-Jorquera G, Wilson RP. 2004. Seasonal variations in the behavioural thermoregulation of roosting Humboldt penguins (*Spheniscus humboldti*) in north-central Chile. *Journal of Ornithology* **145**:35–40.
- Simmonds EG, Sheldon BC, Coulson T, Cole EF. 2017. Incubation behavior adjustments, driven by ambient temperature variation, improve synchrony between hatch dates and caterpillar peak in a wild bird population. *Ecology and Evolution* **7**:9415–9425.
- Sinclair A. 2008. Factors affecting the food availability and breeding season of resident birds and movements of palaeartic migrants in a tropical African savannah. *Ibis* **120**:480–497.
- Sinsch U. 1989. Thermoregulation of the Andean Toad (*Bufo spinulosus*) at high altitudes. *Oecologia* **80**:32–38.
- Sippel S, Meinshausen N, Fischer EM, Székely E, Knutti R. 2020. Climate change now detectable from any single day of weather at global scale. *Nature Climate Change* **10**:35–41.
- Skein L, Alexander M, Robinson T. 2018. Contrasting invasion patterns in intertidal and subtidal mussel communities. *African Zoology* **53**:47–52.
- Skutch AF. 1962. The constancy of incubation. *Wilson Bulletin* **74**:115–152.
- Sládeček M, Vozabulová E, Šálek ME, Bulla M. 2019. Diversity of incubation rhythms in a facultatively uniparental shorebird – the Northern Lapwing. *Scientific Reports* **9**:1–11.
- Slagsvold T. 1982. Clutch size variation in passerine birds: The nest predation hypothesis. *Oecologia* **54**:159–169.
- Slagsvold T. 1984. Clutch size variation of birds in relation to nest predation: On the cost of reproduction. *Journal of Animal Ecology* **53**:945–953.
- Smit B, Boyles JG, Brigham RM, Mckechnie AE. 2011. Torpor in dark times: patterns of heterothermy are associated with the lunar cycle in a nocturnal bird. *Journal of*

- Biological Rhythms **26**:241–248.
- Smit B, Harding CT, Hockey PAR, E. McKechnie A. 2013. Adaptive thermoregulation during summer in two populations of an arid-zone passerine. *Ecology* **94**:1142–1154.
- Smit B, Zietsman G, Martin RO, Cunningham SJ, McKechnie AE, Hockey PAR. 2016. Behavioural responses to heat in desert birds: implications for predicting vulnerability to climate warming. *Climate Change Responses* **3**:1–14.
- Smith PA, Gilchrist HG, Forbes MR, Martin JL, Allard K. 2010. Inter-annual variation in the breeding chronology of arctic shorebirds: Effects of weather, snow melt and predators. *Journal of Avian Biology* **41**:292–304.
- Smith PA, Gilchrist HG, Smith JNM. 2007. Effects of nest habitat, food, and parental behavior on shorebird nest success. *The Condor* **109**:15–31.
- Smith PA, Tulp I, Schekkerman H, Gilchrist HG, Forbes MR. 2012. Shorebird incubation behaviour and its influence on the risk of nest predation. *Animal Behaviour* **84**:835–842.
- Smith PA, Wilson S. 2010. Intraseasonal patterns in shorebird nest survival are related to nest age and defence behaviour. *Oecologia* **163**:613–624.
- Snapp BD. 1976. Colonial breeding in the Barn Swallow (*Hirundo rustica*) and its adaptive significance. *The Condor* **78**:471–480.
- Southwell C, Emmerson L. 2020. Density dependence forces divergent population growth rates and alters occupancy patterns of a central place foraging Antarctic seabird. *Ecology and Evolution* **10**:2339–2351.
- Sparks T. H, Carey PD. 1995. The responses of species to climate over two centuries: an analysis of the Marsham. *Journal of Ecology* **83**:321–329.
- Spearpoint JA, Every B, Underhill LG. 1988. Waders (Charadrii) and other shorebirds at Cape Recife, Algoa Bay, South Africa: Seasonality, trends, conservation, and reliability of surveys. *Ostrich* **59**:166–177.
- Spiby J. 2012. Trends in African Black Oystercatchers *Haematopus moquini* on Robben Island, South Africa: population size and nest characteristics. University of Cape Town. Available from http://nivenlib.pfp.uct.ac.za/pdf/Spiby_Jacky_BSCons_Zoology_2012_thesis.pdf.
- Spiegel CS, Haig SM, Goldstein MI, Huso M. 2012. Factors affecting incubation patterns and sex roles of Black Oystercatchers in Alaska. *The Condor* **114**:123–134.
- Stadler PF, Stephens CR. 2003. Landscapes and effective fitness. *Journal of Theoretical Biology* **8**:389–431.
- Stakel MM, Cimprich DA. 2003. Using video to monitor predation at Black-Capped Vireo nests. *The Condor* **105**:348–357.
- Stearns CS, Koella CJ. 1986. The evolution of phenotypic plasticity in life-history traits: Predictions of reaction norms for age and size at maturity. *Evolution* **40**:893–913.
- Stearns SC. 1977. The evolution of life history traits: A critique of the theory and a review of the data. *Annual Review of Ecology and Systematics* **8**:145–171.

- Steen JB, Gabrielsen GW, J.W. Kanwisher. 1988. Physiological aspects of freezing behaviour in Willow Ptarmigan hens. *Acta Physiologica Scandinavica* **134**:299–304.
- Stern N. 2013. The economics of climate change. *The Future of Nature: Documents of Global Change* **7**:465–475.
- Stillman JH. 2019. Heat waves, the new normal: Summertime temperature extremes will impact animals, ecosystems, and human communities. *Physiology* **34**:86–100.
- Stott P. 2016. How climate change affects extreme weather events. *Science* **352**:1517–1518.
- Studds CE et al. 2017. Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. *Nature Communications* **8**:14895.
- Suggitt AJ et al. 2018. Extinction risk from climate change is reduced by microclimatic buffering. *Nature Climate Change* **8**:713–717.
- Summers RW, Cooper J. 1977. The population, ecology and conservation of the Black Oystercatcher *Haematopus moquini*. *Ostrich* **48**:27–40.
- Svensson E. 1995. Avian reproductive timing: when should parents be prudent? *Animal Behaviour* **49**:1569–1575.
- Swift RJ, Anteau MJ, Ring MM, Toy DL, Sherfy MH. 2020. Low reneating propensity and reproductive success make reneating unproductive for the threatened Piping Plover (*Charadrius melodus*). *The Condor* **122**:1–18.
- Takemura A, Rahman MS, Park YJ. 2010. External and internal controls of lunar-related reproductive rhythms in fishes. *Journal of Fish Biology* **76**:7–26.
- Tattersall GJ, Arnaout B, Symonds MRE. 2017. The evolution of the avian bill as a thermoregulatory organ. *Biological Reviews* **92**:1630–1656.
- Taye ENA. 2019. Breeding ecology and foraging behaviour of Black-winged Stilt (*Himantopus himantopus*) in Ghana. University of Ghana.
- Taylor GT, Ackerman JT, Shaffer SA. 2018. Egg turning behavior and incubation temperature in Forster's terns in relation to mercury contamination. *PLoS One* **13**:e0191390.
- Tetsuji I. 1996. Changes in the concept of "Fitness" in Evolutionary Biology. *Practical Philosophy Research* **19**:67–104.
- Teunissen W, Schekkerman H, Willems F, Majoor F. 2008. Identifying predators of eggs and chicks of lapwing *Vanellus vanellus* and Black-tailed Godwit *Limosa limosa* in the Netherlands and the importance of predation on wader reproductive output. *Ibis* **150**:74–85.
- Theron AK, Rossouw M. 2008. Analysis of potential coastal zone climate change impacts and possible response options in the southern African region. Stellenbosch, South Africa.
- Thierry A-M, Massemin S, Handrich Y, Raclot T. 2013. Elevated corticosterone levels and severe weather conditions decrease parental investment of incubating Adélie Penguins. *Hormones and Behavior* **63**:475–483.
- Thomas CD et al. 2004. Extinction risk from climate change. *Nature* **427**:294–296.
- Thompson III FR. 2007. Factors affecting nest predation on forest songbirds in North America. *Ibis* **149**:98–109.

- Thompson III FR, Dijak W, Burhans DE. 1999. Video identification of predators at songbird nests in old fields. *The Auk* **116**:259–264.
- Thompson M, Cunningham S, Mckechnie AE. 2018. Interspecific variation in avian thermoregulatory patterns and heat dissipation behaviours in a subtropical desert. *Physiology & Behavior* **188**:311–323.
- Thorne KM. 2012. Climate change impacts to the tidal salt marsh habitats of San Pablo Bay, California. University of California.
- Thünken T, Eigster M, Frommen JG. 2014. Context-dependent group size preferences in large shoals of Three-spined Sticklebacks. *Animal Behaviour* **90**:205–210.
- Tieleman BI, Noordwijk HJ Van, Williams JB. 2008. Nest site selection in a hot desert: Trade-off between microclimate and predation risk? *The Condor* **110**:116–124.
- Tinbergen JM, Daan S. 1990. Family planning in the Great Tit (*Parus major*): Optimal clutch size as integration of parent and offspring fitness. *Behaviour* **114**:161–190.
- Tjørve KMC. 2006. From an egg to a fledgling: A perspective on shorebird breeding ecology and chick energetics. University of Groningen. Available from <http://www.rug.nl/research/portal/files/33151015/thesis.pdf>.
- Tjørve KMC, Tjørve E. 2016. The influence of human activity on the breeding success of Eurasian Oystercatchers *Haematopus ostralegus* in southern Norway. *Wader Study* **123**:21–28.
- Tjørve KMC, Underhill LG. 2006. Population increase of African Black Oystercatchers *Haematopus moquini* on Robben Island, South Africa. *Ostrich* **77**:229–232.
- Tjørve KMC, Underhill LG. 2008. Influence of disturbance and predation on breeding success of the African Black Oystercatcher *Haematopus moquini* on Robben Island, South Africa. *Waterbirds: The International Journal of Waterbird Biology* **31**:83–96.
- Tona K, Onagbesan O, Bruggeman V, Mertens K, Decuypere E. 2005. Effects of turning duration during incubation on embryo growth, utilization of albumen, and stress regulation. *Poultry Science* **84**:315–320.
- Tona K, Onagbesan O, De Ketelaere B, Decuypere E, Bruggeman V. 2003. Effects of turning duration during incubation on corticosterone and thyroid hormone levels, gas pressures in air cell, chick quality, and juvenile growth. *Poultry Science* **82**:1974–1979.
- Tortosa FS, Pérez L, Hillström L. 2003. Effect of food abundance on laying date and clutch size in the White Stork *Ciconia ciconia*. *Bird Study* **50**:112–115.
- Troscianko J, Wilson-Aggarwal J, Stevens M, Spottiswoode C. 2016. Camouflage predicts survival in ground-nesting birds. *Scientific Reports* **6**:19966.
- Troy ASR, Conover RR. 2019. The depredation of Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) nests by the Golden-mantled Ground Squirrel (*Callospermophilus lateralis*) and Long-tailed Weasel (*Mustela frenata*). *The Wilson Journal of Ornithology* **131**:629–633.
- Tscharntke T, Tylianakis J. 2010. Conserving complexity: Global change and community-scale interactions. *Biological Conservation* **143**:2249–2250.
- Tulp I, Schekkerman H. 2006. Time allocation between feeding and incubation in uniparental

- arctic-breeding shorebirds: Energy reserves provide leeway in a tight schedule. *Journal of Avian Biology* **37**:207–218.
- Tulp I, Schekkerman H, Bruinzeel LW, Jukema J, Visser GH, Piersma T. 2009. Energetic demands during incubation and chick rearing in a uniparental and a biparental shorebird breeding in the high arctic. *The Auk* **126**:155–164.
- Turner MG et al. 2020. Climate change, ecosystems and abrupt change: Science priorities. *Philosophical Transactions of the Royal Society B: Biological Sciences* **375**:20190105.
- Turpie JK, Hockey PAR. 1993. Comparative diurnal and nocturnal foraging behaviour and energy intake of premigratory Grey Plovers *Pluvialis squatarola* and Whimbrels *Numenius phaeopus* in South Africa. *Ibis* **135**:156–165.
- Underhill L, Whittington P, Calf K. 2001. Shoreline birds of Robben Island, Western Cape, South Africa. *Wader Study Group Bulletin* **96**:37–39.
- Underhill LG. 2014. Assessment of the conservation status of African Black Oystercatcher *Haemantopus moquini*. *International Wader studies* **20**:97–108.
- Underhill LG, Calf KM. 2005. How far is an egg through incubation? *Wader Study Group Bulletin* **106**:39–41.
- Underhill LG, Sherley RB, Dyer BM, Crawford RJM. 2009. Interactions between snakes and seabirds on Robben, Schaapen and Meeuw islands, Western Cape province, South Africa. *Ostrich* **80**:115–118.
- UNESCO World Heritage Committee. 2003. State of conservation of properties inscribed on the World Heritage List, WHC-03/27.COM/7B. Paris, UNESCO Headquarters, Room XII. Available from <https://whc.unesco.org/archive/2003/whc03-27com-07be.pdf>.
- Urfi AJ. 2003. Breeding ecology of birds: Why do some species nest singly while others are colonial? *Resonance* **8**:22–32.
- Vafidis JO, Facey RJ, Leech D, Thomas RJ. 2018. Supplemental food alters nest defence and incubation behaviour of an open-nesting wetland songbird. *Journal of Avian Biology* **49**:e01672.
- van de Pol M et al. 2010. Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? *Journal of Applied Ecology* **47**:720–730.
- van de Pol M, Oosterbeek K, Rutten AL, Ens BJ, Tinbergen JM, Verhulst S. 2009. Biometric sex discrimination is unreliable when sexual dimorphism varies within and between years: an example in Eurasian Oystercatchers *Haematopus ostralegus*. *Ibis* **15**:171–180.
- van De Pol M, Verhulst S. 2006. Age-dependent traits: A new statistical model to separate within- and between- individual effects. *The American Naturalist* **167**:766–773.
- van de Ven TMFN, Mckechie AE, Cunningham SJ. 2019. The costs of keeping cool: behavioural trade-offs between foraging and thermoregulation are associated with significant mass loss in an arid-zone bird. *Oecologia* **191**:205–215.
- Van de Voorde S, Witteveen M, Brown M. 2015. Differential reactions to anthropogenic disturbance by two ground-nesting shorebirds. *Ostrich* **86**:43–52.
- van Noordwijk A. J., de Jong G. 1986. Acquisition and allocation of resources: Their influence

- on variation in life history tactics. *The American Naturalist* **128**:137–142.
- Van Sant MJ, Oufiero CE, Muñoz-Garcia A, Hammond KA, Williams JB. 2012. A Phylogenetic approach to total evaporative water loss in mammals. *Physiological and Biochemical Zoology* **85**:526–532.
- Varpe Ø, Jørgensen C, Tarling GA, Fiksen Ø. 2009. The adaptive value of energy storage and capital breeding in seasonal environments. *Oikos* **118**:363–370.
- Veldsman LM, Kylin H, Bronkhorst P, Engelbrecht I, Bouwman H. 2020. A method to determine the combined effects of climate change (temperature and humidity) and eggshell thickness on water loss from bird eggs. *Environmental Geochemistry and Health* **42**:781–793.
- Verhulst S, Nilsson J-Å. 2008. The timing of birds' breeding seasons: A review of experiments that manipulated timing of breeding. *Philosophical Transactions of The Royal Society B* **363**:399–410.
- Vermeer K, Morgan KH, J Smith GE. 1992. Black Oystercatcher habitat selection, reproductive success, and their relationship with Glaucous-winged Gulls. *Colonial Waterbirds* **15**:14–23.
- Vernon CJ. 2004. Status and abundance of the African Black Oystercatcher *Haematopus moquini* at the eastern limit of its breeding range. *Ostrich* **75**:243–249.
- Vigallon SM, Marzluff JM. 2005. Is nest predation by Steller's Jays (*Cyanocitta Stelleri*) incidental or the result of a specialized search strategy? *The Auk* **122**:36.
- Virzi T, Lockwood JL, Drake D, Grodsky SM, Pover T. 2016. Conservation implications of reproductive success of American Oystercatchers in an urbanized barrier island complex. *Wader Study* **123**:202–212.
- Visco DM, Sherry TW. 2015. Increased abundance, but reduced nest predation in the Chestnut-backed Antbird in Costa Rican rainforest fragments: Surprising impacts of a pervasive snake species. *Biological Conservation* **188**:22–31.
- Visser ME, Both C. 2005. Shifts in phenology due to global climate change: The need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences* **272**:2561–2569.
- Visser ME, Gienapp P. 2019. Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology and Evolution* **3**:879–885.
- Visser ME, Holleman LJM, Caro SP. 2009. Temperature has a causal effect on avian timing of reproduction. *Proceedings of the Royal Society B: Biological Sciences* **276**:2323–2331.
- Vitale N, Brush J, Powell A. 2020. Loss of coastal islands along Florida's big bend region: Implications for breeding American Oystercatchers. *Estuaries and Coasts* **00**:1–10.
- Vleck CM. 1981. Energetic cost of incubation in the Zebra Finch. *The Condor* **83**:229–237.
- Von Holle B et al. 2019. Effects of future sea level rise on coastal habitat. *Journal of Wildlife Management* **83**:694–704.
- Vousdoukas MI, Voukouvalas E, Annunziato A, Giardino A, Feyen L. 2016. Projections of extreme storm surge levels along Europe. *Climate Dynamics* **47**:3171–3190.
- Walsberg GE, Campbell GS, King JR. 1978. Animal coat color and radiative heat gain: a re-

- evaluation. *Journal of Comparative Physiology* **126**:211–222.
- Walsh PT, Evans DM, Hansell M, Ruxton GD. 2007. Factors influencing nocturnal egg-turning frequency in Meadow Pipits *Anthus pratensis*. *Bird Study* **54**:133–136.
- Walther G, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J, Hoegh-guldberg O, Bairlein F. 2002. Ecological response to recent climate change. *Nature* **416**:389–395.
- Ward D. 1990. Incubation temperatures and behavior of Crowned, Black-Winged, and Lesser Black-Winged Plovers. *The Auk* **107**:10–17.
- Watson JJ, Kerley GIH, Mclachlan A, Kerley GIH, Mclachlan A. 1997. Nesting habitat of birds breeding in a coastal dunefield, South Africa and management implications. *Journal of Coastal Research* **13**:36–45.
- Watson M, Wilson JM, Koshkin M, Sherbakov B, Karpov F, Gavrilov A, Schielzeth H, Brombacher M, Collar NJ, Cresswell W. 2006. Nest survival and productivity of the critically endangered Sociable Lapwing *Vanellus gregarius*. *Ibis* **148**:489–502.
- Watts HE, Jimenez D, Pacheco V, Vilgalys TP. 2019. Temperature-correlated shifts in the timing of egg-laying in House Finches *Haemorhous mexicanus*. *Ibis* **161**:428–434.
- Weatherhead PJ, Blouin-Demers G. 2004. Understanding avian nest predation: Why ornithologists should study snakes. *Journal of Avian Biology* **35**:185–190.
- Weatherhead PJ, Sperry JH, Carfagno GLF, Blouin-demers G. 2012. Latitudinal variation in thermal ecology of North American ratsnakes and its implications for the effect of climate warming on snakes. *Journal of Thermal Biology* **37**:273–281.
- Weathers WW. 1981. Physiological thermoregulation in heat-stressed birds: Consequences of body size. *Physiological Zoology* **54**:345–361.
- Weathers WW, Zaun BJ. 2010. Egg-turning behavior and nest attentiveness of the endangered Hawaiian Goose on kauai. *Western Birds* **41**:2–9.
- Webb DR. 1987. Thermal tolerance of avian embryos: a review. *Condor* **89**:874–898.
- Webber AF, Heath JA, Fischer RA. 2013. Human disturbance and stage-specific habitat requirements influence Snowy Plover site occupancy during the breeding season. *Ecology and Evolution* **3**:853–863.
- Weimerskirch H. 1990. The influence of age and experience on breeding performance of the Antarctic Fulmar, *Fulmarus glacialisoides*. *Journal of Animal Ecology* **59**:867–875.
- Weiser EL et al. 2018. Effects of environmental conditions on reproductive effort and nest success of Arctic-breeding shorebirds. *Ibis* **160**:608–623.
- Wen L, He H, Wang Y, Gorimar J, Liu M. 2014. Potential effects of climate change on the Chinese Bulbul (*Pycnonotus sinensis*) in China. *Biologia* **69**:1625–1630.
- White CL, Strauss LR, Stephen K. Davis. 2010. Video evidence of Piping Plover nest predation. *Northwestern Naturalist* **91**:202–205.
- White FN, Kinney JL. 1974. Avian incubation. *Science* **186**:107–115.
- White GC, Burnham KP. 1999. Program mark: Survival estimation from populations of marked animals. *Bird Study* **46**:S120–S139.

- Whittington PA et al. 2016. Recent trends of the Kelp Gull (*Larus dominicanus*) in South Africa. *Waterbirds* **39**:99–113.
- Widlansky MJ, Timmermann A, Cai W. 2015. Future extreme sea level seesaws in the tropical Pacific. *Science Advances* **1**:e1500560.
- Williams A, Ward V, Underhill L. 2004. Waders respond quickly and positively to the banning of off-road vehicles from beaches in South Africa. *Bulletin-Wader Study Group* **104**:79–81.
- Williams GC. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *The American Naturalist* **100**:687–690.
- Williams GE., Wood PB. 2002. Are traditional methods of determining nest predators and nest fates reliable? An experiment with Wood Thrushes (*Hylocichla mustelina*) using miniature video cameras. *The Auk* **119**:1126–1132.
- Wilson AM, Vickery JA, Brown A, Langston RHW, Smallshire D, Wotton S, Vanhinsbergh D. 2005. Changes in the numbers of breeding waders on lowland wet grasslands in England and Wales between 1982 and 2002. *Bird Study* **52**:55–69.
- Wilson S, Martin K, Hannon SJ. 2007. Nest survival patterns in Willow Ptarmigan: Influence of time, nesting stage, and female characteristics. *The Condor* **109**:377.
- Wong BBM, Candolin U. 2015. Behavioral responses to changing environments. *Behavioral Ecology* **26**:665–673.
- Woth K, Weisse R, Von Storch H. 2006. Climate change and North Sea storm surge extremes: An ensemble study of storm surge extremes expected in a changed climate projected by four different regional climate models. *Ocean Dynamics* **56**:3–15.
- Yamamoto T, Takahashi A, Yoda K, Katsumata N, Watanabe S, Sato K, Trathan PN. 2008. The lunar cycle affects at-sea behaviour in a pelagic seabird, the Streaked Shearwater, *Calonectris leucomelas*. *Animal Behaviour* **76**:1647–1652.
- Yorio P, Boersma PDEE. 1994. Causes of nest desertion during incubation in the Magellanic Penguin (*Spheniscus magellanicus*). *The Condor* **96**:1076–1083.
- Zhang L, Shu M, An B, Zhao C, Suo Y, Yang X. 2017. Biparental incubation pattern of the Black-necked Crane on an alpine plateau. *Journal of Ornithology* **158**:697–705.
- Zhao J-M, Yang C, Lou Y-Q, Shi M, Fang Y, Sun Y-H. 2020. Nesting season, nest age, and disturbance, but not habitat characteristics, affect nest survival of Chinese Grouse. *Current Zoology* **66**:29–37.