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**Foraging ecology of gentoo penguins *Pygoscelis papua* at the Falkland Islands**

By:

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*Be bold, be humble, make a splash upon the world...*

## Declaration

I, Jonathan Murray Handley (s212324527), hereby declare that this thesis submitted in the fulfilment of the requirements for the degree, Doctor of Philosophy, is my own work and that it has not previously been submitted for assessment or completion of any postgraduate qualification to another University or for another qualification

Jonathan Murray Handley

A handwritten signature in dark ink, appearing to read 'J. Handley', with a long horizontal flourish extending to the right.

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**M**  **PRU** | Marine Apex Predator  
Research Unit



## ABSTRACT

Marine top predators often occupy broad geographical ranges that encompass varied habitats. Therefore, a pre-requisite towards conserving these animals is to determine the components of their realized niche, and investigate whether a species is a specialist or a generalist. For generalist species, it is also necessary to understand if local specialisation occurs. Uncovering these components can allow us to build models of a species realized niche that may then be used to infer habitat use in unsampled locations. However, fully understanding the components of a marine top predators realized niche is challenging owing to the limited opportunity for *in situ* observations. Overcoming these limitations is a key step in marine top predator research. It will enhance our understanding of trophic coupling in marine systems, and aid in the development of tools to better study these predators in their dynamic environment.

Seabirds, penguins (Spheniscids) in particular, are a group of animals for which investigating their realized niche is of vital importance. This is because numerous species face growing uncertainty in the Anthropocene, and in a time of rapid environmental change there is furthermore a need to better understand the potential use of these birds as indicators of ecosystem health. The aim of this thesis, therefore, is to investigate the foraging ecology of gentoo penguins (*Pygoscelis papua*) at the Falkland Islands. At the Falkland Islands, limited historical information exists regarding this species foraging ecology, with most information coming from a single location at the Falklands. As the Falkland Islands have the world's largest population of gentoo penguins, elucidating factors influencing this population will have global relevance. Furthermore, historical information indicated potential competition with fisheries, and with prospecting for hydrocarbons and an inshore fishery, there is a need to understand the distribution of these birds across the islands. Penguins are also well suited to carry biologging devices allowing for *in situ* observations of inter and intraspecific interactions, as well as habitat specific interactions.

In this study, I sampled birds over three breeding seasons, from four breeding colonies - chosen for their varied surrounding at sea habitat - across the Falkland Islands. I investigated the diet with stomach content and stable isotope analysis, the at-sea distribution with GPS and time depth recorders, and how these birds behaved at sea using custom made animal-borne camera loggers. Furthermore, I developed a method to recognise prey encounter events from back mounted accelerometers, using a supervised machine learning approach.

As part of the first species specific description of diet at this scale for the Falklands, I revealed six key prey items for the birds: rock cod (*Patagonotothen* spp.), lobster krill (*Munida* spp.), Falkland

herring (*Sprattus fuegensis*), Patagonian squid (*Doryteuthis gahi*), juvenile fish (likely all nototheniids), and southern blue whiting (*Micromesistius australis*). The use of animal-borne camera loggers verified that not only do gentoo penguins consume a diverse array of prey items, but they adopted various methods to capture and pursue prey, with evidence of birds following optimal foraging theory.

Prey composition varied significantly between study sites with the at-sea distribution and habitat use of penguins reflecting that of local prey. Birds from colonies close to gently sloping, shallow waters, foraged primarily in a benthic manner and had larger niche widths. However, those at a colony surrounded by steeply sloping, deeper waters, typically foraged in a pelagic manner. Contrasting diet patterns were also prevalent from stable isotope data, and the niche widths of birds relating to both stomach content and stable isotope data were larger at colonies where benthic foraging was prevalent. Therefore, it was clear that surrounding bathymetry played a key role in shaping this species' foraging ecology, and that at the population level at the Falkland Islands birds are generalists. However, at individual colonies some specialisation occurs to take advantage of locally available prey.

I developed habitat distribution models - via boosted regression trees – which transferred well in time but poorly across space. Reasons for poor model transfer might relate to the generalist foraging nature of these birds and the reduced availability of environmental predictors owing to the limited range of these birds. I furthermore developed a method to identify prey encounter events that can also, to a degree, distinguish between prey items. This method will be a promising approach to refine habitat distribution models in future. These habitat distribution models could potentially contribute to marine spatial planning at the Falkland Islands.

Footage from animal-borne camera loggers clearly showed that prey behaviour can significantly influence trophic coupling in marine systems and should be accounted for in studies using marine top predators as samplers of mid to lower trophic level species. Ultimately, flexibility in foraging strategies and inter-colony variation will play a critical role when assessing factors such as inter-specific competition or overlap with anthropogenic activities.

## PREFACE

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Key video footage for this thesis can be found on the You Tube channel: “Handley PhD”

I am the sole author of this thesis. However, various individuals provided valuable discussion regarding analyses. These were Dr Maëlle Connan (Nelson Mandela University), Dr Norman Ratcliffe (British Antarctic Survey), Dr Andréa Thiebault (Nelson Mandela University) and Dr. Gemma Carroll (Macquarie University). While each of these individuals provided the necessary starting direction and constructive debate during the analyses, I primarily wrote all R scripts and analysed all data for this thesis. The relevant papers used for analyses are noted in chapters, however, I gained the necessary core skills to do the analyses through the following means (this list is non-exhaustive):

- June – November 2014: PhD scholarship allowed me to do an internship with Norman Ratcliffe at the British Antarctic Survey
- October 2014: Studied the appendix and first seven chapters, along with additional reference to remaining chapters, of the statistics text book, Mixed effects models and extensions in ecology with R, by Zuur et al. (2009).
- January 2015: Online R Programming Course via COURSERA, John Hopkins University (Distinction). <https://www.coursera.org/learn/r-programming>
- 2-6 February 2015: Movement Ecology Workshop at my university with training from international experts
- April 2015: Online stable isotope tutorials by Andrew Jackson of Trinity College Dublin. <http://www.tcd.ie/Zoology/research/research/theoretical/Rpodcasts.php>
- 20 July – 4 September 2015: BOT 430 Module at my university to learn ArcMap (Distinction)
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- Coding queries: Stack Exchange account

I actively encourage individuals to take up the many online course work opportunities available.

## **PUBLICATIONS ARISING FROM THIS THESIS**

- HANDLEY, J. M., CONNAN, M., BAYLIS, A. M. M., BRICKLE, P. & PISTORIUS, P.** 2017. Jack of all prey, master of some: Influence of habitat on the feeding ecology of a diving marine predator. *Marine Biology* 164.
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## TABLE OF CONTENTS

ABSTRACT.....	I
PREFACE.....	III
PUBLICATIONS ARISING FROM THIS THESIS.....	IV
ASSOCIATED PUBLICATIONS ARISING FROM MY PhD STUDIES.....	IV
TABLE OF CONTENTS.....	V
LIST OF FIGURES.....	VII
LIST OF TABLES.....	X
ACKNOWLEDGEMENTS.....	XII
Chapter 1 General Introduction.....	1
Seabird foraging in the marine environment.....	1
Penguins (Order: Sphenisciformes).....	3
Study species: The gentoo penguin.....	4
Study site.....	9
Rationale and motivation for my study:.....	15
Thesis aims and structure.....	17
Chapter 2 Jack of all prey, master of some: Influence of habitat on the feeding ecology of a diving marine predator.....	20
Abstract.....	20
Introduction.....	20

Methods .....	22
Results .....	28
Discussion .....	38
Chapter 3 Site specific foraging strategies of a colonially breeding seabird revealed through biologging and habitat distribution models.....	44
Abstract .....	44
Introduction .....	44
Methods .....	47
Results .....	53
Discussion .....	61
Chapter 4 Behaviourally mediated predation avoidance in penguins: the need to account for prey behaviour in marine trophic studies.....	66
Abstract .....	66
Introduction .....	66
Methods .....	67
Results .....	68
Discussion .....	73
Chapter 5 Use of machine learning to identify in-situ feeding events by two penguin species ...	76
Abstract .....	76
Introduction .....	76
Methods .....	80
Results .....	85
Discussion .....	89
Chapter 6 General Discussion .....	93
Foraging plasticity in gentoo penguins.....	94
Penguins as sentinels of the marine environment.....	97
Towards the future.....	99

Final thoughts.....	101
References .....	103
Appendix: Chapter 2 (Figures and Tables).....	136
Appendix: Chapter 3 (Model Transferability) .....	157
Appendix: Chapter 4 (Video analysis) .....	162

## LIST OF FIGURES

Figure 1.1: Breeding gentoo penguin at the Falkland Islands .....	4
Figure 1.2: Distribution of the main sites where breeding colonies of gentoo penguins are present. A) Tierra del Fuego, B) Falkland Islands, C) Antarctic Peninsula & The South Shetland Islands, D) South Orkneys, E) South Georgia & The South Sandwich Islands, F) Prince Edward Islands, G) Crozet Islands, H) Kerguelen Islands, I) Heard & McDonald Islands, and J) Macquarie Islands. 5	
Figure 1.3: The Falkland Islands surrounded by the Falkland Islands Interim Conservation and Management Zone (FICZ, light blue), and the Falkland Islands Outer Conservation Zone (FOCZ, dark blue).....	10
Figure 1.4: Gentoo penguin colonies of the Falkland Islands (small dots) and the four study colonies: Steeple Jason (SJ), Cow Bay (CB), Bull Roads (BR) and Bull Point (BP). Isobaths (faint lines) are shown at 50m intervals from 100m to 300m depth .....	11
Figure 1.5: Steeple Jason Island at the Falkland Islands. Green and yellow circles indicate study and adjacent colonies, respectively.....	12
Figure 1.6: Cow Bay at the Falkland Islands. Green and yellow circles indicate study and adjacent colonies, respectively .....	13
Figure 1.7: Bull Roads and Bull Point at the Falkland Islands. Green and yellow circles indicate study and adjacent colonies, respectively.....	14
Figure 2.1: Gentoo penguin colonies of the Falkland Islands (small dots) and the four study colonies: Steeple Jason (SJ), Cow Bay (CB), Bull Roads (BR) and Bull Point (BP). Isobaths (faint lines) are shown at 50m intervals from 100m to 300m depth .....	23
Figure 2.2: Linear model indicating relationship between degree of diet specialisation (V) and trophic niche width (TNW) for gentoo penguins sampled from four colonies Bull Point (BP), Bull Roads (BR), Cow Bay (CB) and Steeple Jason (SJ) over three breeding seasons at the Falkland Islands.	

Solid line represents the best fit from linear model with shaded area depicting the 95% confidence bands. Individual data points for the linear model come from sampling season, site and breeding stage specific sampling periods .....	31
Figure 2.3: Feather stable isotope values ( $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ , centered and rescaled data) for adult gentoo penguins breeding at four colonies: Bull Point (BP), Bull Roads (BR), Cow Bay (CB) and Steeple Jason (SJ) at the Falkland Islands. Feathers were collected from breeding adult birds during concurrent stomach sampling in the austral summer breeding season: 2011, 2012 and 2013. Total (dashed lines, IRic) and core isotopic niche area adjusted for sample size (solid lines, SEAc) are shown .....	35
Figure 2.4: Simulated mixing region for the isotopic mixing model attempted towards the use of diet inference for gentoo penguins at the Falkland Islands. Isotopic signatures of the consumers, individual gentoo penguins, were determined from white adult breast feathers collected in the 2011, 2012 and 2013 breeding periods and are represented by solid circles. Sampling occurred at four colonies; Bull Point (dark red), Bull Roads (dark green), Cow Bay (dark blue) and Steeple Jason (purple). Average source values are represented by white crosses. Probability contours are displayed in black with the outermost contour indicating the 95% mixing region. Samples outside this 95% mixing region are considered inadequate, indicating that an alternative model is needed to explain the diet of the consumer .....	37
Figure 3.1: Probability of tracks overlapping at the 50% utilization distribution. Dashed lines indicate upper and lower confidence intervals associated with the curve after 500 bootstraps. Solid horizontal line indicates the 95% probability of overlapping. Sampling periods are defined by site-season-breeding stage. SJ, BR, CB: Steeple Jason Neck, Bull Roads, Cow Bay. 1213, 1314: 2012/13, 2013/14. I,G: Incubation, Guard .....	54
Figure 3.2: Distribution of gentoo penguins at the Falkland Islands during the 2012 and 2013 breeding seasons. Insets include the (A) incubation period at Steeple Jason Neck and the guards periods of (B,C) Cow Bay and (D,E) Bull Roads during the 2012 and 2013 seasons, respectively. Red bar indicates summed dive effort per cell from all tracks combined. Black bar represents a 10km scale bar. Known breeding gentoo colonies are indicated by black dots, while yellow dots indicate the size of annually monitored colonies during the 2012 breeding pair census (Stanworth 2013) ...	57
Figure 3.3: Three-dimensional representation (blue line) of a typical foraging trip from (top) Steeple Jason, (middle) Bull Roads and (bottom) Cow Bay. Insets show a portion of a cross-sectional typical dive profile. Black bars show 1km scale at given location in image because scale in 3D varies in a linear perspective fashion. Arrow depicts north. Track creation was done by	



interpolating GPS locations to the same time interval as TDR loggers. Visualisation was achieved using ArcScene 10.3 (ESRI) .....	59
Figure 4.1: Gentoo penguin colonies (black dots) of the Falkland Islands (top panel), including the two study colonies (stars), BR Bull Roads and CB Cow Bay. Tracks ( $n_{BR} = 13$ , $n_{CB} = 9$ ) in blue (middle and bottom panel) indicate foraging paths of instrumented birds, while yellow overlays indicate period of time while cameras were recording .....	69
Figure 4.2: The moment before a gentoo penguin strikes a small fish with an upward strike of its head. The silhouette of the small fish aided in its likely identification as a rock cod, either <i>Patagonotothen tessellata</i> or <i>Patagonotothen ramsayi</i> , based on expert opinion (P. Brickle, pers. comm.), and the known biology of fish in this genus at the Falkland Islands (Brickle et al. 2006). Also, the known diet of these birds during my study (Handley et al. 2016, 2017) .....	70
Figure 4.3: Lobster krill <i>Munida</i> spp. (a) assumes defensive position, with pincers open, as bird heads toward it. And, (b) lobster krill is attacking bird with its pincers (attached to the side of the penguin beak) during an attempted prey capture (APC). In both instances, birds were unsuccessful in capturing prey .....	72
Figure 4.4: (a) Probability of gentoo penguin attack on differing swarm density of lobster krill with, (b) example images highlighting percentage cover and pixel conversion (using ImageJ) of swarms in order to generate a proxy for swarm density. Grey bars in panel (a) represent 10% interval bins, the red line is the fitted function of a logistic regression model and the dashed line indicates percentage cover where probability of attack = 0.5 .....	73
Figure 5.1: Overview of the steps required to develop a classification algorithm for identifying prey interactions by penguins as oppose to swimming, using a support vector machine.....	84
Figure 5.2: Frequency histograms denoting the duration (s) that prey encounter events lasted, for gentoo penguins attempting to feed on lobster krill and juvenile fish, and little penguins attempting to feed on fish .....	85
Figure 5.3: Exemplar still images of the moment before striking at a (a) lobster krill and (b) juvenile fish by gentoo penguins, and at a (c) fish by a little penguin .....	86
Figure 5.4: Exemplar accelerometer profiles during a single dive where gentoo penguins were feeding on (a) lobster krill and (b) juvenile fish, and where little penguins were feeding on (c) fish. Accelerometer data is in units of g. Lk = lobster krill, Jf = Juvenile fish.....	87
Figure 6.1: Raster image used for canvas print production. The image depicts 100 possible foraging paths used by a bird through a continuous-time correlated random walk model ('crawl' package, (Johnson et al. 2008)). Bright white colours depict areas of high use .....	99

## LIST OF TABLES

Table 2.1: Stomach samples collected from gentoo penguins breeding at the Falkland Islands. Sampling occurred at four colonies: Steeple Jason (SJ), Cow Bay (CB), Bull Point (BP) and Bull Roads (BR) .....	24
Table 2.2: Detail of metrics used to describe the area of the convex hull (IRic), degree of similarity between two groups (ISim, INes) and the within group distribution of organisms (IDiv, IDis, IEve and IUni), in isotopic niche space, as outlined in Cucherousset and Villéger (2015) 27	27
Table 2.3: Main prey species identified from stomach content analysis of gentoo penguins at the Falkland Islands as indicated by having the percentage index of relative importance (%IRI) >1. Typical habitat of prey items was determined from various sources. NA: Data or source not available.....	28
Table 2.4: Results of ADONIS tests for comparison of major prey items between different stages of the breeding period (incubation (I), guard (G) and crèche (C)) and across colonies for gentoo penguins at the Falkland Islands. Samples were analysed for three seasons, 2011, 2012 and 2013 from four different colonies: Bull Point (BP), Bull Roads (BR), Cow Bay (CB) and Steeple Jason (SJ). Associated nMDS ordination and stacked bar plots can be found in the appendix figures A2.2: A-G, A2.3: A-E .....	30
Table 2.5: Degree of individual diet specialisation (V) for breeding gentoo penguins at the Falkland Islands, determined against only the prey items consumed within a single sampling period and against all prey items consumed across the same season (2011-2013) and breeding stage (guard (G) and crèche (C)). Prey items within each sampling period were identified from the %IRI. See appendix table A2.3 for prey abbreviations. Note, only those prey with %IRI > 1 were used for the analysis, however, the top three prey items for each period are shown for detail.....	32
Table 2.6: Feather carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope values of adult gentoo penguins at the Falkland Islands collected during the breeding seasons of the 2011, 2012 and 2013 austral summers. Collections occurred at Bull Point (BP), Bull Roads (BR), Cow Bay (CB) and Steeple Jason (SJ). Isotopic niche indices include: standard ellipse area corrected for small sample size ( $\text{SEA}_C$ ), the Bayesian estimate of the standard ellipse area with lower and upper bounds of 95% credible intervals ( $\text{SEA}_B$ , Jackson et al. 2011) and, isotopic richness (IRic, Cucherousset and Villéger 2015), the area of the convex hull. A, B, indicate periods where samples were non-significantly different. * indicates average calculated value after bootstrapping to account for varying sample size .....	34

Table 2.7: Inter and intra-colony isotopic diversity metrics (Cucherousset & Villéger 2015): Isotopic divergence (IDiv), dispersion (IDis), evenness (IEve) and uniqueness (IUni) determined from feathers of breeding adult gentoo penguins at the Falkland Islands. Samples collected over three years from four different colonies: Bull Point (BP), Bull Roads (BR), Cow Bay (CB) and Steeple Jason (SJ) .....	36
Table 3.1: Mean (SE) and range of dive and trip characteristics for gentoo penguins at the Falkland Islands from three colonies (BR: Bull Roads, CB: Cow Bay, SJN: Steeple Jason Neck) during the breeding period (Incubation, Guard) of 2012 and 2013. LR reports result from likelihood ratio test used to compare linear mixed effects models (dive characteristics) and general least squares models (trip characteristics) with and without the fixed effect of colony. Significant differences within a variable indicated by differing superscripts .....	55
Table 3.2: Model extrapolative performance indices; area under the curve (AUC) and point biserial correlation (PB Cor) for distribution models developed from tracks of breeding gentoo penguins at the Falkland Islands. Models were developed from two colonies (CB Cow Bay, BR Bull Roads) during two seasons (2012 = 1213, 2013 = 1314), while birds were guarding chicks. Table should be read from top then across to the left. I.e. the CB1213 model tested on the BR1314 data produced an AUC value of 0.86 .....	60
Table 3.3: Boosted regression tree results and model parameters for the distribution models developed for guard stage gentoo penguins at the Falkland Islands. Models developed from two colonies and include BR Bull Roads and CB Cow Bay during the 2012/13 and 2013/14 breeding season .....	60
Table 4.1: Orientation of gentoo penguins while feeding on all prey and the two main prey types observed, lobster krill <i>Munida</i> spp. and small fish (likely <i>Patagonothen</i> spp.). Total number of observations and percentage are shown.....	71
Table 5.1: Details of sampling frequency and devices used on the two species of penguin sampled during my study .....	81
Table 5.2: Performance metrics for a two-class support vector machine to classify swimming vs. prey encounter events in gentoo and little penguins. Metrics represent the mean and standard error following 10-fold cross validation .....	88
Table 5.3: Performance metrics for a three-class support vector machine to classify swimming as opposed to a lobster krill or juvenile fish prey encounter event, in gentoo penguins. Metrics show the mean and standard error following 10-fold cross validation using a 70:30 (train:test) ratio.....	88

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Live the dream!



And of course, the penguins!

## Chapter 1 General Introduction

### Seabird foraging in the marine environment

Seabirds typically form large colonies near regionally productive ocean areas such as coastal margins, zones of upwelling and high latitudes (Boersma & Parrish 1998, Villablanca et al. 2007). They have conservative life history traits such as high adult survival, delayed maturity, slow growth of chicks and small clutch size (Furness 1987, Schreiber & Burger 2002). During the breeding period, they are central place foragers as they must regularly return to their nests to allow incubating partners the opportunity to replenish food stores, and provision chicks once they have hatched (Daunt et al. 2002, Ropert-Coudert 2004, Lescroël & Bost 2005, Weimerskirch 2007). This tie to a central place allows for the study of numerous aspects regarding seabird biology. Furthermore, this tie to a central place also makes seabirds sensitive to local environmental perturbation, allowing behavioural and demographic parameters to be used as indicators of ecosystem health (Piatt et al. 2007b, Boersma 2008). However, this sensitivity can vary depending on the life history strategy of a species, necessitating studies which address these aspects (Furness & Camphuysen 1997, Piatt et al. 2007a, Durant et al. 2009).

One aspect impacting an individual's life history strategy involves the means through which energy is acquired. Thus, one can study the foraging ecology of a species, which involves identifying the relationships which characterise the food web an individual is part of (Stephens & Krebs 1986, Stephens et al. 2007). This knowledge leads to an understanding of a species realized niche, which is critical for the conservation and management of a species. For species with a narrow niche (specialists), adaptation to change may be limited, resulting in population declines or range shifts. However, for those capable of exploiting a broad niche (generalists), they may be more adaptable to global change (Clavel et al. 2011). Some generalist species though, may in fact consist of populations that are specialised at a local scale (Jaeger et al. 2010, Matich et al. 2011). Where the term specialisation includes the relative width of an individual's diet compared to that of the population (Bolnick et al. 2003) and the dispersal patterns of a species across its range (Ceia & Ramos 2015). Thus, it is feasible that conspecifics occupying varied foraging habitats may have different realized niche widths owing to their different ecological settings (Rosenzweig 2007, Newsome, et al. 2015, Corman et al. 2016). This makes it important to determine if a species is a specialist or, if a generalist, then whether that species consists of individuals that all utilize a diverse array of prey items (Type A) or subsets of individuals that utilize specific prey items (Type B) (Van Valen 1965, Bearhop et al. 2004).

When determining resource use by a predator, clearly one needs to consider how both predator and prey can distribute themselves in space and time. Assessing this distribution between predator and prey, however, has been particularly challenging in the “3-D” marine environment. While it is now feasible to get near real time distribution of both predator (through the use of biologging devices) and prey (through ship based acoustic surveys and autonomous underwater vehicles) (Cimino et al. 2016, Carroll et al. 2017), a review (Tremblay et al. 2009) on seabird-environment interactions recognised that:

*“obtaining real distribution maps of seabirds’ prey at appropriate spatial and temporal scales is probably the holy grail of the discipline, yet obtaining these data usually remains out of reach.”*

By example, a recent study used autonomous underwater vehicles (UAV’s) and concurrently tracked two penguin species with GPS and time-depth recorders (TDR’s). While remarkable insight was gained about predator distribution, two types of krill aggregation were detected in the water column; dense and diffuse. However, even with detailed distribution of predator and prey, it was still unclear how the prey aggregations might influence penguin behaviour (Cimino et al. 2016).

The use of animal-borne camera loggers is allowing researchers to answer questions relating to the real-time interactions of predator and prey, and their environment. Many novel insights have been gained through the use of cameras, such as: types of substrate the European shag (*Phalacrocorax aristotelis*) forages over (Watanuki et al. 2008), intra (Takahashi et al. 2004) and inter-specific foraging associations (Sakamoto et al. 2009), interactions with shipping (Grémillet et al. 2010), inferences from a device indicating prey interaction (Watanabe & Takahashi 2013), tests of optimal foraging theory (Watanabe et al. 2014), novel insights into prey distribution and capture (Kokubun et al. 2013, Handley & Pistorius 2015, Sato et al. 2015, Sutton et al. 2015, Baptiste et al. 2016) and seabird communication at sea (Thiebault et al. 2016a). Thus, it is clear that animal-borne camera loggers are revealing unprecedented insight into lives of marine predators. Their continued use will certainly unveil the many cryptic details of seabirds’ lives, once previously beyond the scope of most studies.

Stepping back prior to the use of animal-borne cameras, the original seabird studies relied merely on observations at the colony or at sea, but these early studies were able to infer horizontal and



vertical space use by seabirds (Furness 1987, Tasker & Reid 1997, Schreiber & Burger 2002). Following these observations, the next logical step was to look at the diet of seabird species, as this is readily achievable without the need to handle certain species (Duffy & Jackson 1986, Barrett et al. 2007, Karnovsky et al. 2012). While again, inference from these studies could be made about how seabirds utilized the marine environment, there was still no evidence to justify these inferences. The revolutionary step came from a study on Weddell seals (*Leptonychotes weddellii*), where for the first time the diving metrics of depth and duration could be determined (Kooyman 1966). It is hardly surprising then, that the next logical step was to follow up deploying a similar device on the heaviest seabird, the Emperor penguin (*Aptenodytes forsteri*), and also record its diving behaviour (Kooyman et al. 1971). From this point on, the question of horizontal space use by seabirds remained. Technological innovation thrived following the early development of “dive loggers” and numerous devices, which place comparatively minimal impact to seabirds, have now been developed to study horizontal space use (Tremblay et al. 2009, Wilson & Vandenabeele 2012). Indeed, the integration of multiple devices is now allowing seabird biologists to gain intimate knowledge about seabird foraging ecology. Of the seabirds, penguins are a particularly well-suited family to carry recording devices as their diving nature minimizes the associated cost of carrying a relatively heavy device. While drag does have an impact to hydrodynamics, many devices are now suitably designed to reduce this impact (Bannasch et al. 1994, Vandenabeele et al. 2015).

### **Penguins (Order: Sphenisciformes)**

Penguins are marine birds with synapomorphic traits related to their environment, which include underwater propulsion using flipper-like wings, an upright posture on land, and a unique insulating plumage (Giannini & Bertelli 2004, Triche 2007). Penguins range from the tropics to the south polar circle and fossil evidence suggests that penguins flourished 10-40 million years ago (Borboroglu & Boersma 2013). At present, however, the Sphenisciformes are considered one of the most threatened seabird families (Croxall et al. 2012), with only 5 of the 18 species listed as “Least Concern” on the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species, and the remaining being listed as “Near Threatened” (3), “Vulnerable” (5) and “Endangered” (5) (IUCN 2017). Of the 18 extant species (although this number is still debated), they are assigned to six well defined genera; *Aptenodytes*, *Eudyptes*, *Pygoscelis*, *Spheniscus*, *Megadyptes* and *Eudyptula* (Borboroglu & Boersma 2013, De Roy et al. 2013). They are highly specialised diving birds that forage in three dimensions, tracking their prey throughout

their habitat range. Forming a major component of marine ecosystems in the Southern Ocean, they constitute approximately 80%-90% of the avian biomass (Quintana & Cirelli 2000, Tanton et al. 2004). There are three species within the genus *Pygoscelis* inhabiting Antarctic and sub-Antarctic Islands in the Southern Ocean, (Borboroglu & Boersma 2013, De Roy et al. 2013), the Adélie penguin (*Pygoscelis adeliae*), chinstrap penguin (*Pygoscelis antarctica*) and gentoo penguin (*Pygoscelis papua*, Figure 1.1).

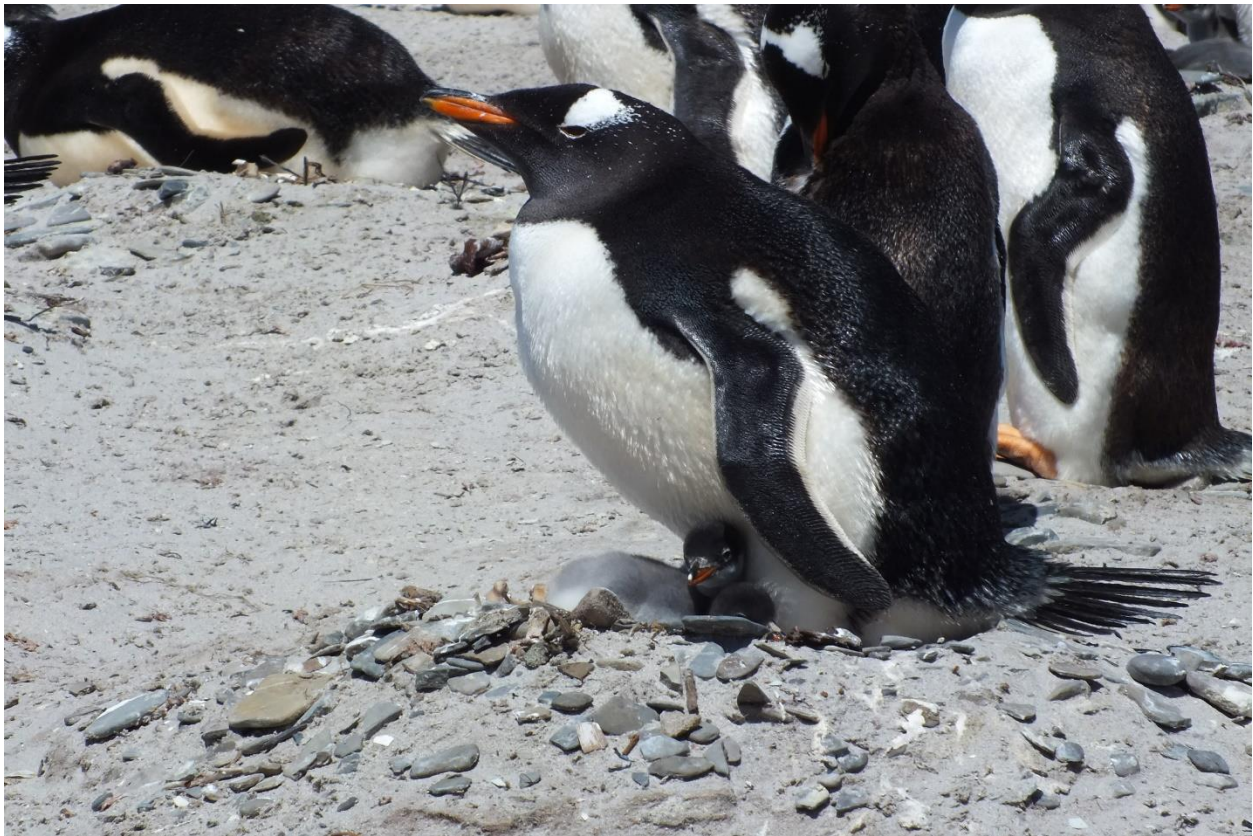


Figure 1.1: Breeding gentoo penguin at the Falkland Islands

### **Study species: The gentoo penguin**

Gentoo penguin breeding colonies are the most widely distributed among the *Pygoscelid* penguins (Figure 1.2), spanning a wide latitudinal and circumpolar distribution (Stonehouse 1970, Dinechin et al. 2012, Levy et al. 2016, Clucas et al. 2017). They extend across Antarctic and sub-Antarctic regions from 46°-65° south and in recent years their range has increased even further southwards, extending as far as Cape Tuxon on the Antarctic peninsula (65°10'S ,64°10'W)

(Lynch et al. 2008, 2012a, Humphries et al. 2017). This diversity in breeding locations is reflected in the degree of genetic diversity across the species range. While defined as a single species, recent genetic evidence via genome-wide data (Clucas et al. 2017), mitochondrial DNA (Dinechin et al. 2012, Clucas et al. 2014, Vianna et al. 2017) and microsatellites (Levy et al. 2016, Vianna et al. 2017), urges for taxonomic revision to recognise ongoing allopatric speciation (Clucas et al. 2017). Currently there are two recognised subspecies, the northern (*Pygoscelis papua papua*) and southern (*Pygoscelis papua ellsworthi*), which are divided by the 60° S latitude line. Morphological evidence shows the northern subspecies to be larger than the southern subspecies (Lynch 2013, Valenzuela-Guerra et al. 2013). However, Clucas et al. (2017) recently suggested a revision to define those birds breeding at the Kerguelen archipelago as a third subspecies, to include birds from South Georgia under the southern subspecies and urge for the characterization of birds breeding at un-sampled archipelagos via genomic data. This thesis focuses on the foraging ecology of gentoo penguins at the Falkland Islands, the northern subspecies.

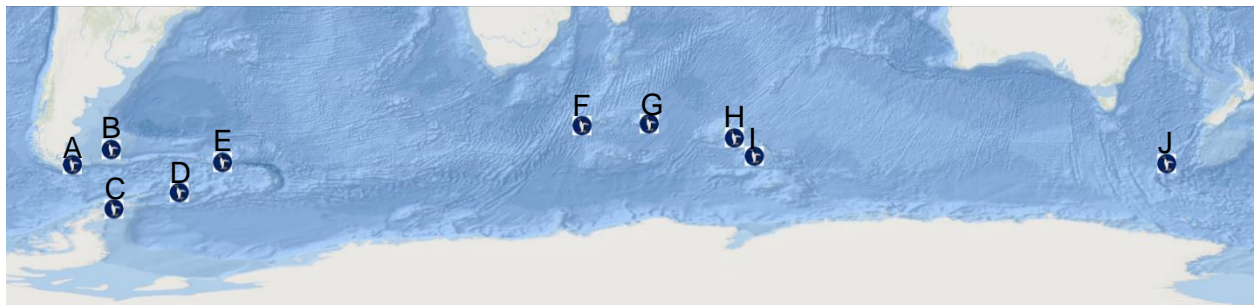


Figure 1.2: Distribution of the main sites where breeding colonies of gentoo penguins are present. A) Tierra del Fuego, B) Falkland Islands, C) Antarctic Peninsula & The South Shetland Islands, D) South Orkneys, E) South Georgia & The South Sandwich Islands, F) Prince Edward Islands, G) Crozet Islands, H) Kerguelen Islands, I) Heard & McDonald Islands, and J) Macquarie Islands

One of the key drivers thought to underpin this genetic variation in the species is their limited dispersal. Despite their wide distribution, they are assumed to be sedentary, in that they appear not to migrate large distances during the nonbreeding season. Rather, they remain confined to inshore waters visiting other colonies within the scale of their specific archipelagos (Wilson et al. 1998, Clausen & Putz 2003, Tanton et al. 2004, Hinke et al. 2017a). This dispersal pattern was also reflected in the first study to use a time-lapse camera system to monitor the attendance of multiple gentoo penguin breeding colonies during the nonbreeding period. Black et al. (2017) observed birds at breeding colonies during the nonbreeding period, but attendance varied both

spatially and temporally with distinct patterns between years and colony locations, particularly for colonies south of 60°S. Additionally, environmental and temporal factors, including sea ice extent directly offshore, photoperiod, and temperature, appeared to dictate gentoo penguin colony attendance outside the breeding season (Black et al. 2017).

Gentoo penguins are colonially breeding seabirds and exhibit a high degree of plasticity in breeding biology across their range (Black 2016). At a colony, close proximity to other individuals has recently been shown to be a key driver of nest site, rather than terrain features (McDowall & Lynch 2017). They may breed as early as two years of age and typically lay two eggs in a clutch (Otley et al. 2005, Holmes et al. 2006). Mate fidelity does appear to vary, and both high and low rates of 90% (Trivelpiece & Trivelpiece 1990) and 0% (Williams 1990) have been recorded, respectively. Typically, birds tend nests for two weeks prior to egg laying, with a three day interval between eggs (Black 2016). Colonies may exhibit inter-annual and intra-annual variation in the timing of peak laying by over a month, and two weeks, respectively (Otley et al. 2005, Juárez et al. 2013). At the Falkland Islands, first laying of eggs typically occurs at the beginning of November with chicks fledging during February (Otley et al. 2005). The gentoo penguin breeding cycle is divided into five stages: (i) Prebreeding, when adults come ashore for courtship activities and pairing; (ii) Incubation, when mates take turns to incubate the eggs; (iii) Chick guard, when mates take turns to brood and guard chicks at the nest; (iv) Crèche, when chicks are left alone and gather with other chicks in crèches and (v) Fledging, when chicks go to sea for the first time, although still being fed by their parents (Polito & Trivelpiece 2008, Lescroël et al. 2009, Black 2016). Fieldwork conducted for this thesis took place during the incubation, chick guard and crèche periods. Incubation lasts for approximately 35 days, with chicks then guarded for 25-30 days, followed by the crèche period through to fledging lasting approximately 80-100 days. There is equal sharing of chick rearing duties during the breeding cycle by parents (Williams & Rothery 1990, Otley et al. 2005, Black 2016).

Previous studies during the breeding period have suggested potential for sex related differences in gentoo penguin diet (Volkman et al. 1980, Bearhop et al. 2006, Miller et al. 2010, Pedro et al. 2015). Often, differences in diet during these studies were marginal and could not be readily accounted for. Authors did suggest that larger bill and body size in males (Valenzuela-Guerra et al. 2013) may be driving this difference. However, other studies have also found no sex related differences in diet (Masello et al. 2010, Polito et al. 2016) or diving behaviour (Croxall et al. 1988, Bost et al. 1994), and rather suggest that differing results across studies might be expected due to temporal and/or spatial variation in prey and foraging habitat availability (Polito et al. 2016).

Furthermore, in a year with anomalous environmental conditions, reduced prey availability at South Georgia was thought to influence the foraging decisions of male and female birds during the winter period. The reduced prey availability, might have been a driver of the different diets observed in this study (Xavier et al. 2017). While further work is still needed to understand potential sex related differences in diet during the nonbreeding period, prey availability seems the most likely reason for varied diet considering their highly varied diet across differing breeding colonies, even at the scale of the archipelago (Lescroël et al. 2004, Clausen et al. 2005, Miller et al. 2010, Handley et al. 2017). Currently, there is no evidence to suggest sex related differences in diet for birds from the Falkland Islands (Masello et al. 2010, 2017).

With respect to their general diet and distribution during the breeding period, gentoo penguins typically remain within inshore waters, feeding over the continental shelf (Lescroël & Bost 2005, Wilson 2010, Miller et al. 2010, Kokubun et al. 2010). Birds seldom travel further than a maximum distance of 40 km during the chick rearing period and trips rarely exceed 24hrs, with the majority of foraging occurring during the day (Croxall et al. 1988, Williams & Rothery 1990, Miller et al. 2009, Masello et al. 2010, Ratcliffe & Trathan 2011, Carpenter-Kling et al. 2017). Similar patterns have been observed at a single island at the Falkland Islands, New Island (Boersma et al. 2002, Masello et al. 2010, 2017). However, birds from this island did travel much further on average (69km) in a year with potentially lower food availability, as indicated by fisheries catch statistics (Masello et al. 2017). While real time distribution of prey (Cimino et al. 2016) would enhance this interpretation, the study does reaffirm that these birds could be particularly susceptible to changes in local prey availability (Bevan et al. 2002) as breeding success was lower in the year birds travelled farthest (Masello et al. 2017).

The breeding success of gentoo penguins was not related to prey composition at the South Shetland Islands, probably because of their ability to forage on multiple prey types (Miller et al. 2009). Studies on gentoo penguin diet across their range have indicated that they are opportunistic feeders, preying upon either benthic or pelagic species as soon as they are available in the inshore waters (Clausen et al. 2005, Ratcliffe & Trathan 2011, Cimino et al. 2016). While being opportunistic, recent evidence from stable isotope analysis does suggest some degree of specialisation within individuals (Polito et al. 2015, Herman et al. 2017). A clear trend across their range, is that birds from southern localities consume a less varied diet, largely consisting of euphausiid crustaceans (Volkman et al. 1980, Miller et al. 2009, Cimino et al. 2016, Juárez et al. 2016), whereas those in northern localities have a more diverse diet with larger components of fish and squid (Adams & Klages 1989, Robinson & Hindell 1996, Lescroël et al. 2004, Clausen et

al. 2005). Considering their restricted foraging range, diet appears to be largely influenced by available habitat within close proximity to breeding colonies (Hindell 1989, Lescroël et al. 2004, Miller et al. 2010). In these studies, benthic prey items were more typical when colonies were situated near a gently sloping, shallower sea floor, whereas pelagic feeding was more typical when surrounding waters rapidly became deep. While originally this behaviour was inferred based on life history characteristics of prey items, studies have further confirmed this through the use of time-depth recorders (Miller et al. 2009, Wilson 2010, Kokubun et al. 2010, Cimino et al. 2016, Carpenter-Kling et al. 2017).

Previously gentoo penguins were listed as “Near Threatened” on the IUCN red list, with threats identified as disturbance by humans, local pollution and potential interaction with fisheries (Birdlife International 2010). However, this status was deemed to be unjustified considering the global population increase over the last two decades (Lynch 2013). Therefore, in 2016 the species was downlisted to “Least Concern” (Birdlife International 2016). Regarding their conservation and management, those found north of the Antarctic convergence generally receive lower levels of environmental protection, compared to those southward of the convergence which fall under areas protected by the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) (Lynch 2013). At the Falkland Islands, the Falkland Islands Interim Conservation and Management Zone (FICZ), and the Falkland Islands Outer Conservation Zone (FOCZ) were established in 1987 and 1990 (Figure 1.3), respectively, as there were concerns about the impacts of overexploitation and unregulated fisheries. The regulation of fisheries and marine activities within these zones is likely to offer a degree of protection for gentoo penguins at the Falkland Islands.

The global population of gentoo penguins was an estimated 314 000 breeding pairs (Woehler 1993), but the most recent surveys show the populations is now an estimated 387 000 breeding pairs (Lynch 2013). The Falkland Islands are home to the largest population with an estimated 132 000 breeding pairs, 34% of the world’s population, following the last island wide survey in 2010 (Baylis et al. 2013). Population growth at the Falkland Islands has occurred rapidly, as the 2005 island wide census estimated the population to only be 21% of the global population (Pistorius et al. 2010). Despite this large increase over the five-year period, population numbers have varied considerably from 64 426 in 1995, increasing by 79% to 113 571 in 2000, and decreasing by 42% to 65 857 in 2005 (Pistorius et al. 2010). The recent estimate is the highest recorded number at the Falklands, even compared to the 1930’s (116 000 breeding pairs) (Bennett 1933). The relatively large year-to-year fluctuation in breeding population size at a given

site are thought to be the result of high levels of skipped breeding among mature individuals and delayed recruitment of first-time breeders (Williams 1990, Williams & Rodwell 1992).

### **Study site**

The Falkland Islands are situated in the south-west Atlantic Ocean (Figure 1.3) (between 51-53°S and 57°30'- 61°30'W), 450km north east of the southern tip of South America. The two main islands (West and East Falkland), and some 750 smaller islands, make up the Falklands archipelago; covering an area of 12,173 km<sup>2</sup> (Otley et al. 2008). The islands have a cool temperate climate dominated by westerly winds and low average annual rainfall (450-600mm/year) (FIG 2008). Their position places them at the south-eastern edge of the highly productive Patagonian Shelf, which is a major feeding area for marine top predators in the South Atlantic (Croxall & Wood 2002). Twenty-two seabird species breed at the Falklands and the surrounding shelf also provides an important nursery ground for larvae of a number of fish and squid species (Otley et al. 2008). The irregular shape and large number of islands, means the Falklands has a very long coastline in relation to its land area, providing a wide variety of coastal habitats. This, in conjunction with the high productivity, supports the reason why the Falkland Islands is home to numerous seabird species. Of the penguin species, three breed sympatrically with gentoo penguins; the king (*Aptenodytes patagonicus*), southern rockhopper (*Eudyptes chrysocome*) and Magellanic penguins (*Spheniscus magellanicus*).



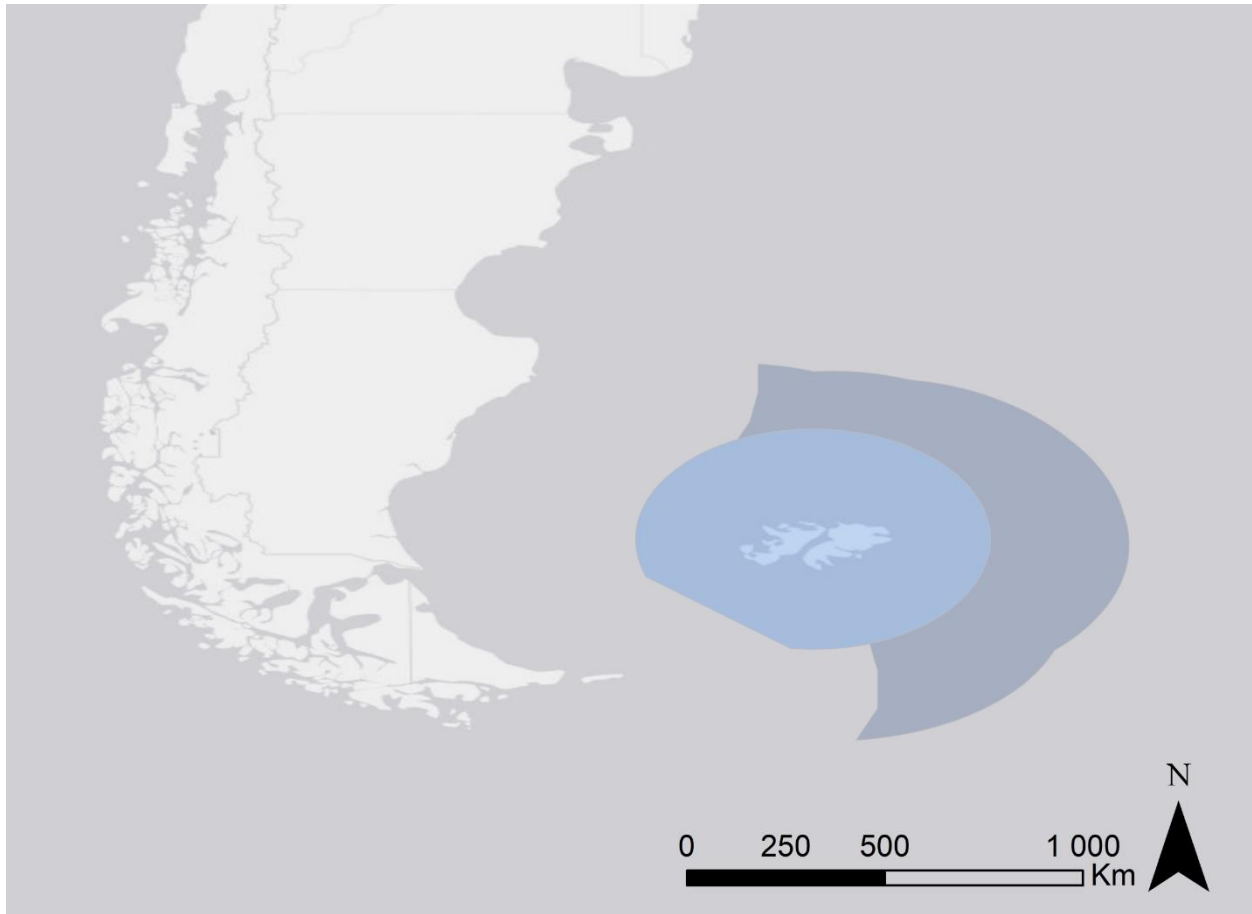


Figure 1.3: The Falkland Islands surrounded by the Falkland Islands Interim Conservation and Management Zone (FICZ, light blue), and the Falkland Islands Outer Conservation Zone (FOCZ, dark blue)

The high productivity in the region comes from the Falklands current that branches off around the southern tip of South America and is derived from the Antarctic circumpolar current. As the current moves northward around the islands, nutrient rich waters then create an area of high zooplankton productivity, which extends northward until it meets the warm Brazilian current (Agnew 2002). The Falkland current splits into two around the Falklands, forming the easterly and westerly current which then converge toward the north of the Islands (Agnew 2002). An important feature of the current promoting the high productivity is the upwelling action which occurs at the Falkland Islands shelf edges, as Antarctic surface waters move onto the shelf from relatively deep water (Agnew 2002). The upwelling causes high oxygen saturation and nutrient levels, which have led to some of the highest primary production values being recorded for the South West Atlantic (Sánchez & Ciechomski 1995).



In my study, I investigated the foraging ecology of gentoo penguins from four of the 75 breeding colonies (Baylis et al. 2013) across the Falkland Islands: Steeple Jason Island, Cow Bay, Bull Roads and Bull Point (Figure 1.4). The colonies were chosen owing to their broad geographic coverage and contrasting environmental conditions, which included varied surrounding bathymetry.

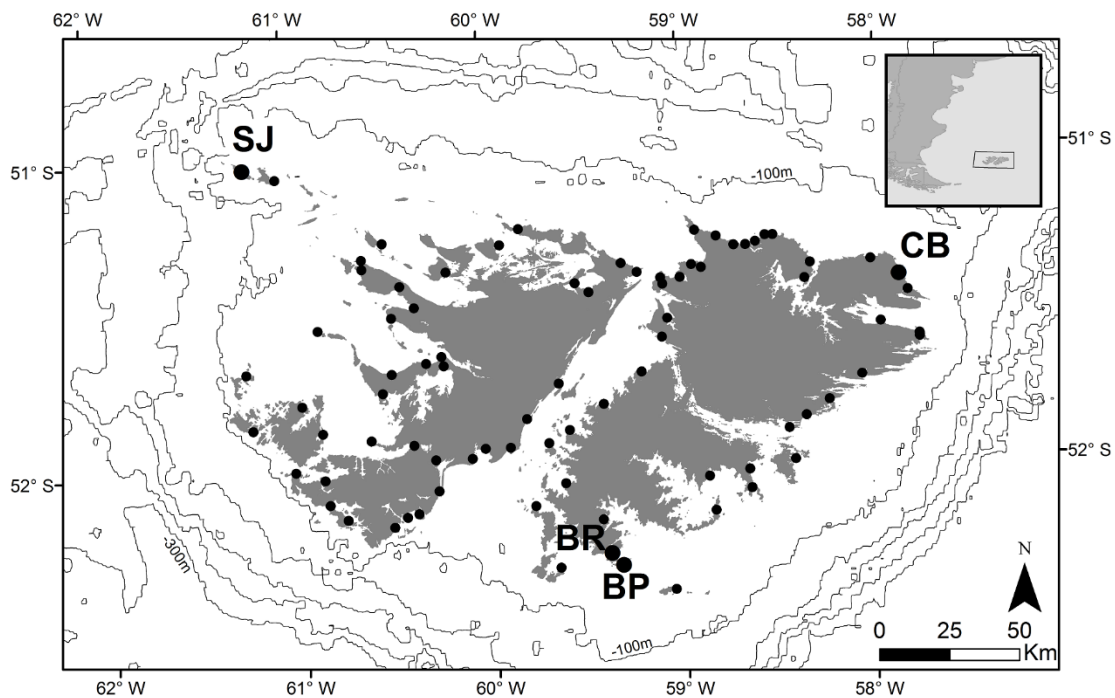


Figure 1.4: Gentoo penguin colonies of the Falkland Islands (small dots) and the four study colonies: Steeple Jason (SJ), Cow Bay (CB), Bull Roads (BR) and Bull Point (BP). Isobaths (faint lines) are shown at 50m intervals from 100m to 300m depth

**Steeple Jason Island (51.0375° S, 61.2097° W, Figure 1.5).** Steeple Jason is an isolated island in the North West of the archipelago that forms the end of the greater chain known as the Jason islands. It is roughly 8km long and 1km wide and supports not only gentoo penguins but the world's largest population of black browed albatross (*Thalassarche melanophris*) as well as rockhopper and Magellanic penguins and other small populations of breeding bird species (Falklands Conservation 2006). There are over 12 000 breeding pairs of gentoo penguins on the island separated into four main rookeries. These rookeries are clearly divisible by large tracts of tussock grass. Within and among rookeries there are multiple entrance/exit points to the sea used by the penguins. My study focused on the largest rookery situated on the middle of the island,

Steeple Jason Neck, which has approximately 3710 breeding pairs (Stanworth 2013). Only those penguins using the most common entrance/exit point were sampled. Steeple Jason Island is surrounded by rapidly deepening waters.

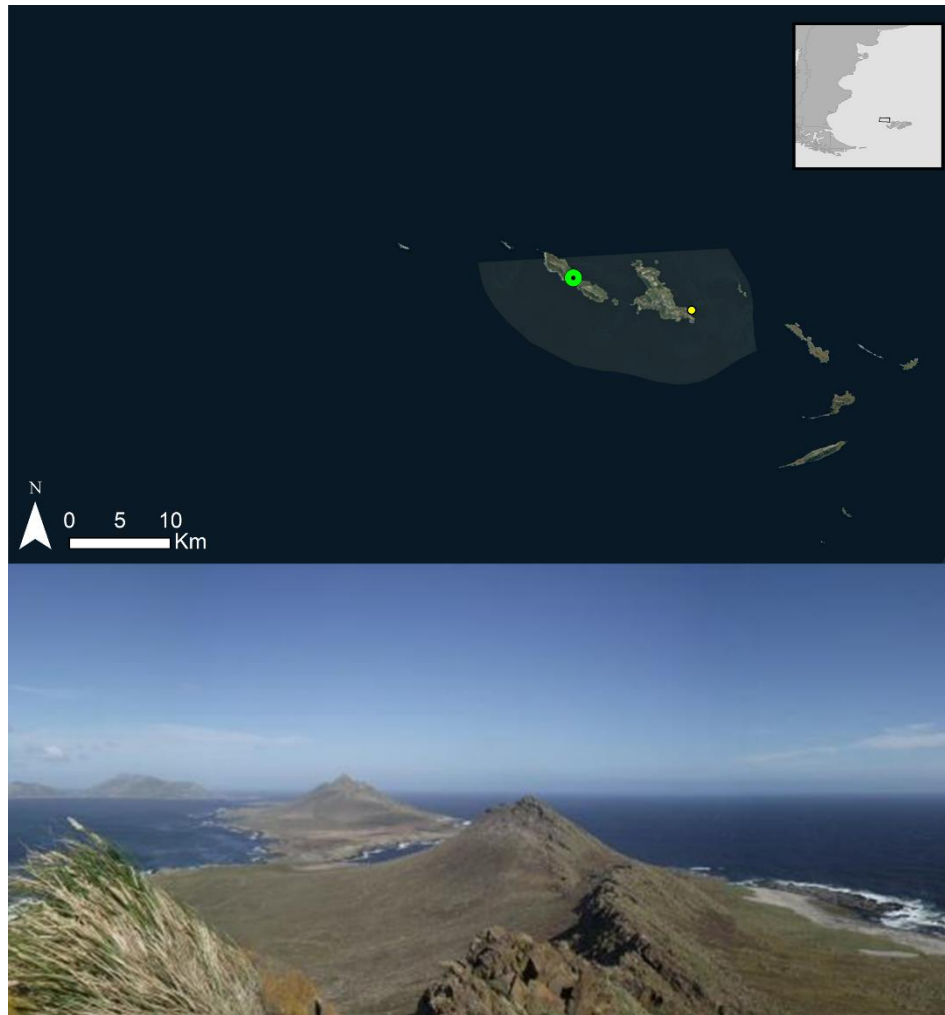


Figure 1.5: Steeple Jason Island at the Falkland Islands. Green and yellow circles indicate study and adjacent colonies, respectively

**Cow Bay ( $51.4288^{\circ}$  S,  $57.8703^{\circ}$ , Figure 1.6).** Cow Bay is a north-easterly facing site that lies at the north east of the archipelago. There are approximately 1821 pairs of gentoo penguins breeding here (Stanworth 2013). The site lies along a lowland peninsula, characterised by low cliffs, sandy and boulder beaches with extensive offshore kelp beds. Magellanic penguins also have burrows along this stretch of coastline and there are other gentoo penguin colonies nearby

(Falklands Conservation 2006). It is also approximately 100km away from areas with intensive oil exploration. The colony is situated about 800m from shoreline with penguins using the west corner of the beach as a single entrance/exit. The surrounding bathymetry comprises of a gently sloping bed, and the colony faces the open ocean.

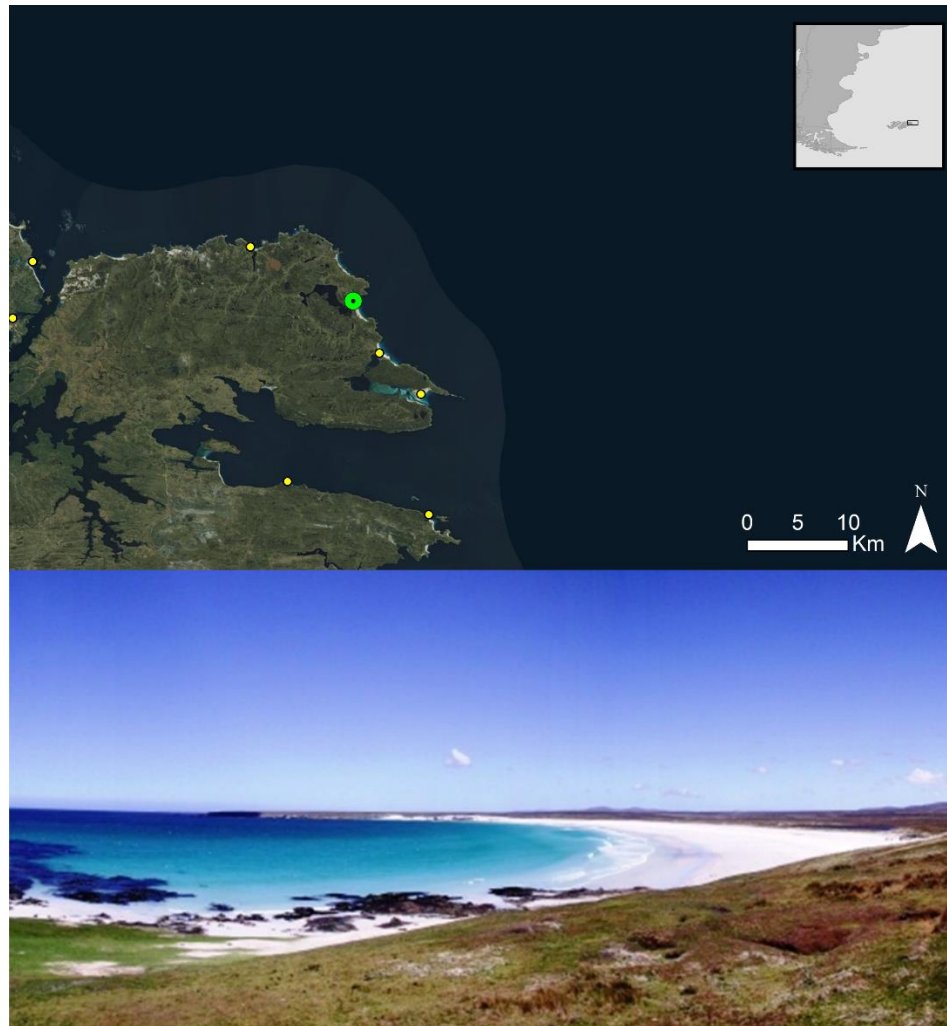


Figure 1.6: Cow Bay at the Falkland Islands. Green and yellow circles indicate study and adjacent colonies, respectively

**Bull Roads ( $52.3096^{\circ}$  S,  $59.3896^{\circ}$  W) and Bull Point ( $52.3478^{\circ}$  S,  $59.3287^{\circ}$  W) (Figure 1.7).** These sites are situated at the southernmost tip of East Falklands and are home to approximately 3400 and 1236 breeding pairs, respectively (Stanworth 2013). The area is low lying with a variety of rocky and sandy beaches. Extensive low-lying dunes cover most of the southern point

(Falklands Conservation, 2006). At Bull Point, birds nest at multiple closely spaced rookeries. While birds do use a variety of entrance/exit points to the sea, there is one primary one which was where birds from my study were sampled. The smaller Bull Roads colony is also roughly 800m from the shoreline and birds use a single entrance/exit point. While both colonies are surrounded by a gently sloping seabed, Bull Point birds tend to head out toward the open ocean, whereas the colony at Bull Roads is situated within a sheltered bay.



Figure 1.7: Bull Roads and Bull Point at the Falkland Islands. Green and yellow circles indicate study and adjacent colonies, respectively

### **Rationale and motivation for my study:**

There are currently key research priorities for seabirds which have global relevance (Lewison et al. 2012, Croxall et al. 2012), and are summarized as follows:

1. Which monitoring methods will best reflect changes in seabird well-being?
2. What drives population dynamics?
3. What drives at-sea spatial ecology?
4. How do seabirds tie into the trophic dynamics of marine food webs?
5. How will seabirds respond to anthropogenic induced change?
6. What degree of gene flow is there between populations?

To an extent, I cover aspects relating to all these questions in this thesis, bar that of gene flow between populations. Principally, the focus of this thesis is to determine a species foraging ecology, and so questions three to five are primarily addressed.

Specific to the context of my study; during the 1980s and early 1990s, populations of gentoo, southern rockhopper and Magellanic penguins declined sharply at the Falkland Islands (Bingham 2002). A lack of comparative data made it impossible to determine whether such declines were associated to natural or anthropogenic factors. To address these issues the Falkland Islands Seabird Monitoring Program (FISMP) was established in the 1980's (Bingham 2002, Pistorius et al. 2010). More recently, the Falkland Islands Biodiversity Strategy was developed (FIG 2008). By 2018, this strategy looks to conserve and enhance the natural diversity, ecological processes and heritage of the Falkland Islands, while maintaining sustainable economic development. As part of this program, the gentoo penguin is identified as requiring a basic action plan for species management.

At present, gentoo penguin populations appear to be on the increase at the Falkland Islands (Stanworth 2013). However, a recent diet study at one colony found that one of their principal prey items was rock cod (*Patagonotothen spp.*) fish, which is now the primary commercial fish caught in Falklands waters (Handley et al. 2016). Considering there has been over exploitation of a commercial species, southern blue whiting (*Micromesistius australis*), in the past (Laptikhovsky et al. 2013), it is not unrealistic to consider a similar future scenario - although I do acknowledge the considerable increase in effort to manage fisheries in Falkland's waters in recent years. While diet of these birds was studied in the past at the Falkland's (Thompson 1994, Clausen & Putz 2002, 2003, Clausen et al. 2005), there is a timely need to revise this knowledge. This will assist in the ability to understand and monitor potential environmental change as decreasing populations

of gentoo penguins at the Kerguelen archipelago (Lescroël & Bost 2006) and Prince Edward Islands (Crawford et al. 2014), are believed to be occurring due to potential competition with fisheries and a change in local food availability because of altered benthic production, respectively. Revising this knowledge, especially across multiple breeding colonies concurrently, will enable me to determine whether rock cod is a key contemporary diet component across the islands. Furthermore, there is limited knowledge of gentoo diet during the pre-molt period, with only a single location, New Island, investigated so far through stable isotope analysis (Weiss et al. 2009, Masello et al. 2010, 2017). Combining dietary and stable isotope data from multiple colonies will provide insight not only into the diet beyond the breeding period, but also help assess if there is a degree of specialisation occurring across colonies.

Knowledge of gentoo distribution during the breeding period is also lacking at the Falkland Islands. While the population at New Island has been well studied (Boersma et al. 2002, Masello et al. 2010, 2017), and a limited number of birds have been tracked during the winter (Clausen & Putz 2003), whether inter-colony variation in horizontal (via GPS) and vertical (via TDR) space use exists is largely unknown.

Across the Spheniscids, there is still much to be learned about fine scale prey interactions. This is now becoming feasible with animal-borne camera loggers. While the first such camera was deployed on an Emperor penguin (*Aptenodytes forsteri*) bound to a man-made ice hole nearly two decades ago (Ponganis et al. 2000), it is only through recent miniaturization that such technology can now feasibly be deployed on even the smallest wild penguin species (Sutton et al. 2015). For gentoo penguins, only still image cameras have been deployed on birds in Antarctica (Takahashi et al. 2008), which gave some of the first insights into krill feeding behaviour. Therefore, there is virtually no knowledge about how gentoo penguins might interact with prey on a fine scale.

Seabirds typically feed in patchy environments (Furness 1987, Schreiber & Burger 2002). Yet, fully elucidating where these patches occur and how a seabird reacts to prey patches is still a growing body of research. Cameras are clearly beginning to reveal insights into fine scale prey interactions, but they have a limited battery life compared to an entire foraging trip and analyses of video footage is a time consuming process with only limited options for automation, which has only been achieved for turtles (Okuyama et al. 2015). While methods for identifying prey encounters by penguins have been developed (Hanuise et al. 2010, Watanabe & Takahashi 2013, Carroll et al. 2014), many of the methods involve complex deployment procedures and are often case specific. Therefore, there is an urgent need to develop a simplified approach for recognizing

prey encounters, which can be easily applied to all species. Thus, while this thesis focuses primarily on the foraging ecology of gentoo penguins, I extend the scope of my study to also investigate prey encounters for little penguins (*Eudyptula minor*).

Little penguins have a constricted range during the breeding period and relatively short trips compared to other species that are deep diving and/or have wider foraging ranges (Borboroglu & Boersma 2013). Similarly to gentoo penguins, they are considered generalist predators and their diet can vary considerably across colonies and between seasons (Cullen et al. 1992, Shaw 2009). In the context of my study, little penguins in south-east Australia, typically feed on small mid-water shoaling fish (e.g. Clupeiformes) (Sutton et al. 2015). In light of their short foraging trips and varied diet, this also makes them a well-suited study species for examining feeding behaviours, as recording a large sample size and broad repertoire of behaviours through animal-borne camera loggers, with limited recording capacity, is more likely.

### **Thesis aims and structure**

The study of marine top predators is a fascinating and challenging discipline to be a part of. While our terrestrial counterparts have often only had to worry about how close they might get to a study species to observe it, marine top predator researchers have had to find ingenious ways of studying these predators to answer the many questions about their biology. Often, this has come in the form of novel hardware; some more ‘home grown’ than others. More recently, with the continued proliferation of computing power there has been a surge in the development of statistical approaches. These improvements have vastly increased our ability to answer some of the fundamental questions of a species biology: what, where, why and how. What resources does a species require? Where might that species be acquiring those resources? Why, and how are those resources acquired? Determining the what and where, has been within our reach for some time now. Albeit, still not for all marine top predators. Determining the why and how part, however, has only more recently come to fruition for a growing number of species.

The key aim of this thesis, is to uncover novel aspects about the foraging ecology of gentoo penguins (*Pygoscelis papua*) at the Falkland Islands. Each core chapter (2-5) is written with intent for publication. Therefore, core chapters are introduced by a publication reference which either indicates where a version of the chapter has been published or is intended to be published. The core chapters are preceded by a chapter specific abstract and key words, and some degree of repetition does occur across chapters. For the first time, I investigate what resources (chapter 2) and where these resources (chapter 3) are consumed by these birds at numerous breeding colonies. Furthermore, I am the first to uncover intricate details about the why and how, of

resource acquirement by these birds (chapter 4). This latter part I achieved by custom making animal-borne camera loggers and developing a novel methodology. Following the newly developed understanding of these species, and with a pressing need to identify prey encounters by marine predators through minimally invasive approaches, I refine a method for identifying prey encounter events by penguins (chapter 5). More specifically, each chapter covers the following content:

Chapter 2 reveals the contemporary diet of gentoo penguins at multiple colonies across the Falkland Islands by using stomach content analysis as an indicator of diet during the breeding period, and stable isotope analysis to determine diet and potential distribution during the pre-molt period. Combining information from both dietary sources I am the first to investigate the degree of diet specialisation occurring across colonies at the Falkland Islands.

Chapter 3 investigates the horizontal and vertical space use by gentoo penguins through GPS and TDR's. I investigate whether inter-colony differences occur. A prime goal of discovering species distributions is for marine spatial planning. In this regard, I am the first to develop habitat distribution models for gentoo penguins using a machine learning approach. For the first time for gentoo penguins, I collected distribution data from multiple colonies during the same phase of breeding, over multiple years. I am the first to test whether habitat distribution models for this species can be transferred in space and time.

Chapter 4 looks at fine scale interactions between gentoo penguins and their prey by using custom made animal-borne camera loggers. I developed a freeware approach, readily applicable to any species equipped with an animal-borne camera logger and that feeds on pelagic prey. Using this approach, I reveal for the first time in a marine central place forager, how multiple prey behaviours can influence capture success. This particularly novel finding means that prey behaviour can significantly influence trophic coupling in marine systems and should be accounted for in studies using marine top predators as samplers of mid to lower trophic level species.

Chapter 5 shows how one can identify prey encounter events when penguins are foraging at sea. Using animal-borne camera loggers on gentoo penguins and little penguins, I classify behaviours where the movement characteristics have been recorded by accelerometers. I then develop a method, which uses a supervised machine learning approach, to distinguish prey encounter events from swimming based on characteristics of accelerometer data. With this algorithm, one will be able to identify prey encounter events from accelerometer signals beyond the recording



duration of a camera. Furthermore, it will ultimately remove the need for cameras in future deployments, saving both time and valuable research funds.

Chapter 6 concludes the thesis. I discuss my study of gentoo penguin foraging ecology, and what my findings mean for the conservation and management of this species at the Falkland Islands. I address the knowledge gaps for gentoo penguins, and make general recommendations toward future studies focusing on marine top predator foraging ecology.

## Chapter 2 Jack of all prey, master of some: Influence of habitat on the feeding ecology of a diving marine predator

**Handley JM**, Connan M, Baylis AMM, Brickle P, Pistorius P (2017) Jack of all prey, master of some: Influence of habitat on the feeding ecology of a diving marine predator. Marine Biology. doi: 10.1007/s00227-017-3113-1

### Abstract

Marine species occupy broad geographical ranges that encompass varied habitats. Accordingly, resource availability is likely to differ across a species range and, in-turn, this may influence the degree of dietary specialisation. Gentoo penguins *Pygoscelis papua* are generalist predators occupying a range of habitats with a large breeding range extending from Antarctica to temperate environments. Using the most extensive stomach content data set on gentoo penguins I investigated their feeding ecology at the Falkland Islands (52° S, 59.5° W), the world's largest population. Sampling occurred in consecutive breeding seasons (2011-2013), across multiple foraging habitats utilizing stomach content data and carbon and nitrogen stable isotope values of feathers. The first species specific description of diet at this scale for the Falklands revealed six key prey items for the birds: rock cod (*Patagonotothen* spp.), lobster krill (*Munida* spp.), Falkland herring (*Sprattus fuegensis*), Patagonian squid (*Doryteuthis gahi*), juvenile fish (likely all nototheniids), and southern blue whiting (*Micromesistius australis*). Niche width, relating to both stomach content and stable isotope data related to the surrounding bathymetry. Birds from colonies close to gently sloping, shallow waters, fed primarily on benthic prey and had larger niche widths. The opposite was observed at a colony surrounded by steeply sloping, deeper waters. Therefore, gentoo penguins at the population level at the Falklands are indeed generalists, however, at individual colonies some specialisation occurred to take advantage of locally available prey, resulting in these birds being classified as Type B generalists. Hence, future studies must account for this intra-colony variation when assessing for factors such as inter-specific competition or overlap with anthropogenic activities.

**Key words:** Spheniscidae, dietary niche, isotopic niche, isotopic diversity, multivariate analyses

### Introduction

Conspecifics occupying varied foraging habitats may have different dietary niche widths owing to their different ecological settings (Rosenzweig 2007, Newsome, et al. 2015, Corman et al.

2016). Therefore, species that are considered to be generalists may in fact consist of populations that are specialised at a local scale (Jaeger et al. 2010, Matich et al. 2011). Here, the term specialisation designates the relative width of an individual's diet compared to that of the population (Bolnick et al. 2003). This makes knowledge of whether a generalist species consists of individuals that all utilize a diverse array of prey items (Type A) or subsets of individuals that utilize specific prey items (Type B) essential to acquire, so as to understand and predict the capacity of populations to adapt to global and environmental changes (Van Valen 1965, Bearhop et al. 2004). Ultimately, differences may occur due to complex interactions between predator and prey which can arise from environmental heterogeneity (Bolnick et al. 2003). For seabirds in particular, only 40 species (11.7% of the total extant species) have exhibited some type of individual specialisation in foraging and/or feeding strategies, but this proportion likely reflects existing studies (Ceia & Ramos 2015).

To gain insight toward the dietary niche width of an organism one can utilize a combination of direct and indirect methods. Using a combination has added value as it allows insight into dietary specialisation over varying temporal scales (Ceia et al. 2012, Thomson et al. 2012). Specifically, the direct method of stomach content analysis, enables identification of prey items to species level and one can determine the mass and size of prey items consumed (Jobling & Breiby 1986; Granadeiro & Silva 2000; Barrett et al. 2007). However, stomach sampling represents a snap shot of ingested prey items (the most recent meal), is invasive and logistically challenging for sustained sampling over extended time periods (Duffy & Jackson 1986, Karnovsky et al. 2012). Accordingly, one can also utilize an indirect method, stable isotope analysis, to investigate carbon and nitrogen isotopic values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ). These values indicate the isotopic niche of a consumer, which can be used to infer its foraging area and trophic position in a given geographic area, respectively (Hobson et al. 1994, Cherel & Hobson 2007, Jaeger et al. 2010). For birds, these values are often measured in feathers as storage and collection is simplified compared to the more intensive requirements for blood sampling (Inger & Bearhop 2008, Bond & Jones 2009). Additionally, feathers are metabolically inert and therefore reflect the trophic ecology of individual birds at the time of deposition (Mizutani et al. 1990, Cherel et al. 2000, Polito et al. 2011a).

The gentoo penguin, *Pygoscelis papua*, is often considered a generalist and opportunist marine predator, with diet being varied and reflecting local prey availability (Clausen et al. 2005). During the breeding season adults seldom travel further than 30 km and typically remain within the confines of the continental shelf (Trivelpiece et al. 1986, Wilson et al. 1998, Miller et al. 2009). However, in rare instances have been recorded to travel as far as 46km (Lescroël & Bost 2005). Hence, gentoo penguin diet is influenced by available habitat within close proximity to breeding colonies (Hindell 1989, Lescroël et al. 2004, Miller et al. 2010). In

these studies, benthic prey items were typically associated with a gently sloping, shallower sea floor in the vicinity of the colony, whereas pelagic feeding was more typical in deep surrounding waters.

The Falkland Islands present a unique opportunity for multi-colony dietary investigation across a wide range of habitat features. This archipelago now hosts the largest population of gentoo penguins with 34% of the global population,  $\approx 132,000$  breeding pairs (Baylis et al. 2013, Lynch 2013). Therefore, understanding factors influencing the foraging ecology of this population is of significance in managing and understanding the species as whole. Dietary studies at the Falkland Islands are currently limited to a description of stomach content analysis at the level of broad taxonomic composition (Pütz et al. 2001, Clausen & Pütz 2002), or more detailed studies relating to a single year (Clausen et al. 2005) or colony (Handley et al. 2016). A detailed, spatially extensive, dietary study of the gentoo penguin at the Falkland Islands is therefore timely. It will also facilitate our understanding of conservation needs for these birds, in light of current and proposed anthropogenic activities for the Islands (Augé et al. 2015).

Here, I use the most extensive dataset that integrates stomach content analysis (detailed dietary analysis during the breeding period), complemented with feathers' stable isotopes, a proxy for foraging distribution and trophic interactions relating to the adult pre-moult diet of gentoo penguins. I selected colonies where the surrounding habitat was either shallow with a gently sloping seabed or deep with a steeply sloping seabed in order to determine how these habitats might influence diet. Specifically, the aims of my study were to (1) give detailed description of dietary items at a large spatial scale across the Falkland Islands, (2) assess temporal (between breeding stages) and spatial (across colonies, controlling for breeding stage) variation in the diet during the breeding period and (3) compare dietary and isotopic measures of gentoo penguin trophic niche width and specialisation in the context of different habitats. Through understanding each of these facets I address the degree of gentoo penguin dietary specialisation at the Falkland Islands.

## **Methods**

### **Study sites**

Fieldwork occurred at the Falkland Islands during the austral summers of 2011/12, 2012/13 and 2013/14 hereafter referred to as 2011, 2012, 2013 respectively. Birds were sampled from four of the 75 breeding colonies: Steeple Jason Island ( $51.0375^{\circ}$  S,  $61.2097^{\circ}$  W), Cow Bay ( $51.4288^{\circ}$  S,  $57.8703^{\circ}$  W) Bull Roads ( $52.3096^{\circ}$  S,  $59.3896^{\circ}$  W) and Bull Point ( $52.3478^{\circ}$  S,  $59.3287^{\circ}$  W) (Figure 2.1), each with approximately 3710, 1821, 1236, 3400 breeding pairs, respectively (Stanworth 2013).

Each of these colonies is surrounded by a unique bathymetry and exposure to the ocean, particularly at Steeple Jason Island. The island lies between a steeply sloping seabed that rapidly drops down to 100m whereas the Cow Bay and Bull Point colonies follow on to gently sloping seabeds facing the open ocean, while the Bull Roads colony is in a sheltered, shallow bay.

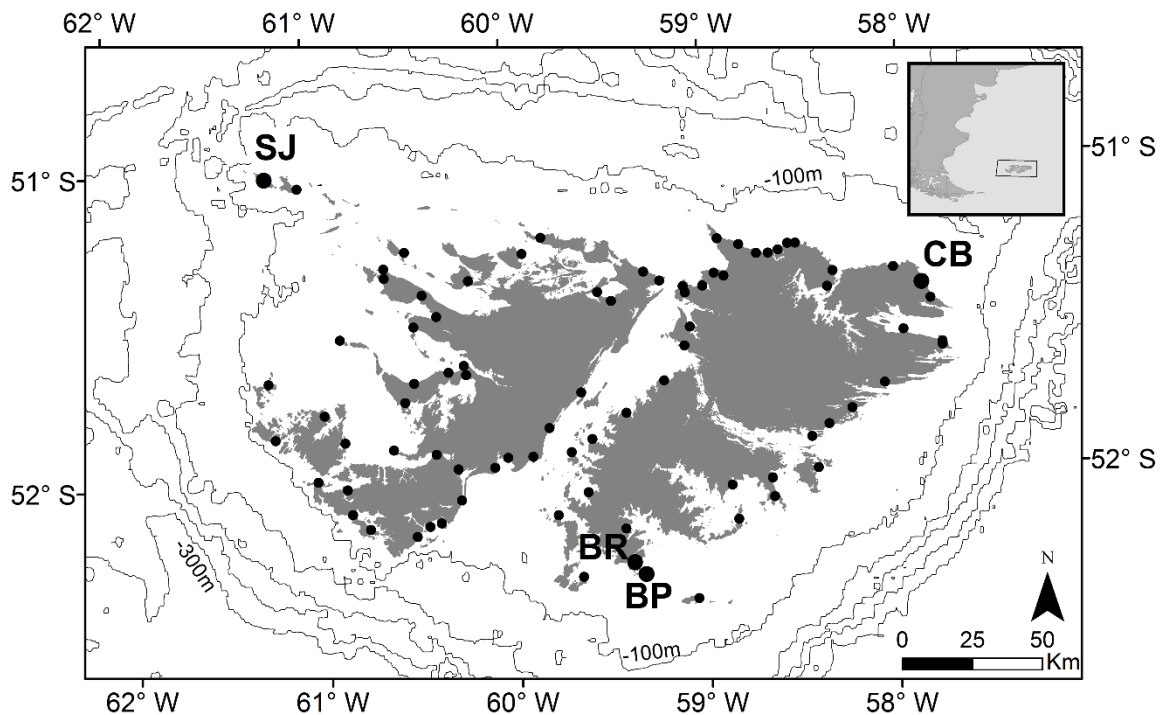


Figure 2.1: Gentoo penguin colonies of the Falkland Islands (small dots) and the four study colonies: Steeple Jason (SJ), Cow Bay (CB), Bull Roads (BR) and Bull Point (BP). Isobaths (faint lines) are shown at 50m intervals from 100m to 300m depth

### Sample collection

Stomach contents were collected from breeding adults during the incubation (I), guard (G) and crèche (C) stages. These occur during early November, late November/early December and January, respectively. Sampling effort varied spatiotemporally owing to logistical constraints. The most samples were collected during the guard period of 2011 from three colonies. Then, in the crèche period of 2012, I was able to collect samples from all four colonies. Ultimately, between 8 and 31 birds were sampled per colony in a given period and year (Table 2.1). Where, a single sampling period refers to all birds sampled from a specific site in a given breeding stage and season.

Table 2.1: Stomach samples collected from gentoo penguins breeding at the Falkland Islands. Sampling occurred at four colonies: Steeple Jason (SJ), Cow Bay (CB), Bull Point (BP) and Bull Roads (BR)

Breeding Stage	Incubation				Guard				Crèche			
Colony	SJ	CB	BP	BR	SJ	CB	BP	BR	SJ	CB	BP	BR
Season												
2011	16				24	30	31			10	8	
2012	11					10	10	10	10	11	10	10
2013						19		17				

Methods associated with collection and sorting of stomach contents are detailed in Handley et al. (2015). Briefly, stomach lavage followed Wilson (1984) and three white breast feathers were also plucked from each bird for subsequent stable isotope analysis. As gentoo penguins molt synchronously at the Falkland Islands, the isotopic values of these feathers would be derived from dietary items consumed during the pre-moult diet period, which occurs towards the end of February. A random sub-sample of birds had feathers chosen for final processing, and in some instances, I also bolstered sample size by using feathers plucked from birds involved in other ongoing studies. I adopted this pragmatic approach to achieve roughly equal sample sizes of 20 birds per sampling period.

### Laboratory analyses

I gathered sagittal otoliths, cephalopod beaks, crustacean carapaces, or other hard part remains and identified these to the lowest possible taxonomic level by comparing them with reference collections maintained by the Falkland Islands Fisheries Department or published reference material (Clarke 1986, Xavier & Cherel 2009). Length and reconstituted mass of samples were calculated from non-eroded hard part remains (Van Heezik & Seddon 1989, Clausen et al. 2005) based on morphometric equations for each species following reference material or from regression equations developed during my study (Appendix: Table A2.1). Wet mass was used in cases where whole prey could be identified, but no reference equation existed or could be developed (Clausen & Pütz 2003).

Regarding stable isotope analysis, two feathers from each bird were cleaned of contaminants and homogenized, in order to obtain an average value, following Connan et al. (2015). A sub sample of homogenized feather material weighing approximately 0.5 mg was analyzed for carbon and nitrogen stable isotope ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) via combustion in a Flash 2000 organic elemental analyzer with the gases passed to a Delta V Plus isotope ratio mass spectrometer (IRMS) via a Conflo IV gas control unit (Thermo Scientific, Bremen, Germany). All samples were processed at the Stable Light Isotope Unit at the University of Cape Town,

South Africa. Results are presented in  $\delta$  notation in per mil units (‰), based on the following equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \cdot 1000$$

Where X is  $^{13}\text{C}$  or  $^{15}\text{N}$  and R is the corresponding ratio  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ . The  $R_{standard}$  values were based on the Vienna PeeDee Belemnite (VPBD) for  $\delta^{13}\text{C}$  and atmospheric nitrogen for  $\delta^{15}\text{N}$ . Replicate measurements of internal laboratory standards (Merck gel:  $\delta^{13}\text{C} = -20.1\text{‰}$ ,  $\delta^{15}\text{N} = +7.5\text{‰}$ ; seal bone  $\delta^{13}\text{C} = -12.0\text{‰}$ ,  $\delta^{15}\text{N} = +15.8\text{‰}$ ; valine  $\delta^{13}\text{C} = -26.8\text{‰}$ ,  $\delta^{15}\text{N} = +12.1\text{‰}$ ) indicated measurement errors  $<0.2\text{‰}$  and  $<0.1\text{‰}$  for stable-carbon and nitrogen isotope measurements, respectively.

### Data analysis and statistics

Data analyses were performed using R version 3.2.1 (R Core 2015). Univariate normality and homoscedasticity were tested for via the Shapiro-Wilks and Bartlett's test respectively. Multivariate analogues used were the multivariate Shapiro-Wilks test (package: mvnrmtest, function: m.shapirotest) and the multivariate Levene's test (package: Vegan, function: betadisper). In the case of linear or generalized linear models, model validation was performed via assessment for normal distribution of residuals, equality of variance and that no excessively influential observations were present (Zuur et al. 2009). Means with standard deviations are presented, and significance was assumed at  $p < 0.05$  unless otherwise stated.

For stomach content data, I identified important prey items using the percentage index of relative importance (%IRI) as this facilitates comparison across sampling periods (Pinkas et al. 1971, Cortes 1997, Huin 2005). The IRI is an integrative metric that accounts for percentage mass, numerical abundance and frequency of occurrence. Analyses could then be conducted using the most important prey species (those with %IRI  $> 1$ ). As the IRI relies on the summed information of each sampling period, yielding no variation in the results, percentage mass (%M) was chosen to compare prey items at the level of the sampling unit (each penguin), as this favours samples with varying prey size (Duffy & Jackson 1986, Ratcliffe & Trathan 2011). Sample size sufficiency was assessed through prey species accumulation curves and the Chao estimator (Chao 1987).

Comparisons were made between breeding stages for each colony in each season, then across different colonies while accounting for breeding stage and season. Differences in species composition were visually assessed with ordination via nonmetric multidimensional

scaling (nMDS) (package: Vegan, function: metaMDS with autotransform = "F") using the %M data based on the major prey items across all sampling periods. Statistical differences were determined via the ADONIS test (package: Vegan, function: adonis with distance = "bray").

Two dietary niche metrics were calculated for each sampling period (package: RInSp) (Zaccarelli et al. 2013). Firstly, the trophic niche width (TNW) was quantified using the Shannon-Weaver diversity index, following Roughgarden (1979). A value of 0 is scored when the entire population consumes a single prey category, increasing with both the number of prey species consumed and the evenness with which they are used. Secondly, diet variation among individuals was determined via the degree of individual diet specialisation ( $V$ ), where a value of '0' indicates that individuals use the same resources in the same proportions, and '1' where individuals all rely on entirely different resources. The relationship between TNW and  $V$  was then assessed using a linear model.

Generalized linear models (GLMs) were used to compare  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values across sampling periods (family = Gaussian, link = identity), followed by the Tukey post-hoc test for pairwise comparisons (package: multcomp, function: glht). Prior to calculating measures regarding the isotopic niche space utilized by the penguins, data were scaled between 0 and 1 according to Cucherousset and Vill  ger (2015). This facilitates the spatial comparison when basal resources may differ and weights each isotope equally. The core isotopic niches across different sampling periods were investigated through the Stable Isotope Bayesian Ellipse package in R (SIBER) (Jackson et al. 2011). Differences in core niche width and overlap were explored by using the standard ellipse areas corrected for small sample size ( $n < 30$ ), SEAc, which represents about 40% of the data. The Bayesian estimate of the standard ellipse area ( $\text{SEA}_B$ ) was used to compare niche widths between groups in a probabilistic manner based on the size of simulated ellipse areas and their estimated posterior distributions (iterations = 10,000). Furthermore 95, 75 and 50% credibility intervals were assessed via density plots. The degree of overlap in these intervals is indicative of the degree of similarity in isotopic niche width between groups.

The methods outlined in Jackson et al. (2011) were developed to facilitate comparison between groups, particularly when there was varying sample size (e.g: Connan et al. 2014, Kiszka et al. 2015, Polito et al. 2015). More recently, Cucherousset and Vill  ger (2015) proposed using complementary methods, which, include comparing the convex hull area, the entire space occupied by organisms in isotopic space (isotopic richness, IRic), something advised against by Jackson et al. (2011). However, Cucherousset and Vill  ger (2015) introduced a bootstrapping approach to account for the varying sample size. They recognised the importance of investigating differences in convex hull area as this fully integrates the



importance of organisms located at the edges of the isotopic niche. Therefore, the complementary metrics, isotopic richness, isotopic similarity (ISim) and isotopic nestedness (INes) were calculated. The bootstrapping approach was utilized when varying sample size was present (iterations = 4000). To account for the distribution of organisms within the isotopic niche space, isotopic divergence (IDiv), isotopic dispersion (IDis), isotopic evenness (IEve) and isotopic uniqueness (IUni) were also calculated. These metrics are briefly outlined below in table 2.2, and were all calculated for scaled data.

Table 2.2: Detail of metrics used to describe the area of the convex hull (IRic), degree of similarity between two groups (ISim, INes) and the within group distribution of organisms (IDiv, IDis, IEve and IUni), in isotopic niche space, as outlined in Cucherousset and Vill  ger (2015)

Metric	Code	Unit [range]	Description	Interpretation
Isotopic Richness	<i>IRic</i>	‰ <sup>2</sup> [0: + ∞]	The convex hull area filled by all organisms	Larger values indicate a large isotopic niche area filled by the organisms.
Isotopic Similarity	<i>ISim</i>	Unitless [0; 1]	Ratio between the volume shared and the volume of the union of the two convex hulls	0 indicates no overlap. 1 indicates complete overlap.
Isotopic Nestedness	<i>INes</i>	Unitless [0; 1]	Ratio between the volume shared and volume of the smallest convex hull	0 indicates no overlap. 1 indicates the smaller hull fits entirely in the larger.
Isotopic Divergence	<i>IDiv</i>	Unitless [0; 1]	Describes the distribution of organisms within isotopic space	0 indicates most organisms are clustered towards centre of gravity of isotopic space. 1 indicates all organisms are towards border of the isotopic space.
Isotopic Dispersion	<i>IDis</i>	Unitless [0; 1]	Describes the weighed-mean distance to the centre of gravity of all points	0 indicates that all organisms have the same stable isotope values. 1 indicates most organisms lie far from the centre of gravity of isotopic values.
Isotopic Evenness	<i>IEve</i>	Unitless [0; 1]	Describes the regularity in the distribution of organisms within isotopic space	0 indicates high degree of clustering with a few organisms far from this cluster. 1 indicates organisms evenly distributed across isotopic space.
Isotopic Uniqueness	<i>IUni</i>	Unitless [0; 1]	Describes the inverse of the average closeness of organisms in isotopic space	0 indicates each organism has at least one organism with the same position in the stable isotope space. 1 indicates most organisms are different from one another.

### Inferring diet: Stable isotope mixing model

To quantitatively assess the contribution of different prey sources towards gentoo penguin diet, I used a SIAR Bayesian stable isotope mixing model, SIAR (Parnell et al. 2010). A species and tissue specific discrimination factor of  $1.3 \pm 0.5\text{‰}$  for  $\delta^{13}\text{C}$  and  $3.5 \pm 0.4\text{‰}$  for  $\delta^{15}\text{N}$  were used (Polito, et al. 2011). Prey samples were dried and ground to a fine powder before lipid removal using cyclohexane (Chouvelon et al. 2011). Any prey item which still had a bulk C:N ratio > 3.5 was subjected to  $\delta^{13}\text{C}$  correction as outlined in Post et al. (2007). I used 17 prey

items (Appendix: Table A2.2) kindly sourced through research cruises undertaken by the Falkland Islands Fisheries Department, and reduced the number of sources to three (Phillips et al. 2005). I assessed the validity of the model using a Monte Carlo simulation approach (1500 iterations) to test the goodness-of-fit of the data to the model using simulated mixing polygons (Smith et al. 2013).

## Results

### Stomach content analysis

A total of 13197 individual prey items were identified over three seasons across the four study colonies. This included 8669 crustaceans, 4650 fish, 587 cephalopods and 11 other items from 237 penguins, comprising a total of 37 prey items (Appendix: Table A2.3). A total of 19 of the 37 prey items were identified to species level and six of these contributed >1% IRI across all sampling periods combined (Table 2.3). The sizes of prey items are presented in, Appendix: Table A2.4. For each individual sampling period, prey species accumulation curves plateaued and there was zero deviation about the Chao estimator, as expected once a species is found in more than two individuals (Appendix: Figure A2.1).

Table 2.3: Main prey species identified from stomach content analysis of gentoo penguins at the Falkland Islands as indicated by having the percentage index of relative importance (%IRI) >1. Typical habitat of prey items was determined from various sources. NA: Data or source not available

Scientific Name	Common Name	Code	% IRI	Habitat	Source
<b>Cephalopod</b>					
<i>Doryteuthis gahi</i>	Patagonian squid	LOL	9.87	Benthic	Arkhipkin et al. (2013)
<b>Crustacean</b>					
<i>Munida</i> spp.	Lobster krill	MUN	25.48	Benthic	Tapella & Lovrich (2006)
<b>Fish</b>					
<i>Patagonotothen</i> spp.	Rock cod	PATA	46.55	Benthic	Brickle (2006)
<i>Sprattus fuegensis</i>	Falkland herring	SAR	11.44	Pelagic	Zenteno et al. (2015)
Fish (juvenile)	Juvenile fish	JF	2.66	NA	NA
<i>Micromesistius australis</i>	Southern blue whiting	BLU	1.02	Pelagic	Brickle et al. (2009)
<b>Others</b>			2.98		

### Intra-annual variation in diet during the breeding period

During different stages of the 2011 and 2012 breeding seasons, significant differences in diet were evident in one of three, and three of four comparisons, respectively (Table 2.4, Figure A2.2 (A-G)). In 2011, this difference was between the incubation and guard stage at Steeple Jason when birds consumed mainly Falkland herring (*Sprattus fuegensis*) compared to rock

cod (*Patagonotothen* spp.) (Figure A2.2 (A)). At the other two colonies during the 2011 breeding season birds consumed equally large proportions of rock cod then Patagonian squid (*Doryteuthis gahi*), or rock cod then lobster krill (*Munida* spp.) at Cow Bay (Figure A2.2 (B)) and Bull Point (Figure A2.2 (C)), respectively.

In 2012 significant differences occurred for all comparisons between the guard and crèche stages at Cow Bay, Bull Point and Bull Roads. At Steeple Jason birds fed equally on large proportions of Falkland herring during the incubation and crèche stages (Figure A2.2 (D)). Differences were largely due to different proportions of rock cod vs. Falkland herring, rock cod and Patagonian squid vs. lobster krill and juvenile fish, and, rock cod and Patagonian squid vs. lobster krill being consumed at Cow Bay (Figure A2.2 (E)), Bull Point (Figure A2.2 (F)) and Bull Roads (Figure A2.2 (G)), respectively.

### **Variation in diet across colonies**

In four of five inter-colony comparisons, significant differences in diet were observed (Table 2.4, Figure A2.3 (A-E)). These occurred during all three years in the guard stages and in one of the two crèche stages investigated. Bull Point birds consumed significantly more lobster krill compared to rock cod dominating at Cow Bay and Steeple Jason during the guard stage of 2011 (Figure A2.3 (A)). During the 2011 crèche stage no differences in diet were evident with birds consuming similar proportions of rock cod then Patagonian squid (Figure A2.3 (B)). During the guard stage of 2012, birds at Cow Bay consumed significantly more rock cod than at Bull Point and Bull Roads where birds consumed a greater proportion of Patagonian squid then lobster Krill (Figure A2.3 (C)). Similarly, the large proportion of lobster krill consumed at Bull Point and Bull Roads during the crèche stage of 2012 led to these colonies having similar diet, whereas, birds at Steeple Jason and Cow Bay consumed significantly more Falkland herring which drove the observed difference in diet across colonies for this sampling period (Figure A2.3 (D)). In the final guard stage sampled, 2013, an influx of southern blue whiting (*Micromesistius australis*) in the diet of birds at Cow Bay drove a significant difference in diet compared to Bull Roads birds where nearly all prey consumed consisted of lobster krill (Figure A2.3 (E)).

Table 2.4: Results of ADONIS tests for comparison of major prey items between different stages of the breeding period (incubation (I), guard (G) and crèche (C)) and across colonies for gentoo penguins at the Falkland Islands. Samples were analysed for three seasons, 2011, 2012 and 2013 from four different colonies: Bull Point (BP), Bull Roads (BR), Cow Bay (CB) and Steeple Jason (SJ). Associated nMDS ordination and stacked bar plots can be found in the appendix figures A2.2: A-G, A2.3: A-E

Season	Colony(ies)	Breeding stage(s)	F. model	R <sup>2</sup>	p value	Fig.
<i>Between breeding periods</i>						
2011	SJ	I vs. G	$F_{(1,38)} = 59.90$	0.61	<b>0.001</b>	A2.2 (A)
	CB	G vs. C	$F_{(1,38)} = 2.00$	0.05	0.092	A2.2 (B)
	BP	G vs. C	$F_{(1,37)} = 1.69$	0.04	0.185	A2.2 (C)
2012	SJ	I vs. C	$F_{(1,19)} = 0.35$	0.02	0.856	A2.2 (D)
	CB	G vs. C	$F_{(1,19)} = 11.55$	0.38	<b>0.001</b>	A2.2 (E)
	BP	G vs. C	$F_{(1,18)} = 3.87$	0.18	<b>0.026</b>	A2.2 (F)
	BR	G vs. C	$F_{(1,18)} = 5.24$	0.23	<b>0.012</b>	A2.2 (G)
<i>Across colonies</i>						
2011	SJ, CB, BP	G	$F_{(2,82)} = 10.45$	0.2	<b>0.001</b>	A2.3 (A)
	CB, BP	C	$F_{(1,16)} = 2.06$	0.11	0.114	A2.3 (B)
2012	CB, BP, BR	G	$F_{(2,27)} = 3.35$	0.2	<b>0.018</b>	A2.3 (C)
	SJ, CB, BP, BR	C	$F_{(3,37)} = 8.68$	0.41	<b>0.001</b>	A2.3 (D)
2013	CB, BR	G	$F_{(1,34)} = 28.88$	0.46	<b>0.001</b>	A2.3 (E)

### Dietary niche metrics

Trophic niche widths were typically lower for birds at Steeple Jason (0.40-0.95) compared to other colonies (1.07-1.51) for all sampling periods except the guard stage of 2012 and 2013 at Cow Bay and Bull Roads, when TNW's were 0.87 and 0.36, respectively. Birds at Steeple Jason also typically demonstrated lower levels in the degree of diet specialisation, V, for all periods bar the aforementioned (Appendix: Table A2.5). In all sampling periods, except the crèche stage of Cow Bay in 2012, the degree of diet specialisation tended more towards zero showing that individuals tended to use the same resources in the same proportions. Within this generalist pattern, there was a significant and strong, positive relationship ( $F_{1,14} = 60.46$ ,  $R^2 = 0.81$ ,  $p < 0.001$ ) between V and TNW (Figure 2.2). This indicated that when a large variety of resources were consumed in a given sampling period across all birds so too did each individual bird consume a larger variety of resources.

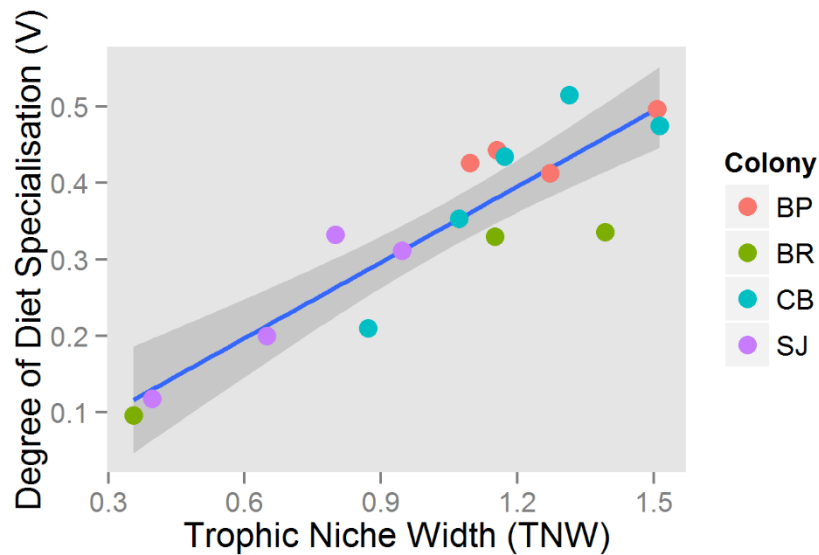


Figure 2.2: Linear model indicating relationship between degree of diet specialisation (V) and trophic niche width (TNW) for gentoo penguins sampled from four colonies Bull Point (BP), Bull Roads (BR), Cow Bay (CB) and Steeple Jason (SJ) over three breeding seasons at the Falkland Islands. Solid line represents the best fit from linear model with shaded area depicting the 95% confidence bands. Individual data points for the linear model come from sampling season, site and breeding stage specific sampling periods

In contrast, the degree of diet specialisation across colonies compared to that within a colony increased after accounting for prey items consumed across the same temporal scale (e.g. all colonies during the guard stage of 2011) (Table 2.5). This reinforces the difference in diet observed across colonies and the increase was particularly large for the crèche and guard stages of 2012 and 2013 when there were influxes of the pelagic prey items in the diet, Falkland herring and southern blue whiting, respectively.

Table 2.5: Degree of individual diet specialisation (V) for breeding gentoo penguins at the Falkland Islands, determined against only the prey items consumed within a single sampling period and against all prey items consumed across the same season (2011-2013) and breeding stage (guard (G) and crèche (C)). Prey items within each sampling period were identified from the %IRI. See appendix table A2.3 for prey abbreviations. Note, only those prey with %IRI > 1 were used for the analysis, however, the top three prey items for each period are shown for detail

Sample Period		V		Prey		
Season/Stage	Colony	Within	Across	Primary	Secondary	Tertiary
2011 G	SJ	0.31	0.41	PATA	MUN	SAR
	CB	0.35	0.42	PATA	LOL	TG
	BP	0.43	0.49	MUN	PATA	LOL
2011 C	CB	0.44	0.49	PATA	LOL	GON
	BP	0.50	0.51	MUN	PATA	JF
2012 G	CB	0.21	0.34	PATA	LOL	JC
	BP	0.44	0.44	PATA	MUN	LOL
	BR	0.33	0.36	PATA	LOL	MUN
2012 C	SJ	0.33	0.66	SAR	LOL	GON
	CB	0.52	0.62	SAR	PATA	LOL
	BP	0.41	0.61	JF	MUN	PATA
	BR	0.34	0.49	MUN	PATA	JF
2013 G	CB	0.48	0.56	BLU	MUN	LOL
	BR	0.10	0.40	MUN	LOL	PATA

### Inter-colony comparison: stable isotope analysis

In 2011, significant differences were present among colonies for both  $\delta^{13}\text{C}$  ( $F_{2,59} = 13.39$ ,  $p < 0.001$ ) and  $\delta^{15}\text{N}$  ( $F_{2,59} = 26.35$ ,  $p < 0.001$ ) (Table 2.6). Post-hoc testing showed only Steeple Jason had significantly lower values compared to either Cow Bay or Bull Point for  $\delta^{13}\text{C}$ . For  $\delta^{15}\text{N}$ , there were significant differences for all pairwise comparisons with the lowest values recorded at Cow Bay followed by Bull Point, then Steeple Jason. These results were illustrated when comparing SEAc, where, Steeple Jason had no overlap with either colony and the SEAc for Cow Bay only encompassed 30% of the larger SEAc for Bull Point (Figure 2.3). Regarding ISim and INes, Steeple Jason was clearly separated in isotopic niche space (ISim/INes = 0/0: SJ vs. CB; = 0.02/0.11: SJ vs. BP), while, Cow Bay was more similar to Bull Roads (ISim/INes = 0.41/0.92: CB vs. BP). The size of the SEA, compared between sites using SEAB, was significantly larger for Bull Point, then Cow Bay and Steeple Jason (probability < 0.01). Similarly, IRic at Bull Point was twice as large compared to Cow Bay and over five times larger than Steeple Jason (Table 2.6).

In 2012, significant differences were also present among colonies for both  $\delta^{13}\text{C}$  ( $F_{3,82} = 100.40$ ,  $p < 0.001$ ) and  $\delta^{15}\text{N}$  ( $F_{3,82} = 15.85$ ,  $p < 0.001$ ; Table 2.6). As in 2011, penguins at Steeple Jason also had significantly lower  $\delta^{13}\text{C}$  values in 2012 compared to all colonies. Unlike 2011,

only Bull Point and Bull Roads had similar  $\delta^{13}\text{C}$  values which were both higher than Cow Bay. Regarding  $\delta^{15}\text{N}$ , Steeple Jason had significantly higher values than all other colonies, with similar values recorded between Cow Bay and Bull Point and the lowest, but similar values recorded between Bull Point and Bull Roads. In 2012, Steeple Jason had zero overlap with any colonies for both SEAc and ISim (Figure 2.3). There was, however, 23% overlap with Cow Bay and the larger SEAc of Bull Point, which overlapped with Bull Roads by 58%. There was no overlap in SEAc between Cow Bay and Bull Roads. Isotopic similarity was strongest between Bull Point and Bull Roads (ISim/INes = 0.49/0.74), then Cow Bay and Bull Point (ISim/INes = 0.25/0.43), and then Cow Bay and Bull Roads (ISim/INes = 0.12/0.24). The size of the SEA<sub>B</sub> was most similar between Bull Point, Bull Roads and Cow Bay (all probabilities > 0.4) and least similar for all pairwise comparisons with Steeple Jason (all probabilities = 0.1) (Figure 2.3). A result further reflected by IRic for Steeple Jason being approximately half the value of all other colonies in 2012 (Table 2.6).

In contrast, the final sampling season, 2013, showed significant differences for  $\delta^{13}\text{C}$  ( $F_{2,57} = 100.40$ ,  $p < 0.001$ ) but no significant differences for  $\delta^{15}\text{N}$  ( $F_{2,57} = 2.62$ ,  $p = 0.080$ ) among colonies (Table 2.6). Significance in  $\delta^{13}\text{C}$  was strong between Cow Bay and Bull Point ( $p < 0.001$ ) or Bull Roads ( $p < 0.001$ ), however, was marginal between Bull Point and Bull Roads ( $p = 0.04$ ). This is illustrated (Figure 2.3) by zero overlap in SEAc for Cow Bay with either colony, and a 16% overlap of the smaller Bull Roads SEAc within that of Bull Point. Cow Bay also had lower overlap in total isotopic niche area compared to Bull Point (ISim/INes = 0.10/0.28) then Bull Roads (ISim/INes = 0.07/0.18), which, had greater overlap between them due to Bull Roads being largely encompassed by Bull Point (ISim/INes = 0.24/0.85). The size of the SEA<sub>B</sub> (Figure 2.3) was similar between Bull Point and Cow Bay (probability = 0.13), however both of these colonies had significantly larger ellipses than Bull Roads (probability < 0.01) (Figure 2.3). This was also reflected by Bull Roads having isotopic richness nearly half of Cow Bay and over a third of Bull Point (Table 2.6).

Table 2.6: Feather carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope values of adult gentoo penguins at the Falkland Islands collected during the breeding seasons of the 2011, 2012 and 2013 austral summers. Collections occurred at Bull Point (BP), Bull Roads (BR), Cow Bay (CB) and Steeple Jason (SJ). Isotopic niche indices include: standard ellipse area corrected for small sample size ( $\text{SEA}_\text{C}$ ), the Bayesian estimate of the standard ellipse area with lower and upper bounds of 95% credible intervals ( $\text{SEA}_\text{B}$ , Jackson et al. 2011) and, isotopic richness (IRic, Cucherousset and Villéger 2015), the area of the convex hull. A, B, indicate periods where samples were non-significantly different. \* indicates average calculated value after bootstrapping to account for varying sample size

Year	Colony	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\text{SEA}_\text{C}$ (‰ <sup>2</sup> )	$\text{SEA}_\text{B}$ (‰ <sup>2</sup> )	IRic (‰ <sup>2</sup> )
2011	BP	20	$-15.2 \pm 0.5^{\text{A}}$	$15.7 \pm 0.7$	0.15	0.14 (0.09/0.22)	0.43
	CB	22	$-15.3 \pm 0.3^{\text{A}}$	$15.1 \pm 0.6$	0.07	0.06 (0.04/0.10)	0.20*
	SJ	20	$-15.7 \pm 0.2$	$16.4 \pm 0.3$	0.03	0.03 (0.02/0.04)	0.08
2012	BP	19	$-14.3 \pm 0.3^{\text{A}}$	$15.6 \pm 0.4^{\text{A, B}}$	0.07	0.07 (0.04/0.10)	0.21
	BR	20	$-14.1 \pm 0.4^{\text{A}}$	$15.5 \pm 0.3^{\text{A}}$	0.07	0.06 (0.04/0.10)	0.17*
	CB	28	$-14.7 \pm 0.3$	$15.8 \pm 0.4^{\text{B}}$	0.07	0.07 (0.04/0.09)	0.19*
	SJ	19	$-15.7 \pm 0.2$	$16.3 \pm 0.5$	0.05	0.04 (0.02/0.07)	0.11
2013	BP	20	$-14.4 \pm 0.3$	$15.0 \pm 0.7^{\text{A}}$	0.11	0.09 (0.06/0.20)	0.34
	BR	20	$-14.2 \pm 0.3$	$15.4 \pm 0.3^{\text{A}}$	0.03	0.03 (0.02/0.05)	0.10
	CB	20	$-15.1 \pm 0.4$	$15.3 \pm 0.4^{\text{A}}$	0.07	0.07 (0.05/0.11)	0.16



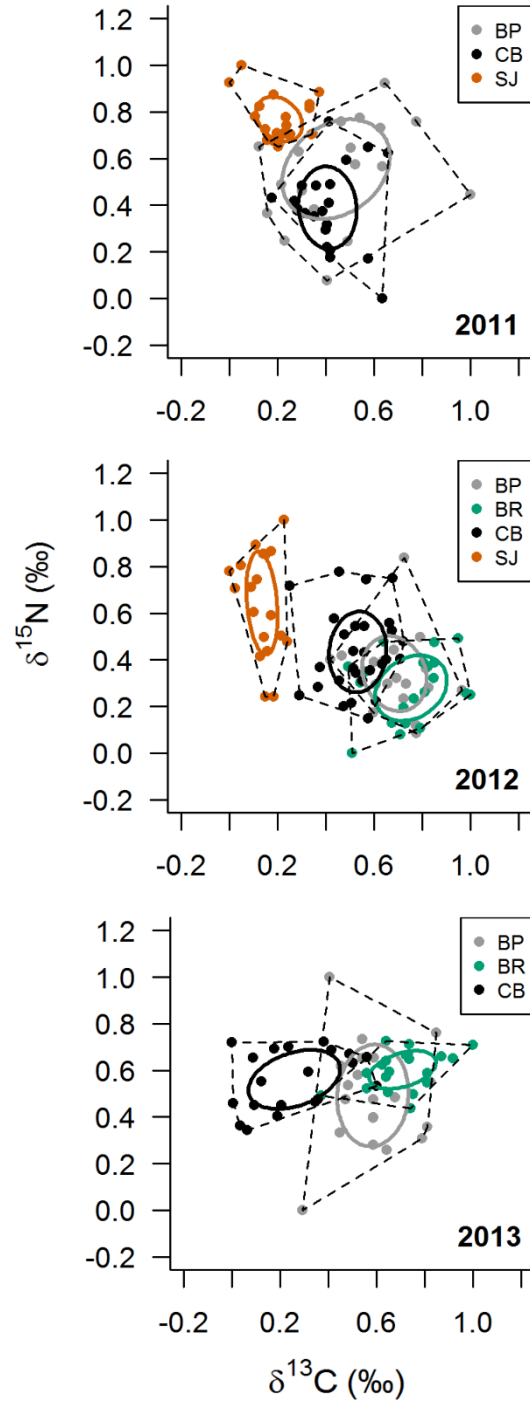


Figure 2.3: Feather stable isotope values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , centered and rescaled data) for adult gentoo penguins breeding at four colonies: Bull Point (BP), Bull Roads (BR), Cow Bay (CB) and Steeple Jason (SJ) at the Falkland Islands. Feathers were collected from breeding adult birds during concurrent stomach sampling in the austral summer breeding season: 2011, 2012 and 2013. Total (dashed lines, IRic) and core isotopic niche area adjusted for sample size (solid lines, SEAc) are shown

### Inter-colony comparison: Isotopic diversity metrics

In all years IDiv approximated 1 (Table 2.7) indicating that groups were further apart and hence different in isotopic space confirming the lack of overlap for SEAc or the convex hull. Similarly, as IDis also typically tended towards 1 this supported the IDiv results and indicates that across groups there were different isotopic values. Typically, the range of resources used each year across all colonies was higher than for the range of resources used at a specific colony as indicated by IEve tending towards 1. Notably though, were the typically lower (although all tending towards 1) values of IDiv, IDis and IEve in 2012 which were supported by having the lowest IUni value. This indicates that groups were more similar, which was driven by the similarity amongst sites in niche space overlap, except for Steeple Jason in 2012 (Figure 2.3).

### Intra-colony comparison: Isotopic diversity metrics

Within each colony the typical pattern across all years showed IDis tending towards 0 indicating that individuals within these groups have similar isotopic values (Table 2.7). This was supported by the IUni values tending towards 0, showing that most of the weight belonged to organisms that are isotopically similar. The typically high IEve values indicate broad resource use over the entire range of the resources within isotopic niche space. The only exception is at Cow Bay in 2013 where IDis tended more towards 1, indicating that individuals within this group had different isotopic values which can also be seen by a lack of individuals within the core isotopic niche area for that year (Figure 2.3).

Table 2.7: Inter and intra-colony isotopic diversity metrics (Cucherousset & Villéger 2015): Isotopic divergence (IDiv), dispersion (IDis), evenness (IEve) and uniqueness (IUni) determined from feathers of breeding adult gentoo penguins at the Falkland Islands. Samples collected over three years from four different colonies: Bull Point (BP), Bull Roads (BR), Cow Bay (CB) and Steeple Jason (SJ)

Year	----- Inter-colony -----				----- BP -----				----- BR -----				----- CB -----				----- SJ -----			
	IDiv	IDis	IEve	IUni	IDiv	IDis	IEve	IUni	IDiv	IDis	IEve	IUni	IDiv	IDis	IEve	IUni	IDiv	IDis	IEve	IUni
2011	0.79	0.71	0.57	0.6	0.76	0.48	0.82	0.32					0.73	0.39	0.71	0.35	0.76	0.42	0.69	0.45
2012	0.63	0.51	0.59	0.47	0.67	0.34	0.76	0.23	0.76	0.49	0.73	0.3	0.72	0.46	0.8	0.3	0.71	0.5	0.76	0.33
2013	0.96	0.94	0.96	0.95	0.71	0.38	0.71	0.28	0.7	0.38	0.76	0.27	0.75	0.61	0.8	0.49				

### Inferring diet: Stable isotope mixing model

Assessing the validity of the model using the approach outline by Smith et al. (2013), and discussed in methods above, indicated that consumers fell well beyond the required mixing space suitable towards the use of a potential stable isotope mixing model (Figure 2.4). Therefore, such a model was not pursued.

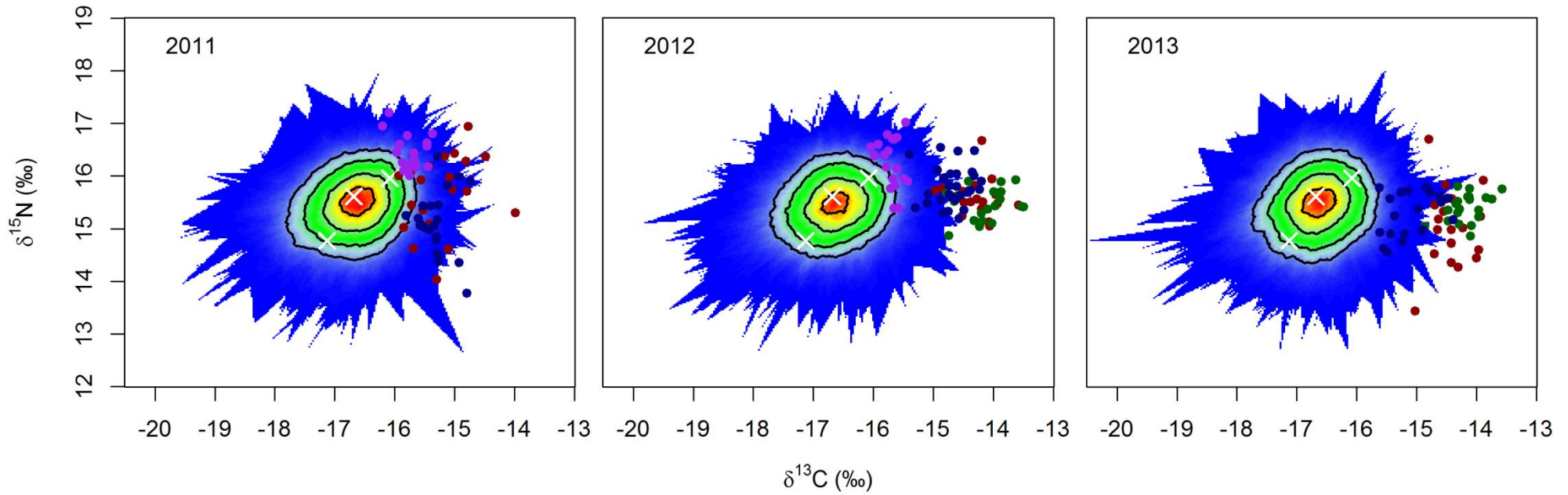


Figure 2.4: Simulated mixing region for the isotopic mixing model attempted towards the use of diet inference for gentoo penguins at the Falkland Islands. Isotopic signatures of the consumers, individual gentoo penguins, were determined from white adult breast feathers collected in the 2011, 2012 and 2013 breeding periods and are represented by solid circles. Sampling occurred at four colonies; Bull Point (dark red), Bull Roads (dark green), Cow Bay (dark blue) and Steeple Jason (purple). Average source values are represented by white crosses. Probability contours are displayed in black with the outermost contour indicating the 95% mixing region. Samples outside this 95% mixing region are considered inadequate, indicating that an alternative model is needed to explain the diet of the consumer

## Discussion

My study is the first detailed multi-year study on gentoo penguin diet at the Falkland Islands. Through a combination of stomach sampling and stable isotope analysis, I found that gentoo penguin diet differed between select breeding colonies around the Islands. These results point toward the important role of available habitat within close proximity to gentoo penguin breeding colonies and the influence of habitat on prey diversity and consequently gentoo penguin diet.

In summary, six main prey items were of major significance across all sampling periods. These were, in order of importance, rock cod fish, lobster krill, Falkland herring, Patagonian squid, juvenile fish and southern blue whiting. Between different stages within a breeding period, significant difference occurred four out of seven times and when accounting for these different breeding stages, across colony difference in diet occurred four out of five times. Birds from the Steeple Jason colony generally had the narrowest trophic niche width and degree of diet specialisation. When looking at all sampling periods, results from the linear model indicate that when gentoo penguins feed on a broader array of prey items so too does each individual bird consume a larger variety of prey items. The differences observed in diet were also reflected in the across colony degree of diet specialisation when birds always had higher values than when looking at the within colony component. This was particularly so when birds consumed pelagic prey at some colonies. Clear differences in isotopic values were observed across the colonies with Steeple Jason birds always having the lowest  $\delta^{13}\text{C}$  and highest  $\delta^{15}\text{N}$  values. These differences were also reflected in the isotopic niche space, where, similarly to TNW, birds from Steeple Jason almost always occupied the smallest, separated niche space, for both  $\text{SEA}_\text{B}$  and  $\text{IRic}$ . The smallest occupied isotopic niche space recorded was for birds from Bull Roads in 2013 when birds from the Steeple Jason colony were unable to be sampled.

## Temporal and spatial diet variation

Prey switching may be necessitated by differing demands for energy requirements during the breeding season (Williams & Rothery 1990, Le corre et al. 2003, Quillfeldt et al. 2011). This is particularly relevant when considering the significant differences in diet that I observed between the guard and crèche stages of the 2012 breeding season. As chicks got older, diet changed from rock cod to either; Falkland herring, a combination of juvenile fish and lobster krill, or lobster krill at Cow Bay, Bull Point and Bull Roads respectively. Of these prey items, Ciancio et al. (2007) showed that rock cod had the lowest energy content by wet mass ( $4,798 \text{ j.g}^{-1}$ ) compared to Falkland herring ( $7,148 \text{ j.g}^{-1}$ ) and lobster krill ( $11,008 \text{ j.g}^{-1}$ , although their measure was for dry mass). Hence, the calorific values of prey are consistent with the hypothesis that gentoo penguins

might change diet to meet increased energetic demands of growing chicks, as has been suggested for other penguins (e.g. Jansen et al. 2002, Browne et al. 2011). Notably, when higher energy content prey items are consumed there is often an associated increase in reproductive success, higher fledgling mass and higher growth increments not only for penguins (van Heezik 1990) but also for flying species such as black-legged kittiwakes *Rissa tridactyla* and tufted puffins *Fratercula cirrhata* (Romano et al. 2006).

However, without simultaneous at-sea surveys of prey availability I cannot distinguish whether the prey switching behaviour I report is a result of prey availability, or prey preference. More typically, prey availability, rather than prey preference, is believed to be the driving force behind gentoo penguin diet switching. This is because annual variation in the diet of gentoo penguins (Volkman et al. 1980, Adams & Klages 1989, Coria et al. 2000, Libertelli et al. 2004), and at different sites within an archipelago (Lescroël et al. 2004, Clausen et al. 2005, Miller et al. 2010) has been recorded when there were known differences in prey availability based on at-sea surveys.

In my study, birds at Steeple Jason fed primarily on Falkland herring followed by rock cod, those at Cow Bay fed mainly on rock cod with influxes of Falkland herring and southern blue whiting, and, at the two colonies in the south of the islands, Bull Point and Bull Roads, birds consumed mostly lobster krill then Patagonian squid and rock cod. The locations of these colonies, and their proximity to the shelf edge or position in different water masses appears to play a key role in determining prey availability. Most notable is the major division between the west and east side of the Islands. The Steeple Jason colony, in the west, is situated in a separate water mass, the western branch of the Falkland Current, which is derived from the Antarctic Circumpolar Current (Agnew 2002, Arkhipkin et al. 2010, Ashford et al. 2012). The eastern branch of the Falkland current is stronger, however, both bring upwelled nutrients and create highly productive waters around the islands due to retention of nutrients in localised eddies (Agnew 2002, Arkhipkin et al. 2010, Ashford et al. 2012).

Around the Falklands, Falkland herring move inshore after spawning in September and October (Agnew 2002), with the largest populations being found towards the north-west of the islands during at-sea surveys (Laptikhovsky et al. 2001, Agnew 2002). This indicates greater availability around Steeple Jason. The other pelagic prey item consumed, southern blue whiting, typically occurred towards the north-east of the Falkland Islands (Niklitschek et al. 2010, Arkhipkin et al. 2013) during trawls from October to December (Arkhipkin et al. 2013), rendering it a suitable prey item for gentoo penguins at Cow Bay.

Similarly, the presence of the benthic rock cod fish in high proportions for birds at Cow Bay and as a major dietary component for birds in southern colonies is well explained by its distribution. Juvenile individuals (< 150 mm) typically utilize the bottom waters over the shelf (Laptikhovsky & Arkhipkin 2003, Brickle et al. 2006) and recent at-sea surveys found the highest abundance of small fish (< 300 mm) towards the north-east in October and north-west in February with fish still in the north-east during this time (Arkhipkin et al. 2013). The juvenile fish also occur in the Patagonian squid fishing grounds (Laptikhovsky & Arkhipkin 2003) which helps to explain the co-occurrence of these prey items in the diet of gentoo penguins in southern colonies. These Patagonian squid typically concentrate near the bottom during the day, the time when gentoo penguins typically forage, with smaller individuals (dorsal mantle length, DML < 80 mm) inhabiting shallow waters, < 80 m, and larger individuals (DML 90-100 mm) being found in deeper waters, 100-200 m, which is still over the shelf where the birds typically feed (Masello et al. 2010, Miller et al. 2010). At the Falkland Islands, the squid are abundant to the south and east of the islands, however, the most abundant concentrations, with particular respect to the study colonies, have been found towards the north east (Arkhipkin et al. 2013). Finally, the high consumption of benthic, adult lobster krill in the south of the islands fits well with the surrounding calmer shallow waters as high concentrations of this prey item are better suited to these conditions following a pelagic juvenile dispersal phase (Zeldis 1985, León et al. 2008, Meerhoff et al. 2013).

My results clearly show that at the scale of the archipelago gentoo penguin diet is diverse. This relates to both the type of prey consumed and the associated habitat utilized by these prey. Hence, it is clear that gentoo penguins can utilise different parts of the water column at various colonies across the Falklands, as documented at other locations (Hindell 1989, Lescroël et al. 2004, Clausen et al. 2005, Miller et al. 2010). This is understandable as across their range gentoo penguins seldom travel farther than 30km from the colony during the breeding season (Trivelpiece et al. 1987, Wilson et al. 1998, Miller et al. 2009, Handley 2014). This distance makes large shallow areas of the surrounding shelf readily available for birds at Cow Bay, Bull Point and Bull Roads, but far less accessible to those birds at Steeple Jason where the 100m isobath is in close proximity to the island. Although gentoo penguins have been recorded to dive as deep as 210 m (Bost et al. 1994), their typical depth range of 30-50 m (Williams et al. 1992, Miller et al. 2009, Kokubun et al. 2010) makes them far more suited to the consumption of benthic prey around the eastern part of the Falkland Islands.

Initial insights from stable isotope values indicate that birds at Steeple Jason may, in particular, be utilizing different areas at sea and foraging at different trophic levels as  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values

were always lower and higher, respectively, compared to other colonies. This is in contrast to what one would expect should birds be feeding on similar prey items beyond the breeding period because  $\delta^{15}\text{N}$  values are typically higher for rock cod and lobster krill, the benthic prey items (Quillfeldt et al. 2015, Table A2.2). Furthermore, the conclusion regarding varied habitat use is biased as the  $\delta^{13}\text{C}$  isoscape values appear to be higher in the south and east of the Falklands (Quillfeldt et al. 2010), along with the  $\delta^{15}\text{N}$  isoscape values typically being lower to the east (Quillfeldt et al. 2015). Additionally, all the  $\delta^{13}\text{C}$  values are higher than the average of  $-16.26\text{‰}$  for gentoo penguins recorded at New Island on the west of the Falklands (Weiss et al. 2009), nearest to the Steeple Jason study colony. Therefore, similarly to Weiss et al. (2009) I also suggest that gentoo penguins during the pre-moult stage remain foraging in inshore waters. This is further supported by the value for  $\delta^{13}\text{C}$  from my study being more similar to that of the imperial cormorant *Phalacrocorax articeps* ( $\delta^{13}\text{C} = -15.38\text{‰}$ ) at New Island, an inshore foraging species (Weiss et al. 2009).

### **Niche metrics**

Polito et al. (2015) provided the first evidence to suggest gentoo penguins, at least within part of their range, are Type B generalists. By incorporating stomach content data representing breeding period diet and insights from stable isotope values of feathers, a proxy for the pre-moult diet, this thesis supports the proposed idea that gentoo penguins are Type B generalists, particularly when looking at the island wide population.

Deep waters surrounding the Steeple Jason colony probably prevents benthic foraging due to energetic constraints. Therefore, it is unsurprising that birds at Steeple Jason typically had the lowest degrees of individual diet specialisation,  $V$ , and that this degree of specialisation increased as the trophic niche width of the birds increased. This increase is likely an artefact of increased availability to multiple foraging opportunities at the other colonies where birds may more feasibly forage benthically or pelagically. The fact that birds at Steeple Jason fed on rock cod, a prey item considered benthic in nature, during the 2011 guard stage, can possibly be explained by the larger rock cod consumed during this time (Table A2.4). These fish were most likely feeding in pelagic waters as diet of rock cod changes when larger adults consume more planktonic prey compared to juveniles which feed benthically (Laptikhovsky & Arkhipkin 2003).

During the pre-molt period, towards the end of February, both the core isotopic niche space and isotopic richness were also generally lower for birds at Steeple Jason. This may be due to limited dispersal during this time for which no knowledge exists yet as to where birds might be at sea.

However, unlike their congeners, gentoo penguins do not migrate large distances during the winter, outside the breeding period (Wilson et al. 1998, Clausen & Putz 2003, Tanton et al. 2004). Therefore, prior to molting these birds probably remain foraging pelagically in the inshore environment, close to their colony, which would explain their relatively low niche space being occupied. In addition, isotopic divergence and dispersion tended more towards 0 when looking at the intra-colony isotopic diversity metrics showing that within a colony, individuals were more similar. This supports the notion that at the colony level across the Falkland Islands gentoo penguins are Type B generalists.

The influence of habitat affecting the realized niche of individuals has been recognised across a wide range of taxa for terrestrial, aquatic and marine organisms such as the gray wolf *Canis lupus* (Darimont et al. 2009), American alligator *Alligator mississippiensis* (Rosenblatt et al. 2015), sea otter *Enhydra lutris* (Newsome et al. 2015), tiger shark *Galeocerdo cuvier* (Simpfendorfer et al. 2001) and bull shark *Carcharhinus leucas* (Matich et al. 2011). It is clear that habitat heterogeneity can place an upper bound on an individual's niche width (Araújo et al. 2011, Schriever & Williams 2013). This habitat heterogeneity, however, is not the only factor that can affect the niche width of a population. Indeed both intra and inter-specific interactions have been recognised to affect the degree of individual diet specialisation and thus the niche width of a population (Araújo et al. 2011, Matich et al. 2011). To fully elucidate the role of these factors for gentoo penguins at the Falkland Islands would require simultaneous quantification of prey availability and I strongly advocate for this research in the future.

### **Inferring diet: Stable isotope mixing model**

Making inferences about the dietary contribution of different source items is difficult as different proportions of prey can still result in the same overall isotopic value (Bond & Jones 2009). To overcome this, knowledge of prey items consumed during the time of investigation is important as a baseline comparison. Furthermore, significant differences in prey item isotopic values should be evident in order to distinguish between potential sources. After reducing a mixing model with 17 potential sources to a three-source model (following Phillips et al. (2005)), which only included isotopically distinct putative prey sources for gentoo penguins, this was still not the case. Firstly, there was no clear separation between the pelagic feeding, Falkland herring, southern blue whiting and Patagonian squid. Secondly, it was clear from the simulated mixing region for the mixed model that the majority of consumers in my study fell well beyond the required mixing space suitable towards the use of a potential stable isotope mixing model (Figure 2.4). This may indicate that an alternate prey item is consumed during the pre-moult stage or that the available diet-tissue



discrimination factor is inadequate (Inger & Bearhop 2008, Phillips et al. 2014), even though it is species and tissue specific (Polito et al. 2011a). The isotopic values for potential prey items from my study are similar to Quillfeldt et al. (2015). Therefore, should birds continue to feed on similar prey items consumed during the breeding period it looks feasible that birds at Steeple Jason should have the lowest  $\delta^{15}\text{N}$  values as these were typically highest for rock cod and lobster krill, benthic prey items. However, this was not the case, again reiterating the observed values from the Quillfeldt et al. (2015)  $\delta^{15}\text{N}$  isoscape. I suggest, that in addition to requiring suitable baseline isotopic values on a suitable spatial and temporal scale (Quillfeldt et al. 2015), future studies will need to investigate the diet-tissue discrimination factors that may be present for prey alternative to forage fish (e.g: cephalopods and crustaceans) often used in feeding trials.

## **Conclusions**

This thesis has provided the first, island wide, species specific prey description, for gentoo penguins at the Falkland Islands over three consecutive breeding seasons (2011-2013). The data re-iterate the great flexibility in foraging strategies in gentoo penguins which are largely driven by local conditions. This probably to a large extent explains the resilience to environmental change observed in this species (with an increasing global population as opposed to its congeners which are dietary specialists across their range; see Borboroglu and Boersma (2012)). Furthermore, my study highlights how gentoo penguins would require a multi-faceted approach towards their conservation and management owing to spatial variability in prey consumption. Finally, in my attempts to identify prey consumed during the pre-molt period through the use of stable isotope mixing models I was unsuccessful. Critically, future work should focus on determining more prey specific trophic enrichment factors and if possible try to source prey items from a more inshore environment to facilitate the use of stable isotope mixing models towards diet reconstruction.

## Chapter 3 Site specific foraging strategies of a colonially breeding seabird revealed through biologging and habitat distribution models

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### Abstract

Colonial seabirds inhabiting multiple locations can be subjected to contrasting environmental conditions at sea. A pre-requisite towards conserving these top predators is determining how they use their surrounding environment. This information can then be incorporated into habitat distribution models. Following this, if cross validation of models is supported, these can potentially indicate the likely space use by a species within and outside un-sampled locations. I aimed to investigate the at-sea distribution and develop habitat distribution models for a generalist diving species, the northern gentoo penguin *Pygoscelis papua papua*, during its breeding period over two seasons at the Falkland Islands. Using biologging technologies, I show that these birds are inshore foragers but adopted different foraging strategies across three different colonies in terms of diving behaviour and horizontal space use. Distribution models developed through boosted regression trees showed good cross validation through time but were poor across space. Foraging strategies are likely driven by local prey availability and access to the surrounding seabed. Poor transferability in space for distribution models is likely driven by paucity in data pertaining to environmental descriptors. Nonetheless, results show that as elsewhere, within its range, gentoo penguins at the Falkland Islands forage with a broad array of strategies which may be facilitating the current population growth. However, in a region undergoing anthropogenic change, this distribution data should ultimately be used in multispecies studies to facilitate the identification of important areas at sea utilized by multiple species.

**Keywords:** *Spheniscidae*, GPS, TDR, habitat model, marine spatial planning, foraging ecology

### Introduction

Marine habitats used by predators that occupy a broad geographic range, can be highly heterogeneous resulting in varied foraging strategies across a species (Lescroël & Bost 2005, Newsome et al. 2015, Corman et al. 2016). In light of this variation, a single approach to species management may not be suitable. Additionally, logistical constraints such as cost and availability of personnel may make it unfeasible to sample multiple locations a species utilises. One such

approach to overcome this challenge is through habitat distribution models which may be used to infer a species realized distribution in un-sampled regions (Potts & Elith 2006, Franklin 2010, Torres et al. 2015, Lascelles et al. 2016). The first step in developing these models, however, requires a fundamental understanding of the foraging strategies and habitat preferences of a species. If model predictions are robustly transferable for a species across space and time, the inferred distribution data can contribute to multispecies studies, facilitating greater understanding of ecosystem processes and the complex interactions therein (Ceia & Ramos 2015). Habitat distribution models can also help identify areas which may be important to a suite of species (Raymond et al. 2015, Lascelles et al. 2016, Thiers et al. 2016, Hinke et al. 2017a).

The Southern Ocean, defined here as those areas south of the Subtropical Front (Constable et al. 2014), is an area where knowledge of species distributions is of critical importance. Recent evidence shows that this region is susceptible to the impacts of climate change (Constable et al. 2014, Gutt et al. 2015), ocean acidification (Orr et al. 2005, Kawaguchi et al. 2013) and anthropogenic perturbations such as pollution (Wilcox et al. 2015) and overfishing (Cury et al. 2011). The Southern Ocean is also home to vast seabird populations, many of which are vulnerable to these threats (Trathan et al. 2014, Krüger et al. 2017). Disentangling how a species may respond to environmental change, first requires an understanding of its realized niche. For those with a narrow niche (specialists) adaptation to change may be limited, resulting in population declines or range shifts. However, for those capable of exploiting a broad niche (generalists), they may be more adaptable to global change (Clavel et al. 2011). This realized niche is not only restricted to the diet of a species but also includes the potential specialisation in the foraging, searching and diving behaviour, site fidelity, consistency in the migratory and foraging routes and consistency in the non-breeding areas (Ceia & Ramos 2015).

Penguins *Spheniscidae* are one group of seabirds that form a major component of the Southern Ocean, constituting approximately 80-90% of the avian biomass (Croxall 1984). The genus *Pygoscelis* is comprised of three penguin species which inhabit the Southern Ocean. Two of these, the Adélie (*Pygoscelis adeliae*) and chinstrap (*Pygoscelis antarcticus*) penguins, are considered as specialists and forage on krill in offshore waters at shallow depths (Wilson 2010, Kokubun et al. 2010, Polito et al. 2015). The third, the gentoo penguin (*Pygoscelis papua*) is considered as a generalist typically feeding on available prey in neritic waters and foraging behaviour being determined by local habitat characteristics (Lescroël et al. 2004, Lescroël & Bost 2005, Miller et al. 2009, 2010, Kokubun et al. 2010). Recent genetic evidence (Clucas et al. 2014, 2017, Levy et al. 2016, Vianna et al. 2017) validated the separation of gentoo penguins into two

distinct sub-species, and possibly a third (Stonehouse 1970, Dinechin et al. 2012). These include the northern (*Pygoscelis papua papua*) and southern (*Pygoscelis papua ellsworthii*) subspecies, and potentially an Indian ocean subspecies which seem to have evolved because of an oceanographic barrier, the Antarctic Polar Front acting as a physical boundary to introgression (Levy et al. 2016, Clucas et al. 2017). Additionally, limited dispersal beyond the breeding period (Clausen & Putz 2003, Tanton et al. 2004, Hinke et al. 2017a) and archipelago specific natal philopatry (Stonehouse 1970, Tanton et al. 2004, Ratcliffe & Trathan 2011), play a role in the divergence of these subspecies.

At the Falkland Islands, the diet of the northern gentoo penguin has been well-studied and shows that birds feed on locally available prey (Thompson 1994, Putz et al. 2001, Clausen & Putz 2002, Clausen et al. 2005, Handley et al. 2017). However, there is still limited knowledge regarding their foraging, searching and diving behaviour. This relates to breeding birds from, New Island at the Falkland Islands, where birds were observed to forage close to their colonies (Boersma et al. 2002, Masello et al. 2010, 2017) or for two birds during winter, indicating how their range extended as they travelled to various locations around the Falklands while always remaining above the continental shelf (Clausen & Putz 2003). Considering these birds breed at 75 colonies across the Falkland Islands, if birds differ in foraging behaviour and habitat preference in relation to spatial heterogeneity of available habitat, this may impair one's ability to make predictions of distributions around un-surveyed colonies based on predictions from models developed on surveyed ones. This comes at a time when there are increasing anthropogenic pressures on penguins, particularly those which have a higher contact with human populations such as those breeding in South America, Africa and Oceania (Trathan et al. 2014). More specifically to the Falkland Islands, there is also a pressing need to understand the distribution of not only gentoo penguins but multiple species in light of the proposed hydrocarbon developments within the exclusive economic zone (Augé et al. 2015).

Here, I explore the foraging behaviour of gentoo penguins at the Falkland Islands during the breeding period. I tracked birds over two seasons, from three colonies which were selected for their isolation from each other and contrasting surrounding habitat. Specifically, my aims were to (1) describe the general foraging characteristics of gentoo penguins at the Falkland Islands, (2) investigate whether contrasting foraging strategies are used through space and time, and (3) develop habitat distribution models to predict at sea distribution around un-sampled colonies. These data and predictions will make an important contribution toward marine spatial planning in the Falkland Island's waters (Augé et al. 2015).

## **Methods**

### **Study sites**

Birds were sampled at three of 75 breeding colonies at the Falkland Islands during the austral summers of 2012/13 and 2013/14 hereafter referred to as 2012 and 2013, respectively. These included: Steeple Jason Neck (51.0375° S, 61.2097° W), Cow Bay (51.4288° S, 57.8703° W) and Bull Roads (52.3096° S, 59.3896° W) (See Results) each with approximately 3710, 1821 and 1236 breeding pairs, respectively (Stanworth 2013). Each colony is unique in terms of their surrounding bathymetry and exposure to the open ocean. Steeple Jason Island is exposed to the open ocean and has a steeply sloping seabed that rapidly drops down to 100m. Cow Bay, which, faces the open ocean, and Bull Roads, which is in a sheltered shallow bay, both have sea-beds that gradually slope away.

### **Logger Deployment**

To reduce the possible bias in foraging parameters owing to varied clutch or brood size (Williams & Rothery 1990), loggers were deployed on birds incubating (early November) or guarding (December) two eggs or chicks, respectively. For incubating birds, a deployment was only undertaken once two eggs had been laid and both partners had been observed to complete a foraging trip.

Nests were monitored from approximately 14:00 onward as this was the time when most birds began returning to the colony. Following return of a partner, and only once courtship behaviour and change overs had occurred, the individual previously tending the nest was caught with a net attached to a 2m pole. In 2013, however, I captured birds in the morning as adults headed to the sea owing to a concurrent investigation utilising animal-borne camera loggers (Handley & Pistorius 2015). This was necessary as the video cameras had to be switched on immediately. The weight of the bird was recorded prior to deployment with a Pesola spring balance, and each bird was given a unique mark on the breast with a green waterproof marker (ROTO.STIK).

Loggers were secured to the feathers on the midline of the bird's back using overlapping layers of waterproof adhesive TESA® tape (Beiersdorf, AG, GmbH, Hamburg, Germany). Tape ends were sealed with cyanoacrylate glue (Loctite 401®) and tape above the GPS antennae was removed otherwise it would not receive satellite signals when the tape became wet.

Handling time was kept to a minimum, mostly below 15 minutes and always below 20 minutes. Birds were then released toward their nest to allow pair bonding behaviour with partners, or facing

the sea in 2013 so as they could resume their foraging trip. A continual watch was maintained between 11:00 and 23:00 for returning birds so they could be recaptured away from the colony, minimising further disturbance. Retrieval of the device took less than five minutes. Final morphometric measurements of bill length and depth were taken, along with retrieval mass.

Three types of GPS devices were used during my study, each being tapered anteriorly to minimise drag (Bannasch *et al.* 1994). These included: earth & OCEAN Technology's (Kiel, Germany) 2-AA model (140x39x26.5mm, 147g), SIRTRACK's® Fastloc 2 model (69x28x21mm, 39g) and Catnip Technology's CatTraQ GPS logger (44x27x13mm, 22g). In addition to location, pressure and temperature were recorded with a CEFAS G5 TDR (31x3mm, 2.7g, CEFAS Technology Ltd., Lowestoft, UK). The maximum weight (including when cameras were used (Handley & Pistorius 2015)) of device combinations never exceeded 172.7g accounting for approximately 2.7% mass of a bird, which is below the recommended upper limit of 5% external body mass for penguins (Phillips *et al.* 2003, Wilson & McMahon 2006).

GPS units were programmed to maximise positional fix rates, yet still capture a complete foraging trip. The 2-AA and CatTraQ units were programmed to record locations every minute. Additionally, the 2-AA unit was set with a 10 minute fall back time and the pressure control disabled. This causes the unit to search for satellites at one second intervals when no fix is obtained and is beneficial for diving animals with short surface intervals. If locations are recorded continuously for 10 minutes (e.g. when the animal is on land or continually at the surface) the unit falls back to one minute fix intervals, avoiding excessive battery use. The Fastloc 2 unit employs a snapshot technique different to traditional GPS fixing, and requires post processing of data with SIRTRACK® software which reduces fix acquisition times and maximizes the likelihood of obtaining positions during short surface intervals between dives. The units were set to record fixes at two minute intervals owing to battery limitations. TDR loggers were programmed to sample pressure and temperature every 1s at 12-bit resolution.

### **Foraging characteristics**

Data were analysed using R version 2.15.0 and 3.2.1 (R Development Core Team). The former was required for the 'availability' package (Raymond *et al.* 2016), discussed below.

**TDR data.** Summary statistics of dive behaviour were determined from TDR data using the 'diveMove' package (Luque 2007). These included the time relating to the onset of a dive, dive duration, maximum dive depth and bottom time during a dive. The package allowed for an accurate time budget summary of bird departure to sea and return to land. This summary was

amended, if needed, through visually inspecting the temperature trace for a rapid change in ambient temperature. Owing to sensitivities of the transducer within TDR's, pressure readings often need to be zero offset corrected, i.e. if a device consistently records below or above sea level (expected to be 0m depth) the data requires correction. This was achieved manually through visual inspection of the pressure trace during the calibration step. Dives were classified as benthic, as opposed to pelagic, if the maximum depth of a series of dives was uniform and the difference was within  $\pm 10\%$  of the maximum depth reached during the preceding dive (Carpenter-Kling et al. 2017).

**GPS data.** CatTraQ loggers tended to duplicate locations at sea, so these duplicates were removed using Microsoft Excel. The *speedfilter* function ('trip' package, (Sumner 2015)), based on the algorithm by McConnell et al. (1992), was used to remove erroneous locations when the average transit speed between them was  $> 8 \text{ km.h}^{-1}$  (Adams et al. 1987). Furthermore, the diving nature of penguins results in intermittent positional fixes. Therefore, the filtered data was processed using a continuous-time correlated random walk model (implemented in the 'crawl' package, (Johnson et al. 2008)) to generate the most likely path used by a bird, through simulation of 100 possible tracks. With this path, locations were interpolated at one minute intervals in order to calculate total path length, maximum distance from the colony, trip duration and average travelling speed (using the 'move' package, (Kranstauber & Smolla 2015)). Furthermore, from the 100 possible tracks, estimates of uncertainty in the path followed between GPS positions could be accounted for.

Dive locations were interpolated to the most likely path based on the onset of a dive. Using these locations, a similar approach to Lascelles et al. (2016) was followed to determine the representativeness of samples to that of the sample population. Dive locations have an added advantage in that they likely represent the choice of an animal to search for food, compared to the assumption made that feeding takes place within regions of area restricted search (Weimerskirch et al. 2007). Kernel density distributions representing the 50% utilization distribution (UD) were generated (using the 'adehabitatHR' package (Calenge 2006)) to identify the area of core use for the sample population. A bootstrap approach ( $n=500$ ) was then used to compare the overlap between the area used by the sample population versus randomly selected tracks, where the number of randomly selected tracks was increased iteratively from 1 to the number of tracks for a given sample population. The width parameter,  $h$ , was determined using Silverman's ad-hoc method (Silverman 1986), as the common problem of convergence failure using least-squares cross validation (LSCV) occurred (Getz et al. 2007, Erdmann et al. 2011).

## Habitat use

**Species data.** The 100 simulated possible dive locations for each of the recorded dives for each bird were gridded as an estimate of dive effort per cell ( $0.005^\circ \times 0.005^\circ$ ). Each grid was summed across all birds to produce a surface for the sampled population. A high-resolution grid was used initially as GPS loggers provide high quality location data. Importantly, although a degree-based grid implies that cell area will vary depending on location, the narrow range of latitude used by the birds meant that this would not warrant concern for my study. Gridding the uncertainty in locations accounts for their precision and also provides some degree of smoothing compared to simple gridding of the most likely primary positions (Ratcliffe et al. 2014). It also avoids the need for further smoothing by kernel density estimation and the making of assumptions inherent in that method (Sumner et al. 2009). Similarly to previous studies, I assumed that the pooled sample of tracked birds was representative of the distribution patterns of the sample population (Louzao et al. 2013, Torres et al. 2015). Again, the sufficient number of tracks used was further justified through the bootstrap procedure outlined above.

**Available area and absences.** An important prerequisite in determining habitat use by an animal is to determine the grid extent size or area available to that animal (Franklin 2010). This available area is an indication of where animals could have travelled were they not to have any preference in foraging habitat. Currently, no consensus exists as how best to determine this available area and a broad array of approaches have been used (Aarts et al. 2008, Wakefield et al. 2011, Torres et al. 2015, Van Eeden et al. 2016). Therefore, I incorporated the approach outlined in Raymond et al. (2015), via the 'availability' package (Raymond et al. 2016). Specifically, habitat availability was estimated by simulating 100 tracks per observed track. These simulated tracks were bound by a land mask and were statistically similar to the observed tracks (i.e. constraints on trip duration, turning angles, travel speed and departure locations were maintained). The available habitat was then considered to be that area encompassed by the maximum and minimum latitude and longitude reached across all simulated tracks combined. Absences were those cells within this area not used by the birds.

**Covariates.** Satellite derived dynamic variables such as sea surface temperature, sea surface height, chlorophyll-a concentration, eddy kinetic energy and sea level anomaly are often used as proxies for prey availability, which is a likely driver of why an animal may use a specific habitat. The short foraging range typical of gentoo penguins observed in my study and elsewhere, meant that I could only include the physical static variables of distance to coast line, distance to colony (a land mask was used when determining this distance, thereby, accounting for land which would



limit dispersal) and depth. This was because the cell size for the dynamic variables was too coarse and only the depth data (855m x 885m) offered by the General Bathymetric Charts of the Oceans (GEBCO, <http://www.gebco.net>) was deemed appropriate. Furthermore, their inclusion is justified by the requirements for a parsimonious, predictive and yet biologically relevant model (Aarts et al. 2008). Data from the TDR devices also showed birds to be performing benthic dives (see Results) at sites where gentoo penguins feed primarily on benthic prey (Handley et al. 2017, Chap 2). These are the same sites which were considered for habitat modelling.

### **Statistical analyses: foraging characteristics**

Analyses were limited to data obtained from sample periods during which accompanying GPS and TDR data (that were representative of the sample population; see above), along with diet data (Handley et al. 2017), collected over same stage of breeding were available. Means with standard error are presented, and significance was assumed at  $p < 0.05$  unless otherwise stated.

Linear mixed effects models ('nmlme' package, (Pinheiro et al. 2016)) were used initially to compare dive and trip characteristics derived from TDR's and GPS's, respectively, following Zuur et al. (2009). Specifically, colony was specified as a fixed effect while random effects were either trip nested within individual (dive variables: dive duration, maximum depth, bottom time) or just individual (trip characteristics: path length, maximum distance from colony, trip duration and proportion of benthic dives). All models were fitted with normal errors and an identity link. Following model selection, the random component of models relating to trip characteristics was dropped, therefore, final models for these variables were fitted using general least squares (gls) models. To account for heterogeneity in the data across colonies (per stratum), models were weighted with the 'varIdent' variance structure. Furthermore, as successive dives might be similar I assessed for temporal auto-correlation through auto-correlation function (ACF) plots. This was present for all dive variables; therefore, these models were fitted with a first-order autocorrelation structure ('corAR1'). Model selection was done using backward stepwise deletion and ANOVA tests. During model selection, maximum likelihood was used, while final parameters were estimated from the selected model using restricted maximum likelihood. Variance component estimates from the final model were obtained via the 'varcomp' function in the 'ape' package (Paradis et al. 2004).

### **Statistical analyses: distribution model**

**Model development.** My aim was to produce a habitat distribution model that predicted the spatial distribution of birds, which could be scaled across the Falklands. A binary response

variable was used, whereby presence in a cell was scored 1 and absence 0. I considered a second stage, and implementing a hurdle model approach, however, my results indicated this to be unjustified. Initial data exploration, using variance inflation factors, where a value of  $>3$  indicates collinearity (Zuur et al. 2009), revealed high collinearity among covariates. Therefore, a boosted regression tree (BRT) approach (package 'gbm', (Ridgeway 2015)), an approach that incorporates both regression and machine learning, was used. This method, reviewed by (Elith et al. 2008), is regarded as robust and able to cope with outliers, non-linear relationships, and correlated and interacting variables (Elith et al. 2008, Torres et al. 2015). Additionally, while overfitting on training data may occur via BRT, prediction to independent data is often superior to other methods (Elith et al. 2008, Franklin 2010). Tuning parameters, learning rate (lr) and tree complexity (tc), for BRT were optimized using 10 fold cross-validation via the 'gbm.step' function (package 'dismo', (Hijmans et al. 2016)) in order to determine the optimal number of trees (nt) for prediction. The recommendation outlined in Elith et al. (2008), of fitting models with at least 1000 trees, was followed. As BRT models are probabilistic there are no p values; rather, variable importance is determined through their relative contributions during model building. Partial dependence plots can be used to show the effect of a variable on the response after accounting for the average effects of all other variables in the model. A further advantage of BRT over approaches such as Generalized Additive Models, is that BRT can handle sharp discontinuities, which often occur when modelling the distributions of species that occupy only a small proportion of the sampled environmental space (Elith et al. 2008), as was evident in my data.

**Model extrapolative performance.** The ability of a model to be extrapolated in time and space was assessed via cross-validation of that model against the distribution of birds from the same colony but in a different year, then against the distribution of birds from a different year and colony, respectively. The representative sample of tracking data from Steeple Jason was obtained during the 2012 incubation period, as opposed to the data collected during the guard periods at Bull Roads and Cow Bay. Furthermore, bird behaviour at the Steeple Jason colony was significantly different for nearly all dive and trip characteristics. Therefore, distribution models were only considered for birds during the guard period at Cow Bay and Bull Roads in each of the 2012 and 2013 seasons, when birds were foraging benthically. Three performance metrics were used as each has their own advantage. Firstly, for discrimination, the area under the curve (AUC) of the receiver-operating characteristic curve (package 'ROCR', (Sing et al. 2005)), which describes the overall ability of the model to discriminate between the two cases, i.e., species presence and absence. AUC values range from 0.5 to 1 where a value of 0.5 can be interpreted as random predictions and values above 0.5 indicate a performance better than random (Franklin 2010).

Accordingly, values between 0.5-0.7 indicate poor model performance, 0.7-0.9 are moderate, and >0.9 high (Swets 1988). Secondly, for correlation, the point-biserial correlation between observed and predicted probabilities. And thirdly, for calibration, which determines whether predictions were proportional to conditional probability of habitat suitability, I used calibration plots implemented via the function 'calibration' (package 'sdm', (Naimi & Araújo 2016)). These plots can be interpreted as follows: when the predicted probability is plotted against prevalence, values that differ from the 1:1 line (slope = 1) suggest an uncalibrated model. Values above the line indicate a model that has underestimated species prevalence, while values below indicate overestimation (Franklin 2010).

## **Results**

### **Data outcome and quality**

In total, 101 birds were equipped with both GPS and TDR units during my study. Of these, batteries from two deployments failed prior to completion of a trip, four birds were not recaptured and in nine cases devices failed owing to water penetration. Typically, all birds were recaptured after a single trip but in some cases only after a second trip. Birds were sampled during the incubation period of 2012 for all colonies, and during the guard period of 2012 and 2013 for Cow Bay and Bull Roads only. The test for sample representativeness indicated that too few tracks were obtained for the incubation period of 2012 at Cow Bay (n=4) and Bull roads (n=4), as indicated by accumulation curves either only reaching the 95% probability of overlapping for the last track or not reaching it at all (Figure 3.1). Therefore, the across colony comparison was made among 78 deployments (86 trips) from the 2012 incubation period at Steeple Jason, and the 2012 and 2013 guard periods of Cow Bay and Bull Roads (Table 3.1).

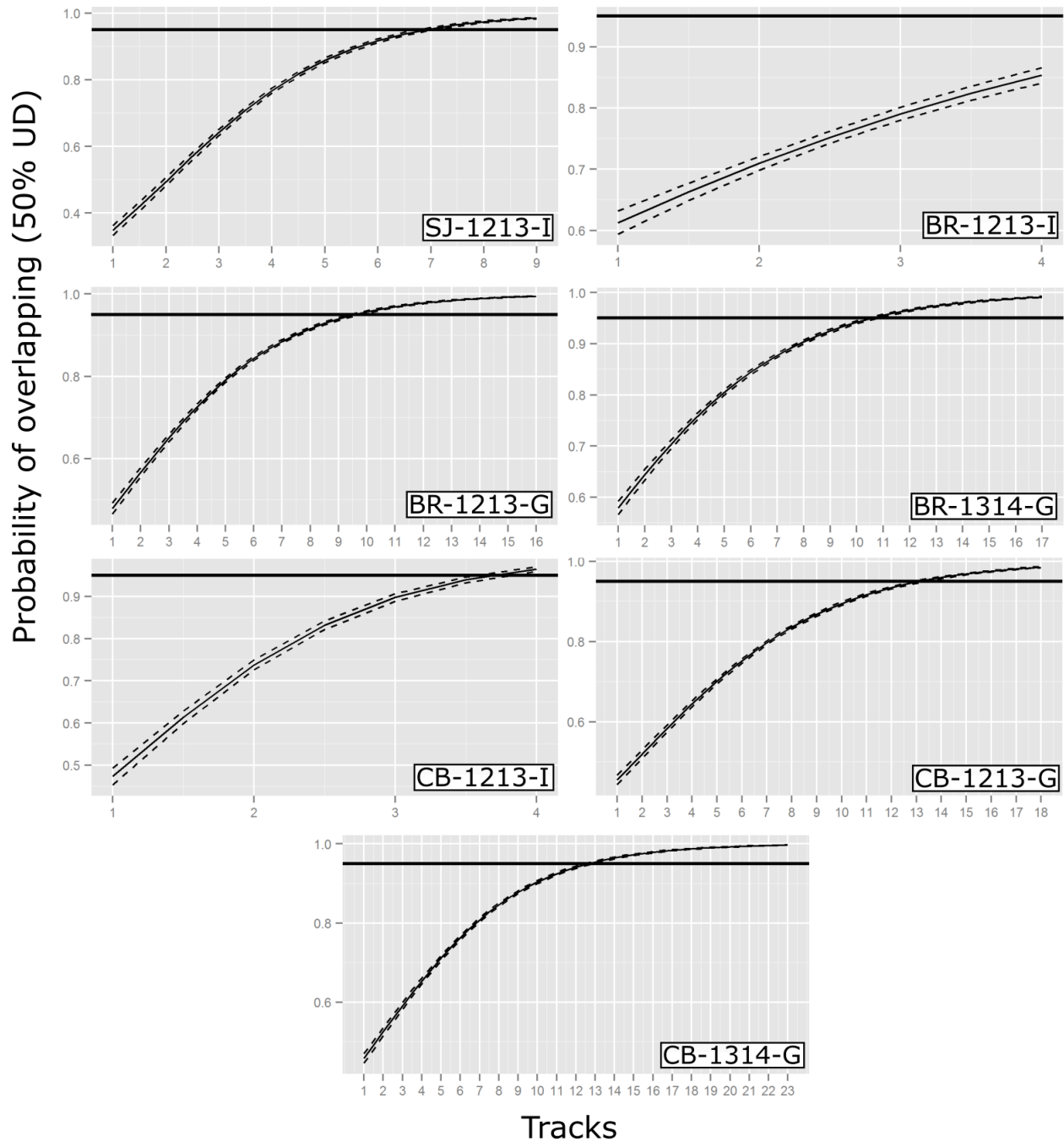


Table 3.1: Mean (SE) and range of dive and trip characteristics for gentoo penguins at the Falkland Islands from three colonies (BR: Bull Roads, CB: Cow Bay, SJN: Steeple Jason Neck) during the breeding period (Incubation, Guard) of 2012 and 2013. LR reports result from likelihood ratio test used to compare linear mixed effects models (dive characteristics) and general least squares models (trip characteristics) with and without the fixed effect of colony. Significant differences within a variable indicated by differing superscripts

	<b>BR (n<sub>bird</sub>=34, n<sub>tracks</sub>=36)</b>		<b>CB (n<sub>bird</sub>=36, n<sub>tracks</sub>=41)</b>		<b>SJN (n<sub>bird</sub>=8, n<sub>tracks</sub>=9)</b>				
	<b>Mean (SE)</b>	<b>Range</b>	<b>Mean (SE)</b>	<b>Range</b>	<b>Mean (SE)</b>	<b>Range</b>	<b>LR</b>	<b>df</b>	<b>p</b>
<b>Dive characteristics</b>									
Dive duration (s)	132.7 (4.4)	1-294 <sup>A</sup>	128.2 (4.0)	1-318 <sup>A</sup>	48.1 (7.4)	1-193 <sup>B</sup>	75.3	8	<0.0001
Maximum depth (m)	37.8 (1.4)	3.0-77 <sup>A</sup>	44.2 (1.5)	3-152 <sup>B</sup>	19.0 (2.5)	3-103 <sup>C</sup>	59.3	8	<0.0001
Bottom time (s)	85.0 (3.1)	1-214 <sup>A</sup>	77.5 (2.7)	1-225 <sup>A</sup>	20.2 (5.0)	1-130 <sup>B</sup>	84.3	8	<0.0001
<b>Trip characteristics</b>									
Proportion benthic dives	0.74 (0.02)	0.44-0.92 <sup>A</sup>	0.70 (0.02)	0.43-0.95 <sup>A</sup>	0.18 (0.02)	0.11-0.36 <sup>B</sup>	68.6	6	<0.0001
Avg. travel speed (km.h <sup>-1</sup> )	2.4 (0.1)	1.4-4.0 <sup>A</sup>	3.2 (0.1)	1.32-4.83 <sup>B</sup>	4.0 (0.4)	1.68-5.33 <sup>C</sup>	29.4	6	<0.0001
Trip duration (hrs)	22.6 (2.5)	6.13-77.8 <sup>A</sup>	23.7 (2.2)	5.6-85.9 <sup>A</sup>	12.9 (3.1)	6.5-34.5 <sup>B</sup>	6.9	6	0.03
Max distance (km)	17.2 (1.2)	8.1-44.4 <sup>A</sup>	28.9 (2.1)	8.5-58.7 <sup>B</sup>	16.1 (2.2)	6.9-23.28 <sup>A</sup>	23	6	<0.0001
Path length (km)	49.5 (3.8)	23.14-118.41 <sup>A</sup>	71.9 (4.9)	19.8-143.2 <sup>B</sup>	44.7 (4.7)	22-58.0 <sup>A</sup>	16.9	6	<0.0001

### **At-sea distribution**

In all cases, birds foraged inshore, above the continental shelf. Birds at Cow Bay used the largest areas at sea, comprising 893km<sup>2</sup> and 1054km<sup>2</sup> in the 2012 and 2013 guard period, respectively. Birds at Bull Roads used much smaller areas, encompassing only 299km<sup>2</sup> and 279km<sup>2</sup> for the same seasons and breeding period as Cow Bay. During the 2012 incubation period at Steeple Jason, birds only used an area of 284km<sup>2</sup>. At Cow Bay, birds spread out from the colony in a north-eastern direction. At Bull Roads, birds moved to the east and largely stayed within the confines of the surrounding bay and outer islands. Those at Steeple Jason headed to the west foraging in typically deeper waters than those birds at Cow Bay and Bull Roads (Figure 3.2).

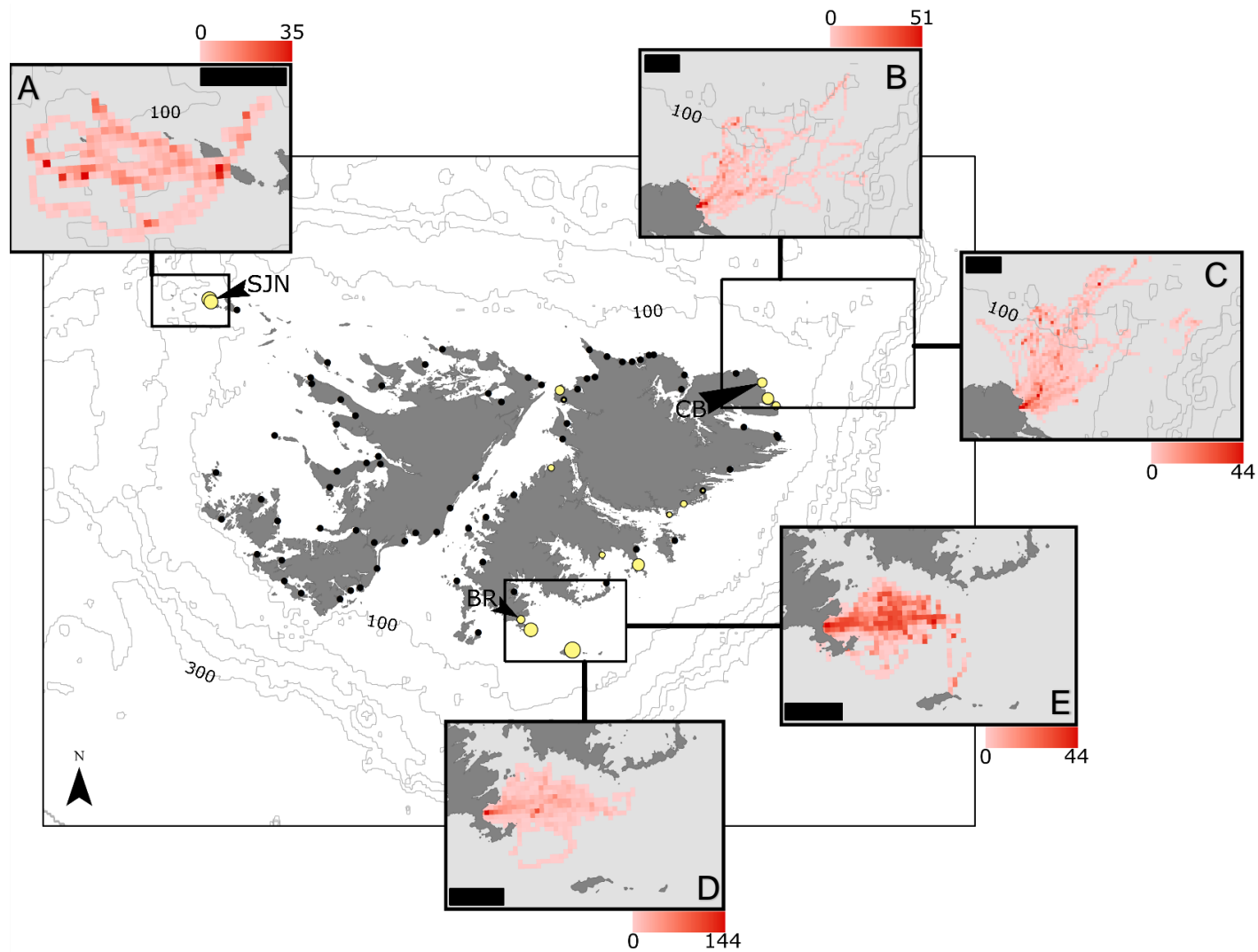


Figure 3.2: Distribution of gentoo penguins at the Falkland Islands during the 2012 and 2013 breeding seasons. Insets include the (A) incubation period at Steeple Jason Neck and the guards periods of (B,C) Cow Bay and (D,E) Bull Roads during the 2012 and 2013 seasons, respectively. Red bar indicates summed dive effort per cell from all tracks combined. Black bar represents a 10km scale bar. Known breeding gentoo colonies are indicated by black dots, while yellow dots indicate the size of annually monitored colonies during the 2012 breeding pair census (Stanworth 2013)

## **Dive and trip characteristics**

Birds had significantly different dive characteristics (dive duration, maximum depth, bottom time) among the three colonies (Table 3.1) and in all models colony and only trip were retained as the fixed and random effect, respectively. Birds dived for similar durations and spent a similar amount of time at the bottom of a dive at Cow Bay and Bull Roads but for significantly shorter periods at Steeple Jason. Similarly, at Steeple Jason birds dived to significantly shallower depths, compared to Bull Roads, then Cow Bay. For all these dive characteristics, Cow Bay had the highest maximum values. Variance components estimates indicated that residual, random variation within a trip was 76%, 79% and 78% while the variability in dive characteristics accounted for by the trip was 24%, 21% and 22% for dive duration, maximum depth and bottom time, respectively. These high within variance components estimates are clearly understood when looking at the range across dive characteristics (Table 3.1) and cross-sectional plots of a bird's dive behaviour during a foraging trip (Figure 3.3). The typical pattern observed for birds during a trip at Cow Bay and Bull Roads indicated a high proportion of benthic dives, where it was evident that birds sequentially reached deeper depths during the outbound phase of the journey followed by sequential shallower dives during the inbound phase (Figure 3.3). This was in contrast to Steeple Jason, where significantly fewer, and only a small proportion of the dives were classified as benthic (Table 3.1). The consistent foraging behaviour during a trip was also evident when looking at the distribution of dive effort per cell as generally speaking there were no major hot spots (Figure 3.2).

Trip characteristics derived from GPS data also showed significant differences among colonies (Table 3.1). At Steeple Jason, birds travelled significantly faster than those at Cow Bay, then Bull Roads. Birds at Steeple Jason also had significantly shorter trip durations compared to the other two colonies where trip durations were similar. Regarding travel distance, birds from Steeple Jason and Bull roads reached on average similar maximum distances from the colony, and also travelled similar distances during a trip, however, for both variables these were significantly lower than those at Cow Bay.



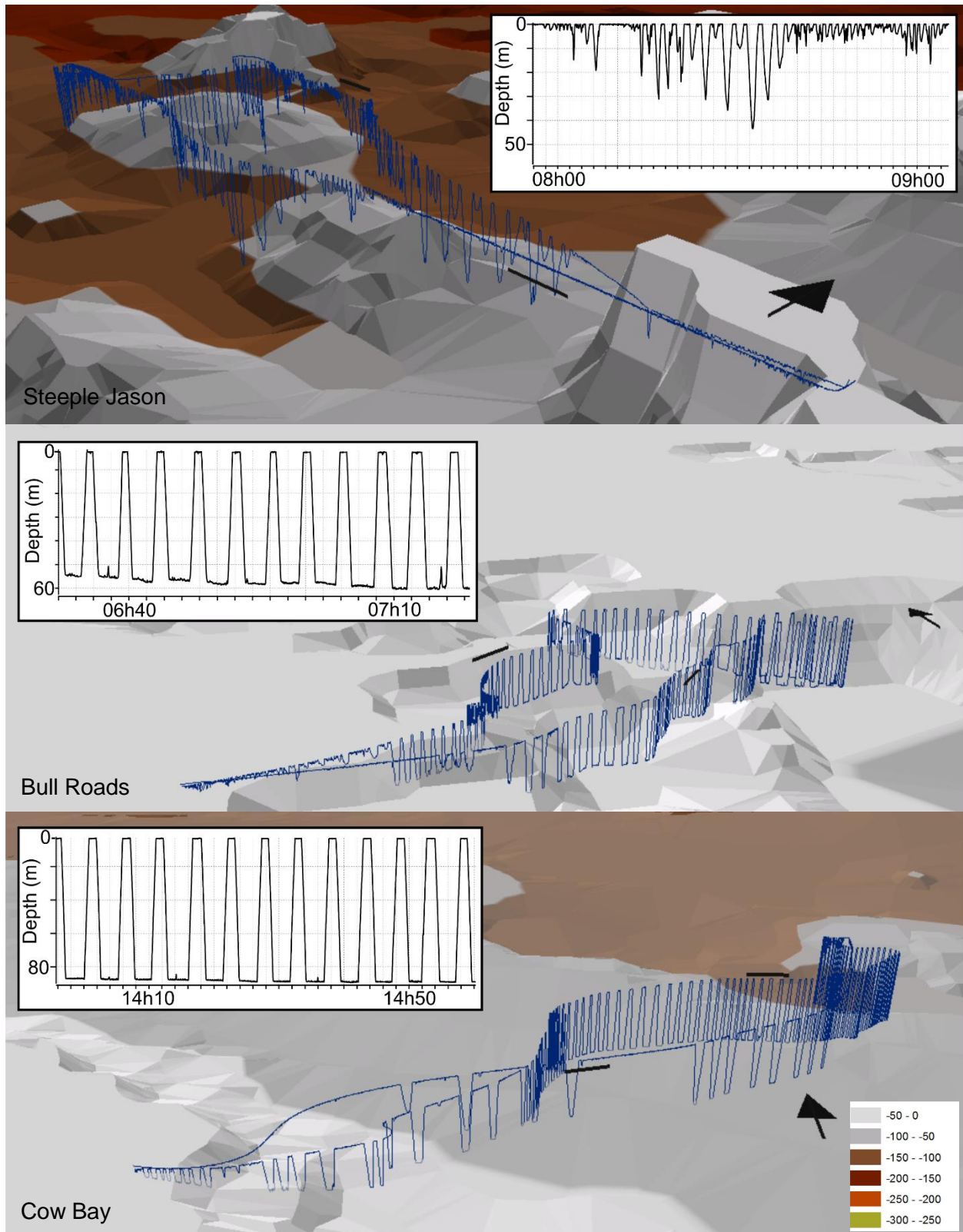


Figure 3.3: Three-dimensional representation (blue line) of a typical foraging trip from (top) Steeple Jason, (middle) Bull Roads and (bottom) Cow Bay. Insets show a portion of a cross-sectional typical dive profile. Black bars show 1km scale at given location in image because scale in 3D varies in a linear perspective fashion. Arrow depicts north. Track creation was done by interpolating GPS locations to the same time interval as TDR loggers. Visualisation was achieved using ArcScene 10.3 (ESRI)

## Distribution models

In all cases models performed well when assessing diagnostics against the training data (i.e. the data generated from a single colony during the guard period of a specific season) (Table 3.2). Distance to colony was always the most important variable (49%-66%) in terms of contributing to the explanation of distribution (Table 3.3). At Bull Roads, depth played a greater importance (23-28%) in model building compared to distance from the coastline (10-16%). At Cow Bay, distance to the coastline was more important (27-35%) than depth (16-20%) (Table 3.3). AUC scores were always above 0.9 and point-biserial correlation was high (0.76-0.84). Similarly, calibration plots showed good fit around the line of best fit (line from (0,0) to (1,1)) (Figure A3.1-A3.4).

Table 3.2: Model extrapolative performance indices; area under the curve (AUC) and point biserial correlation (PB Cor) for distribution models developed from tracks of breeding gentoo penguins at the Falkland Islands. Models were developed from two colonies (CB Cow Bay, BR Bull Roads) during two seasons (2012 = 1213, 2013 = 1314), while birds were guarding chicks. Table should be read from top then across to the left. I.e. the CB1213 model tested on the BR1314 data produced an AUC value of 0.86

AUC	BR1213	BR1314	CB1213	CB1314
BR1213	<b>0.97</b>	0.93	0.77	0.73
BR1314	0.96	<b>0.97</b>	0.86	0.83
CB1213	0.75	0.74	<b>0.99</b>	0.94
CB1314	0.76	0.76	0.94	<b>0.99</b>

PB Cor	BR1213	BR1314	CB1213	CB1314
BR1213	<b>0.8</b>	0.66	0.42	0.34
BR1314	0.72	<b>0.76</b>	0.46	0.37
CB1213	0.38	0.39	<b>0.81</b>	0.56
CB1314	0.37	0.38	0.6	<b>0.84</b>

Table 3.3: Boosted regression tree results and model parameters for the distribution models developed for guard stage gentoo penguins at the Falkland Islands. Models developed from two colonies and include BR Bull Roads and CB Cow Bay during the 2012/13 and 2013/14 breeding season

Model	Parameters (% contribution)			Tree complexity (TC)	Learning rate (LR)	No. of trees
	Dist to col.	Dist. to coast	Depth			
BR1213	54.6	16.6	28.8	3	0.01	2450
BR1314	66.1	10.3	23.6	3	0.01	1050
CB1213	49.1	35.3	15.6	3	0.05	1900
CB1314	52.4	27.7	19.9	3	0.05	1750

Between seasons, the Bull Roads models performed better than the Cow Bay models when comparing the training to the test data (e.g. Bull Roads model from 2012 vs. Bull Roads model from 2013). Season to season for Bull Roads, AUC scores were always above 0.9, while point

biserial correlation was between 0.66 and 0.72 (Table 3.2). Calibration plots indicated well calibrated models. These results are further supported when comparing the predicted distribution to actual distribution of birds at Bull Roads (Appendix Chapter 3, Figure A3.1, A3.2).

The season to season Cow Bay models, although having poorer predictive capacity than the Bull Roads models, still showed fair performance temporally (AUC > 0.9, point biserial correlation 0.56-0.6) (Table 3.2). The Cow Bay 2012 model predicted to the Cow Bay 2013 data was reasonably well calibrated, however, when contrasting models and data were used the calibration plot indicated that the observed prevalence was lower than estimated for the Cow Bay 2013 model. The poorer predictive performance is also evident when comparing predicted distribution versus actual distribution, where one can see that birds tended to forage in an area slightly further north in 2013 (Appendix Chapter 3, Figure A3.3, A3.4).

Spatially, inter-colony model extrapolative ability was poor. AUC values only suggested moderate performance (0.7-0.9) and point-biserial correlation was typically below 0.4 in all cases (Table 3.2). When comparing the 2012 models, calibration plots indicated under-estimation of species prevalence for the Cow Bay model on the Bull Roads data and over estimation vice versa. Similarly, calibration plots from models in 2013 indicated over estimation in both cases (Supplementary material, Figure A3.1-A3.4). This over estimation is clearly evident in predicted distribution extending farther out to sea or for a greater region along the coastline, for the Cow Bay to Bull Roads and Bull Roads to Cow Bay models, respectively (Appendix Chapter 3, Figure A3.1-A3.4).

## **Discussion**

### **General foraging**

My results clearly show that, similar to the other subspecies (e.g, Lescroël & Bost 2005, Wilson 2010, Miller et al. 2010, Kokubun et al. 2010), the northern subspecies of gentoo penguin at the Falkland Islands can also utilise multiple foraging strategies at sea. Birds from the Cow Bay and Bull Roads colonies, which were exposed to gently sloping seabeds, primarily performed benthic dives, whereas, those at Steeple Jason, exposed to a steeply sloping seabed, primarily performed pelagic dives in deeper water. In all cases birds remained foraging in neritic waters; a trait that is highly preserved across the range of all gentoo penguins (Ratcliffe & Trathan 2011). These results confirm the suggested spatial use from the concurrent dietary investigation which occurred at these sites, where Handley et al. (2017) show that birds from each colony tended to feed on specific prey items, most likely as a consequence of local prey availability. The major prey items consumed at the benthic diving sites, Cow Bay and Bull Roads, were small rock cod fish *Patagotothen* spp. and adult lobster krill crustaceans *Munida* spp., respectively. Life history data

for both of these prey items, given their size at consumption, clearly shows that their expected distribution is at or near the sea floor (Zeldis 1985, Laptikhovsky & Arkhipkin 2003, Brickle et al. 2006, Meerhoff et al. 2013). Conversely, at Steeple Jason the main prey item was Falkland herring *Sprattus fuegensis* which is typically found in coastal, pelagic waters, where it schools at or near the surface down to 70m depth (Whitehead et al. 1985).

The alignment between dive behaviour and the vertical distribution of prey has been observed not only for gentoo penguins elsewhere (Miller et al. 2010, Kokubun et al. 2010), but also across many marine taxa (Schreer et al. 2001, Chiaradia et al. 2007, Elliott et al. 2008). Notably, in a study comparing 12 species of pinnipeds and seabirds (Schreer et al. 2001), the percentage of dive type did not appear to be influenced by body size, but rather by water depth and preferred prey. In their study, at those colonies that were surrounded by waters of limited depth, there were a much higher proportion of benthic dives. Comparatively, gentoo penguins in my study had the shallowest dives when birds were in the deepest waters. Therefore, it is not that gentoo penguins perform the deepest dives that physiology and water depth allow. Rather, in shallow waters they target the bottom, whereas in deep water they target shoals in the water column.

Across their breeding range many authors recognise that local bathymetry plays a key role in determining the type of diving strategy adopted by gentoo penguins (Lescroël & Bost 2005, Miller et al. 2010, Kokubun et al. 2010, Carpenter-Kling et al. 2017). This is, perhaps, enhanced by the limited range of these birds during the breeding period. Certainly, for other penguin species such as the little penguin *Eudyptula minor* and yellow eyed penguin *Megadyptes antipodes*, which also forage within a limited range, local bathymetry has also been recognised to play a primary role in determining dive behaviour (Chiaradia et al. 2007, Mattern et al. 2007, Chilvers et al. 2014). This is in contrast to penguin species which forage over a broader range such as the sympatrically breeding congeners at the Antarctic peninsula, the Adélie *Pygoscelis adeliae* and chinstrap *Pygoscelis antarcticus* penguins (Wilson 2010, Miller et al. 2010, Kokubun et al. 2010), and the locally sympatric Magellanic penguin *Spheniscus magellanicus*. For example, when investigating dive behaviour across four colonies along the Argentinian coast, bathymetry played no appreciable role for Magellanic penguins (Sala et al. 2014). Notably though, during the dives in which Magellanic penguins targeted Falkland herring/Feugian sprat they performed the shallowest dives, which accords with the shallow dive behaviour and clupeid-based diet observed at Steeple Jason.

Regarding the restricted range of the birds, the area used at sea by birds at Cow Bay was still four times larger than that at the other two colonies. Comparison with Steeple Jason is probably influenced by the different strategy of diving used by these birds. Furthermore, the data from

Steeple Jason was obtained from incubating birds, a time when birds are not constrained by the need to regularly provision chicks (Barlow & Croxall 2002, Rey et al. 2012, Cottin et al. 2012). As trip duration was similar between the two benthic diving gentoo colonies it is understandable that the birds at Cow Bay would need to travel faster, compared to those at Bull Roads, in order to cover a larger area. The restricted range then between Bull Roads and Cow Bay could be an artefact of reduced intra-specific competition owing to smaller colony size (Lewis et al. 2001) or because of the physical constraints placed on the colony through its position at the head of a bay (Chiaradia et al. 2007). Undoubtedly, the interaction of these two factors could also play a role. Furthermore, Cairns (1989) proposed that seabirds from neighbouring colonies would occupy non-overlapping feeding zones and that colony population size would be a function of the size of these zones. This pattern of segregated feeding and avoidance of intraspecific competition has been observed for gentoo penguins from the New Island colony at the Falklands. Here, gentoo penguins tracked from two colonies only 8 km apart either used entirely separate areas of sea (Masello et al. 2010) or had minimal overlap (Masello et al. 2017). If indeed colony size is a function of the size of feeding zones, my data also support this hypothesis as the surrounding shelf waters extend to great distances at Cow Bay, hence the larger foraging range. Birds at the Cow Bay colony would also be unimpeded in the same way as neighbouring colonies that surround Bull Roads might do. Furthermore, the model proposed by Cairns (1989) supports how such a large gentoo penguin population can occupy Steeple Jason as birds at this colony have nearly no competition from other colonies.

### **Habitat use and realized distribution**

Clearly, gentoo penguins across the Falkland Islands utilise a relatively small range of surrounding ocean within the vicinity of their colonies during the breeding period. Within this range though, birds forage in an opportunistic manner that reflects the surrounding habitat and available prey. This opportunistic nature is supported by the distribution of dive effort per cell being fairly uniform across the foraging area used around each colony. It is also supported by distance to the colony being the predictor variable that explained the most importance in all habitat models. Both of these metrics show that gentoo penguins share potential distribution patterns but differences in habitat availability across the region results in different colonies having variable realized distribution patterns. Following on from this, the associated generalist nature observed for this species probably explains why, despite a robust approach to model development, habitat models showed poor transferability in space.

In reviews of multispecies studies, it was found that the distributions of ecologically specialised species are easier to model than those tolerant to a large variety of environmental conditions.

Furthermore, ecological adaptation by sub-populations can result in different habitat preferences in discrete parts of a species' range (Hernandez et al. 2006, McPherson & Jetz 2007). An additional challenge in habitat distribution modelling for a generalist species, and indeed any species, is obtaining suitable data about the environment (Elith & Leathwick 2009, Franklin 2010). Many habitat modelling studies, with particular emphasis to the marine environment, have focused on species with larger foraging ranges compared to gentoo penguins (e.g, Oppel et al. 2012, Raymond et al. 2015, Torres et al. 2015). In these studies, it is possible to utilise a broader range of available environmental predictor variables owing to a reduced restriction of grain size (i.e. the scale at which a predictor variable is measurable). Also, the increased range used will increase the number of cells over which data is available. Thus, introducing necessary variation to the model, which could enhance model fit.

The added advantage of modelling the distribution of far ranging species is that one might include proximal predictors (direct, e.g., temperature) to a habitat distribution model. My study was limited to the use of mainly distal predictors (indirect, e.g., depth). Although others have used a similar approach (Aarts et al. 2008, Thiebot et al. 2011), extrapolation of models derived from distal predictors can be inherently challenging owing to the combination of these variables possibly not being present in new locations (Elith & Leathwick 2009, Franklin 2010). While this might be also true of proximal predictors at a new location, if one does understand the mechanistic factors limiting distribution, then one could with greater certainty choose to limit where a model is predicted too. Considering the surrounding habitat from the two colonies represented an enclosed bay and an open ocean facing site, this further helps to explain poor transferability of models and why, for example, when the Bull Roads model was transferred to Cow Bay there was a biased prediction for birds to be closer to the coast as oppose to extending their range further out to sea. Beyond the varied habitat structure and a generalist nature of the gentoo penguins, is also the possibility that as a higher trophic level species, biotic factors could play a larger role in determining distribution than abiotic factors, as was the case in a review of 1329 bird species distribution models (McPherson & Jetz 2007).

## **Conclusions**

Having such diverse foraging strategies within a species implies some sub-populations could fare better than others when exposed to differing environmental conditions. However, when comparing the breeding success of birds over five years, gentoo penguins at the South Shetland Islands consistently fledged chicks successfully at similar rates, while over the same period diet composition and diving patterns were variable. Thus, gentoo penguins appear to be successful breeders under a range of conditions (Miller et al. 2009). This appears not only to be the case for

gentoo penguins, but for a variety of seabirds, that forage in contrasting manners (Harding et al. 2013, Sala et al. 2014, Berlincourt & Arnould 2015). From an evolutionary stand point, this helps answer why these birds could be faring so well compared to their specialist congeners. Across their range, including at the Falklands, gentoo penguin population numbers are increasing while the opposite is largely occurring for the Adélie and chinstrap penguins (Miller et al. 2010, Kokubun et al. 2010, Baylis et al. 2013, Borboroglu & Boersma 2013, Hinke et al. 2017b). Indeed, broadly speaking, generalist species appear to be faring better than specialists in the face of global change (Clavel et al. 2011, Le Viol et al. 2012).

In light of varied foraging characteristics for gentoo penguins at the Falkland Islands, it still may present the challenge then as to how one effectively conserves or manages such a species, despite populations currently increasing. At the Falkland Islands, there are limited terrestrial threats. Therefore, future work would benefit from tracking birds during the nonbreeding period and simultaneous tracking of birds residing at neighbouring colonies to determine if the hypothesis proposed by Cairns (1989), of each colony utilizing separate water masses, applies to these birds. This would be particularly useful for colonies in the north-east of the Falklands where there is current exploration for offshore hydrocarbons (Augé et al. 2015). However, the inshore foraging nature of these birds also means that they, fortunately, should receive protection under the umbrella of further ranging species, as has been the case in other marine spatial planning programs (Raymond et al. 2015, Lascelles et al. 2016, Thiers et al. 2016, Hinke et al. 2017a). Finally, an exciting future approach that should also be considered is the use of individual based models which could allow researchers to better understand the multiplicity of factors (for example, prey distribution, predation pressure and inter-specific competition) driving foraging behaviour and distribution at sea (Grimm et al. 2016).

## **Chapter 4 Behaviourally mediated predation avoidance in penguins: the need to account for prey behaviour in marine trophic studies**

**Handley JM**, Thiebault A, Stanworth A, Schutt D, Pistorius P (2017) Behaviourally mediated predation avoidance in penguin prey: the need to account for prey behaviour. (Submitted to Royal Society Open Science)

### **Abstract**

Studies involving the ecology of marine predators, in the absence of direct *in situ* observations, often assume that their diet is reflective of the diversity and relative abundance of their prey. This interpretation ignores species-specific behavioural adaptations in prey that could influence prey capture and vulnerability to predation. Therefore, I use a novel biologging approach to elucidate the factors influencing prey capture by a seabird, the gentoo penguin *Pygoscelis papua*. For the first time, I show that aggressive behavioural defence mechanisms by prey can influence prey capture by a seabird. Furthermore, I provide evidence demonstrating that these birds, which were observed hunting solitarily, target prey when they are most discernible. Specifically, birds targeted prey primarily while ascending and when prey were not tightly clustered. In conclusion, I show that prey behaviour can significantly influence trophic coupling in marine systems and should be accounted for in studies using marine top predators as samplers of mid to lower trophic level species.

**Key words:** animal-borne camera logger, predator-prey interaction, Spheniscids, *Munida* spp.

### **Introduction**

Behavioural interactions between predator and prey are complex, with detailed observation in the field or experimental approaches being required to elucidate factors which influence these interactions. This has resulted in most related studies focusing on either terrestrial systems or species easily manipulated in an *ex situ* context. Furthermore, because of the difficulty in observing predators, studies focusing on predator-prey interactions tend to focus rather on prey, and their response or adaptation to predation (Lima 2002, Quinn & Cresswell 2004). Considering these challenges, studies in the marine realm (e.g., Torres et al. 2008; Carroll et al. 2017) where sampling of higher order predatory species is often logistically and financially difficult, have primarily focused on predator-prey relationships in terms of third-order selection (usage of various habitat components within the home range) (Johnson 1980). Often though, these studies have yielded inconclusive results when relating demographic parameters or distribution, as well dietary composition of predators, to the availability and abundance of prey (Piatt et al. 2007a, Fauchald



2009). This necessitates *in situ* studies which can provide empirical evidence about the actual procurement of food items from those available at that site (fourth-order selection) (Johnson 1980).

There are multiple factors that influence prey selection in terrestrial predators. These relate both to intrinsic factors, including variable energetic requirements associated with self-maintenance and reproduction, and extrinsic factors such as antipredator behaviour employed by prey target species (Krause & Ruxton 2002, Lima 2002, Davies et al. 2012). For marine central place foragers, such as seals and seabirds, there is however limited knowledge regarding how both predator and prey may influence the success of capture or not during an interaction. I address this problem by investigating interactions between gentoo penguins (*Pygoscelis papua*) and their prey. I achieved this with animal-borne camera loggers and a widely applicable, freeware approach, developed during my study; suitable for other point of view studies where predators forage on pelagic prey items.

## Methods

Gentoo penguin foraging behaviour was studied at the Bull Roads (BR) (52.3096° S, 59.3896° W) and Cow Bay (CB) (51.4288° S, 57.8703° W) colonies of the Falkland Islands, each with approximately 1236 and 1821 breeding pairs, respectively (Stanworth 2013). Fieldwork took place during the guard period of chick rearing in December 2013. Thirty-eight birds were equipped with a: CEFAS G5 TDR (CEFAS Technology Ltd, Lowestoft, UK), CatTraQ GPS logger (Catnip Technologies) and custom waterproofed Replay XD 1080 HD camera (Stable Imaging Solutions, LLC, USA). Devices were set to record at 1 second intervals, 1 minute intervals, and 30 frames per second, respectively. The cumulative mass of devices was 172.7g, accounting for an average of 2.7% mass of the instrumented birds.

Devices were deployed on adult birds as they departed towards the sea. Units were secured to the feathers with waterproof adhesive TESA® tape (Beiersdorf AG, GmbH, Hamburg, Germany) on the midline of the birds back. Prior to securing the camera, the device was turned on and a reference time taken from a watch which was synchronized with the GPS time. Cameras could record for up to 90 minutes, limited by battery life. A watch was kept for returning birds exiting the sea until 23h00 daily, so birds could be recaptured before they entered the colony after one foraging trip.

Dive data were processed using the diveMove package (Luque 2007) in R 3.1.2 (R Core Team 2013), while GPS data were processed following steps outlined in Carpenter-Kling et al. (2017). A novel, freeware approach was developed to analyse the video data. Specifically, video was converted from the format .MOV to .AVI using MPEG Streamclip (Version 1.2) to annotate the

footage using the frame based coding option in Solomon Coder (Version 16.06.26). The bird's position and orientation in the water column was coded for, based on physical features (sea surface or sea floor) and light intensity levels. Prey size was estimated by comparing it to the penguin bill size. Merging of data from different devices, and quantification of annotated video files, was done with custom codes in R. Unique behavioural events (still images) were then extracted by frame number, using FFmpeg (Version N-82324-g972b358).

Data were tested for normality and homogeneity of variance using Shapiro-Wilk and Bartlett tests, respectively, prior to the selection of an appropriate parametric or nonparametric test to be used. The probability of a bird attacking a swarm of lobster krill *Munida* spp., one of the most observed prey species (see Results), in relation to the density of the swarm, was assessed using a generalized linear mixed effects model (GLMM, family=binomial, link=logit). Models with and without the fixed effect, were compared using ANOVA tests (Zuur et al. 2009). Lobster krill swarm density was determined by selecting the image which best encompassed a swarm as the bird moved toward it. Using ImageJ (Version 1.46r), images were then converted to a binary pixel image, where background was scored as zero and lobster krill cells as one. A region of interest which encompassed the lobster krill swarm was defined and a proxy of swarm density could be determined based on the percentage cover of pixels scored as one. Data are presented as mean and standard deviation, and significance was assumed at  $p < 0.05$ , unless otherwise stated. Online supplementary material and a step-wise example of software use, along with custom R code and example data files are provided with the submitted manuscript.

## Results

Suitable footage was obtained from 14 and 17 birds at Bull Roads (BR) and Cow Bay (CB), respectively, yielding a total of 35.6 hours of footage while birds were at sea. On average, the first 69 ( $\pm 12.6$ ) minutes of a trip were recorded and all birds, apart from one, were observed attempting to capture prey (APC). At both colonies, birds began foraging soon once at sea and no significant difference was observed between colonies for time to first APC (Mann-Whitney  $U = 139$ ,  $p = 0.28$ , BR 20.8 minutes [7.6-35.4], CB 18.2 minutes [1.8-32.0], median [range]). Similarly, for those birds which had valid GPS data (Figure 4.1) ( $n_{BR} = 13$ ,  $n_{CB} = 9$ ), no significant difference was observed for distance to first APC (Mann-Whitney  $U = 57$ ,  $p = 0.75$ , BR 1454m [595-1695], CB 1248m [184-2767], median[range]).

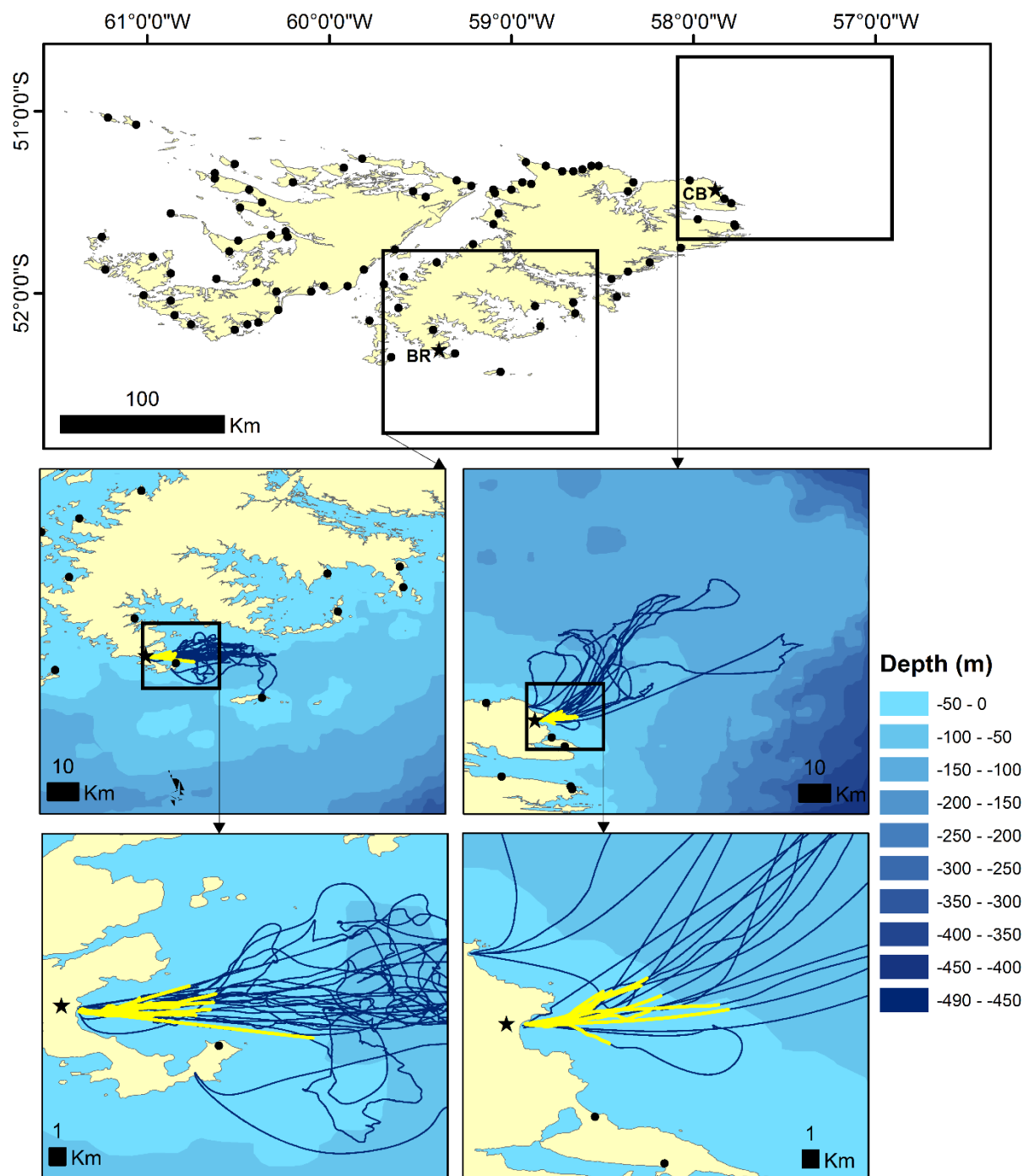


Figure 4.1: Gentoo penguin colonies (black dots) of the Falkland Islands (top panel), including the two study colonies (stars), BR Bull Roads and CB Cow Bay. Tracks ( $n_{BR} = 13$ ,  $n_{CB} = 9$ ) in blue (middle and bottom panel) indicate foraging paths of instrumented birds, while yellow overlays indicate period of time while cameras were recording

A total of 1932 APC's were identified from the definitive striking movement of a bird's head (YouTube: Handley PhD Video 1 shows examples of each type). These APC's were on lobster-krill *Munida* spp. (n = 599), small fish (n = 375, likely juvenile rock cod, either *Patagonotothen tessellata* or *Patagonotothen ramsayi*, <30-40mm standard length, Figure 4.2), larger fish (n = 4, unidentified, > 70mm standard length) and adult squid species (n = 4, likely Patagonian squid *Doryteuthis gahi*). In addition to those APC's where prey were visible, there were also 88 events on unidentifiable items (item 1, n= 27; item 2, n= 51) and 872 events where birds showed the characteristic head striking movement but no prey item could be observed. It is probable that the majority of these 872 events were also APC's for small fish or possibly, but less likely, the amphipod, *Themisto gaudichaudii*, based on previous dietary studies in the region (Handley et al. 2016, 2017) and the similar characteristic in head strike movement.



Figure 4.2: The moment before a gentoo penguin strikes a small fish with an upward strike of its head. The silhouette of the small fish aided in its likely identification as a rock cod, either *Patagonotothen tessellata* or *Patagonotothen ramsayi*, based on expert opinion (P. Brickle, pers. comm.), and the known biology of fish in this genus at the Falkland Islands (Brickle et al. 2006). Also, the known diet of these birds during my study (Handley et al. 2016, 2017)

Regarding the two main prey items, lobster krill and small fish, birds did not appear to pursue either of these prey species. Rather, birds swam in a uniform fashion using quick strikes of the head to capture prey which were present within the trajectory of the bird. When birds clearly missed these prey items (n = 109), they did not appear to deviate from their course and continued swimming uniformly. This contrasted with the eight larger squid and fish, where it was clear that birds pursued prey. Based on the orientation of the birds, nearly no APC's occurred while descending. Instead, they primarily fed while ascending, followed nearly equally by feeding in the water column where orientation was unclear (pelagic foraging) or with upward strikes of the head while foraging along the sea floor (Table 4.1). Furthermore, for the lobster krill, there were relatively few APC's while foraging along the seafloor (n = 9), despite clear evidence in 64

separate events where lobster krill was present on the seafloor (WebVideo 1). Rather, APC's on lobster krill occurred primarily while birds were ascending or foraging pelagically (Table 4.1).

Table 4.1: Orientation of gentoo penguins while feeding on all prey and the two main prey types observed, lobster krill *Munida* spp. and small fish (likely *Patagonothen* spp.). Total number of observations and percentage are shown

Orientation	All (%)	Lobster krill (%)	Small fish (%)
Surface (stationary)	0 (0)	0 (0)	0 (0)
Surface (swimming below)	1 (0.1)	0 (0)	0 (0)
Descend	26 (1.3)	5 (0.8)	5 (1.3)
Seafloor (Head down)	65 (3.4)	9 (1.5)	4 (1.1)
Seafloor (Head up)	479 (24.8)	4 (0.7)	107 (28.5)
Pelagic	525 (27.2)	182 (30.4)	86 (22.9)
Ascend	836 (43.3)	399 (66.6)	173 (46.1)
<b>Total</b>	1932 (100)	599 (100)	375 (100)

There were 29 events, involving 10 different birds, where it was observed that lobster krill could avoid capture by defending themselves (Figure 4.3, You Tube: Handley PhD Video 2). Furthermore, footage by five birds from Bull Roads showed them encountering lobster-krill swarms ( $n = 44$ ) during their foraging trip. For 16 of these swarms, birds headed towards them and fed from the periphery. However, for the other 28 swarms, birds headed towards them but did not feed from them at all (You Tube: Handley PhD Video 3). Using a proxy for swarm density (Figure 4.4), the probability of attack increased significantly as swarm density decreased (McFadden  $R^2 = 0.39$ ,  $Z_{42} = -2.9$ ,  $p = 0.004$ ), with birds more likely to feed on swarms where density was below 75% (Figure 4.4).

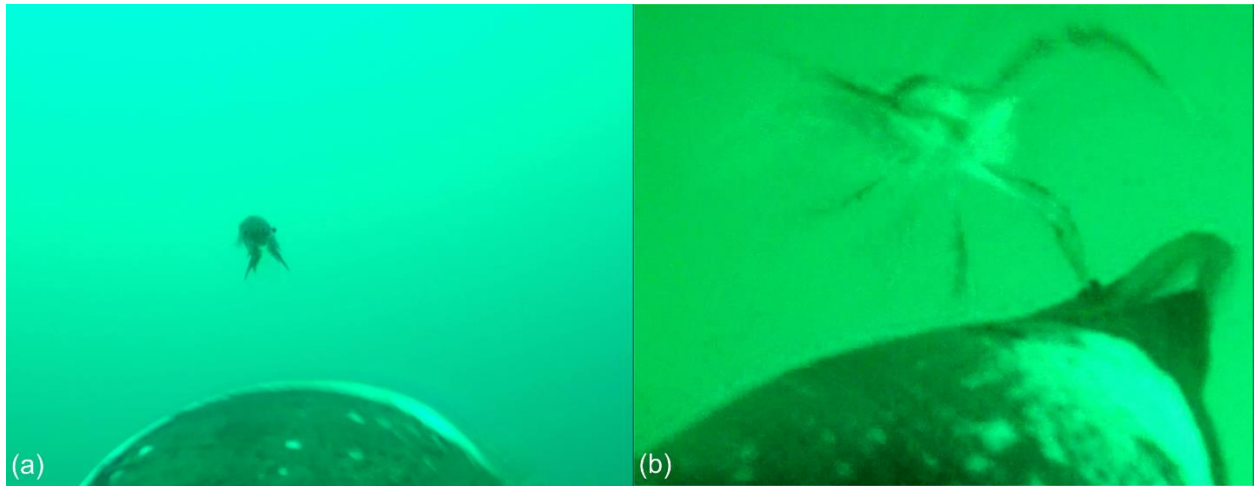


Figure 4.3: Lobster krill *Munida* spp. (a) assumes defensive position, with pincers open, as bird heads toward it. And, (b) lobster krill is attacking bird with its pincers (attached to the side of the penguin beak) during an attempted prey capture (APC). In both instances, birds were unsuccessful in capturing prey

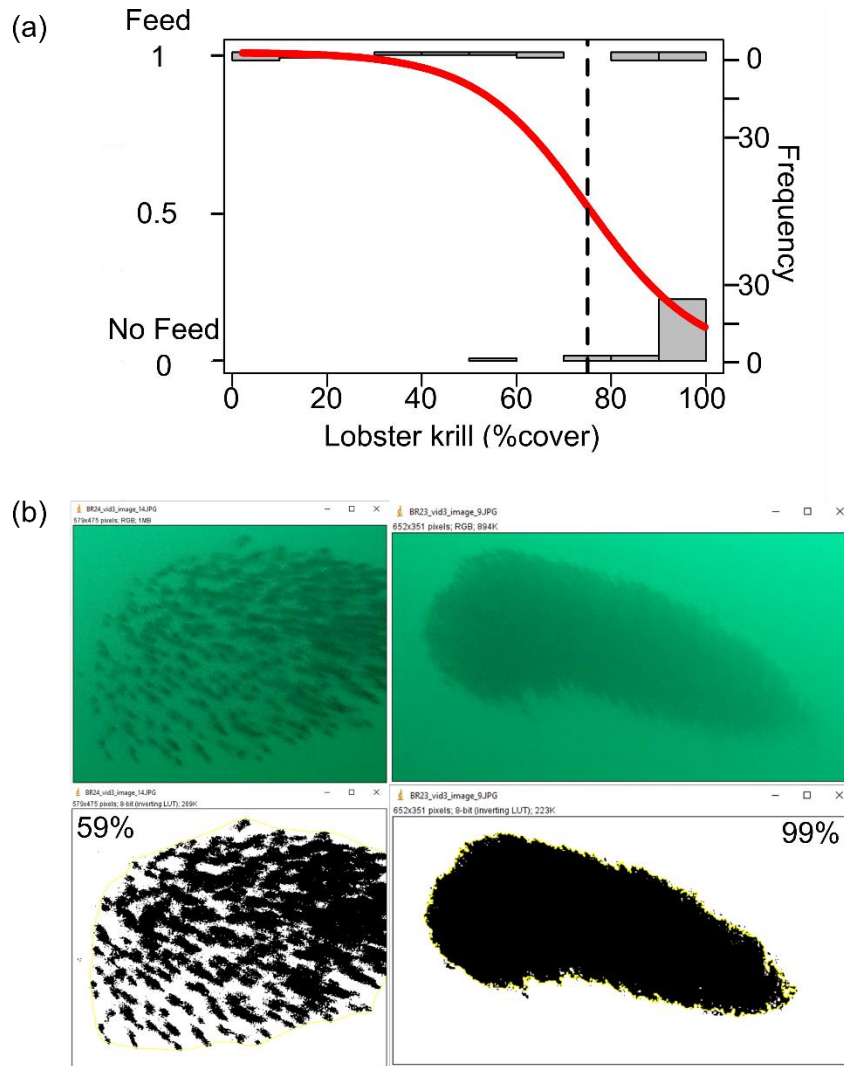


Figure 4.4: (a) Probability of gentoo penguin attack on differing swarm density of lobster krill with, (b) example images highlighting percentage cover and pixel conversion (using ImageJ) of swarms in order to generate a proxy for swarm density. Grey bars in panel (a) represent 10% interval bins, the red line is the fitted function of a logistic regression model and the dashed line indicates percentage cover where probability of attack = 0.5

There was no evidence of cooperative feeding, and birds from both colonies had negligible interactions (percentage of trip time), with both conspecifics (BR = 0.43%[0.86], CB = 3.66%[0.86]) and other penguin species (BR = 0%[0], CB = 0.13%[0.17]).

## Discussion

I provide the first evidence of a reduction in foraging success for a marine central place forager attributable to multi antipredator tactics incorporated by prey. These include active defence, as well as group formation, both of which influenced foraging success. These antipredator tactics reinforce the concern for marine top predator studies assuming a direct relationship between

relative prey availability and dietary composition (Piatt et al. 2007a, Durant et al. 2009). Clearly, as has often been recognised in terrestrial systems (e.g., Grant et al. 2005; Rajaratnam et al. 2007), the context in which prey and predator find themselves must be considered. The increasing use of animal-borne camera loggers on a growing number of species, in both terrestrial (e.g., Rutz and Troschianko 2013) and marine systems (e.g., Sutton et al. 2015), is clearly revealing new insights regarding predator-prey interactions that have often been over simplified in the past.

The active defence observed by lobster krill means that birds must consider the tradeoff between the short-term gain in energy versus the possible long-term reduction in foraging efficiency should the bird become injured. For many species (see, Mukherjee and Heithaus 2013), where individuals have sustained sub-lethal injuries from prey, these individuals are often limited to catch sub-optimal prey with the net-effect being reduced fitness. Clearly, the method used by gentoo penguins to capture lobster krill and most prey, which involves attacking individual items from below, helps to minimize handling time and capture prey individuals before they can orientate themselves into a defensive position. This might further explain why birds seldom attacked lobster krill on the seafloor. These individuals are likely able to defend themselves better given their orientation, and also size, as larger adults typically aggregate on the seabed (Zeldis 1985).

The aggregation of lobster krill into swarms clearly had an impact on whether gentoo penguins captured these prey items or not. Prey which aggregate can reduce susceptibility to predation through attack dilution, increased overall vigilance, communal defence and predator confusion (Krause & Ruxton 2002, Davies et al. 2012). Disentangling which one, or combination, of these mechanisms is driving swarming behaviour in lobster krill is challenging. However, the fact that birds favoured individuals on the periphery and in less dense swarms, lends support to these predators being influenced by the confusion effect whereby it may be harder to single out prey items when they are tightly packed presenting a greater visual barrier (Flynn & Ritz 1999, Jeschke & Tollrian 2007).

To overcome prey defensive ability and increase the chance of singling out prey in a school, or swarm, predators often utilise a cooperative hunting strategy (Packer & Ruttan 1988, Krause & Ruxton 2002, Davies et al. 2012). This was not the case for the gentoo penguins. Across the Spheniscids, evidence suggests that birds may forage individually or cooperatively (Takahashi et al. 2004, 2008, Berlincourt & Arnould 2014). However, even for species that show cooperative foraging, they may still be more successful when targeting aggregating prey alone (Sutton et al. 2015). This appears to be in contrast to a situation where multispecies assemblages attacking grouped prey, increased the feeding success of each individual (Thiebault et al. 2016b). These studies, however, were not able to consider prey defensive ability. Therefore, my study reinforces



that prey ability to avoid predation must be considered when exploring broader facets relating to predator-prey dynamics (Piatt et al. 2007a, Durant et al. 2009, Fauchald 2009).

Notably, birds did not deviate from their general swimming direction when they missed lobster krill or small fish, but actively chased after the eight larger prey items. This is in line with optimal foraging theory (Emlen 1966, Macarthur & Pianka 1966), as it appears penguins are more likely to exert a greater amount of energy, by pursuing prey, when the returns would be higher. Ultimately, this behaviour, and those discussed above, imply that birds are cognitively aware of the consequences presented by each prey type. It is also not unreasonable to assume that gentoo penguins may be aware of potential prey availability within their home range when one considers the 'predator pass-along effect' (Lima 2002). This mechanism suggests that a predator might spread the risk over many hunting sites to manage prey behaviour, ultimately benefiting its long-term energy intake.

The implications of my study are that consideration must be given to the mechanisms through which predator and prey interact, and that caution must be taken against over simplifying trophic studies involving marine top predators (Johnson 1980). By not doing so, we may arrive at naïve conclusions when relating demographic parameters or distribution, as well as dietary composition of predators, to the availability and abundance of prey (Piatt et al. 2007a, Durant et al. 2009, Fauchald 2009).

## Chapter 5 Use of machine learning to identify *in-situ* feeding events by two penguin species

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### Abstract

Identifying feeding events by predators is important for investigating both pure and applied questions in animal ecology. However, for diving marine predators, observing feeding events at sea has traditionally been impossible, necessitating the use of coarse proxies of prey encounter. Advances in biologging technology, including miniaturization of devices, provide an opportunity to overcome these barriers and give unprecedented insight into the feeding ecology of marine predators in the wild. In my study, I used animal-borne camera loggers to link fine-scale prey encounter events (PEEs) to back mounted triaxial accelerometer signals, in two species of marine predators: the gentoo penguin (*Pygoscelis papua*) and little penguin (*Eudyptula minor*). Using support vector machines (SVM) - a powerful supervised machine learning technique - I aimed to assess the feasibility of this approach and develop species-specific models capable of distinguishing PEEs in penguins from background swimming behaviours. I observed gentoo and little penguins to primarily target juvenile fish and lobster krill (*Munida* spp.), and small pelagic fish, respectively. Therefore, I developed a two-class model (PEE vs. swimming) for both species and a three-class model (PEE juvenile fish vs. PEE lobster krill vs. swimming) for gentoo penguins. Two-class models had a sensitivity for PEE's of 72.3% and 87.8% for gentoo and little penguins, respectively. The three-class model for gentoo penguins showed that it is feasible to distinguish between prey types using my approach, although sensitivity was lower for juvenile fish which were captured in a passive manner compared to lobster krill. I discuss avenues for future research and applications of these models, and will provide the necessary R code with which to develop a two-class and multi-class SVM classifier.

**Key words:** Spheniscidae, foraging ecology, seabird, acceleration, video

### Introduction

Understanding where, when and how much food animals consume is fundamental to the study of animal ecology. In the marine environment, identifying these feeding events by wild animals is a particularly vexing challenge, owing to the difficulties in observing organisms underwater. However, identifying these events will enhance our ability to distinguish important feeding areas (Weimerskirch et al. 2007, Sommerfeld et al. 2013), recognise which environmental variables

might be driving distribution of some study species (Doniol-Valcroze et al. 2012) and determine the extent to which the behaviour of organisms align with optimal foraging theory (Heaslip et al. 2014, Watanabe et al. 2014, Foo et al. 2016), among others (Pelletier et al. 2014). Therefore, there is an important need to develop suitable methods that can be applied to accurately identify feeding events in a broad array of typically unobservable marine predators while they forage at sea.

There have been various approaches for identifying feeding events by marine predators in the past. These include, for example; the use of oesophageal and stomach temperature loggers capable of recording a drop in internal temperature as prey is presumably consumed (Ancel et al. 1997, Bost et al. 2007); a Hall sensor-magnet system, capable of identifying subtle changes in the inter-mandibular angle due to jaw movement (Wilson et al. 2002, Liebsch et al. 2007); changes in the profile of the vertical cross section of a dive, such as wiggles, as determined through time-depth recorders (Halsey et al. 2007, Hanuise et al. 2010); looking at peaks in signals from accelerometer devices, thought to be indicative of prey pursuit (Ropert-Coudert et al. 2006, Zimmer et al. 2011) or head movement toward prey has also been used (Gallon et al. 2012, Foo et al. 2016). Most recently, the use of a dual accelerometry approach where concurrent placement of an accelerometer on the head and body of a predator allowed the researchers to determine peaks in the accelerometer signal associated with prey, through validation by an animal-borne camera logger (Watanabe & Takahashi 2013).

Many of these methods of identifying feeding events have provided remarkable insight into the feeding behaviours of marine predators. However, not all are readily applicable to any species, and some (e.g., oesophageal, Hall-sensor) are more invasive, and necessitate considerable handling time of the animal to both deploy and retrieve the device. Furthermore, in many instances the identification of feeding events is speculative, without observations in an *in-situ* context. This is a critical step, as it is only with visual verification that one can validate a technique for assessing prey capture (Hanuise et al. 2010). Even with visual verification, however, a method may only be context dependent. This was the case for the threshold based measurement from accelerometer signals, used to identify feeding events by Adélie penguins (*Pygoscelis adeliae*) (Watanabe & Takahashi 2013). Their method worked well for birds that were foraging pelagically, however for those foraging along the seafloor there were a high number of false positives as birds moved their head in search of prey. Therefore, there is still much scope to refine methods and make them minimally invasive so they can be applied to a suite of marine predators for identifying feeding events across a broad range of contexts.

Of the methods mentioned above, accelerometers are proving to be one of the most valuable tools through which feeding behaviours by marine predators can be distinguished (e.g., Kokubun *et al.* 2011; Gallon *et al.* 2013; Ydesen *et al.* 2014; Volpov *et al.* 2015; Foo *et al.* 2016). This is because these devices are minimally invasive and have the capacity to provide high frequency data detailing the specific movement patterns of an organism (Brown *et al.* 2013). However, movement patterns in the accelerometer signal relating to specific behaviours of interest first need to be identified. This identification will then facilitate the automated development of behaviour classification in the absence of direct observations (Bidder *et al.* 2014, Hammond *et al.* 2016, Fehlmann *et al.* 2017, Sur *et al.* 2017). This can be achieved by coupling an accelerometer with an animal-borne camera logger that provides the opportunity for objective classification of behaviours (Watanabe & Takahashi 2013, Volpov *et al.* 2015). As the recording capacity of animal-borne camera loggers is greatly reduced compared to the accelerometers, the initial classification of a movement pattern in the accelerometer signal allows for further identification of feeding events in the signal beyond the recording period of the camera.

A growing body of research is now focusing on the optimal way to link the observed movement patterns in accelerometer data to specific events (Nathan *et al.* 2012, Bidder *et al.* 2014, Resheff *et al.* 2014, Sur *et al.* 2017). This typically involves the use of a machine learning algorithm (James *et al.* 2013). These are powerful tools that assume that the data-generating process is complex and unknown, and so try to learn the response (e.g. the movement pattern of an animal when it is feeding) by observing inputs (e.g. accelerometer data) and finding dominant patterns (Elith *et al.* 2008). The advantage of this approach over previous studies which have typically used peaks from a single axis of the accelerometer data to identify feeding events (Ropert-Coudert *et al.* 2006, Zimmer *et al.* 2011, Tanoue *et al.* 2012, Watanabe & Takahashi 2013, Watanabe *et al.* 2014, Volpov *et al.* 2015, Foo *et al.* 2016), is that a machine learning algorithm can readily incorporate data from all three axes typically enabled in an accelerometer. In this way, they can account for varied behaviour that may not be reflected by a peak in acceleration data owing to varied patterns of movement in a single dimension (Viviant *et al.* 2010, Kikuchi *et al.* 2014). While a suite of algorithms exist, the support vector machine (SVM) is one algorithm which has been shown to have good predictive ability (Nathan *et al.* 2012, Resheff *et al.* 2014, Hammond *et al.* 2016, Ladds *et al.* 2016). However, the use of this machine learning approach for identifying feeding behaviours by marine predators has to date only been developed in a captive setting, where the range of feeding behaviours and prey items may not represent the full suite of behaviours exhibited by the species in the wild (Carroll *et al.* 2014, Ladds *et al.* 2016).

Penguins (Spheniscidae) face a multiplicity of threats in the Anthropocene, including changes to prey availability and distribution (Trathan *et al.* 2014). There is therefore a growing need to identify

feeding events by these species in the wild. The gentoo penguin (*Pygoscelis papua*) and little penguin (*Eudyptula minor*) are well suited species for the development of an approach using accelerometers on wild birds, where signals can be verified through animal-borne camera loggers. This is because compared to the other penguin species, these two are relatively accessible, are both listed as Least Concern on the IUCN Red List and during the breeding period have relatively short trips compared to other species that are deep diving and/or have wider foraging ranges (Borboroglu & Boersma 2013). These features of the two species increase the likelihood of feeding behaviours being recorded while a bird is carrying an animal-borne camera logger that is only capable of recording for a small portion of the entire foraging trip. Furthermore, it is only through the recent miniaturisation of cameras that *in-situ* insight into the feeding behaviour of these birds is now possible (Handley & Pistorius 2015, Sutton et al. 2015).

Both the gentoo and little penguins are considered generalist predators and their diet can vary considerably across colonies and between seasons, likely affected by local prey availability (Cullen et al. 1992, Lescroël et al. 2004, Shaw 2009, Handley et al. 2017). In the context of my study, where I deployed instruments on gentoo penguins at the Falkland Islands, they typically feed on lobster krill crustaceans (*Munida* spp.) and rock cod fish (*Patagontochen* spp.) (Handley et al. 2016, 2017). Little penguins in south-east Australia, typically feed on small mid-water shoaling fish (e.g. Clupeiformes) (Sutton et al. 2015). Gentoo penguins are approximately five times heavier than little penguins and have a stroke frequency - which is not related to swimming speed but rather inversely to body mass - of nearly half (Clark & Bemis 1979, Sato et al. 2007).

An SVM algorithm has been developed that can successfully identify feeding events by captive little penguins (Carroll et al. 2014). There is now a need to test and develop a similar approach for wild penguins. Using different species with varied diet and swimming kinematics will further reveal the applicability of such an approach over varied contexts. Therefore, I investigated the feasibility of using back mounted accelerometers to identify prey encounter events (PEEs) in wild penguins, by validating signals from accelerometers with footage derived from animal-borne camera loggers. I define a PEE as any event where a bird actively attempts to capture a prey item. I hypothesise that attempts to capture prey will cause the birds to sufficiently alter their swimming kinematics and therefore, should produce a contrasting signature to the general swimming pattern in the accelerometer data. Using a supervised classification approach and a machine learning algorithm, the SVM, should allow for the development of an automated classifier to distinguish between swimming and PEEs. The approach used in my study will serve as a model for other penguin species, and will also be widely applicable to many marine taxa for which body size constraints warrant deployment of only a single accelerometer on the animal.

## Methods

### Data collection

Adult gentoo and little penguins were sampled from two colonies at the Falkland Islands and Australia, during the December 2013 chick-guard period, and between October and January during the 2014/15 and 2015/16 breeding seasons, respectively. The colonies for gentoo penguins were Bull Roads (52.3096° S, 59.3896° W) and Cow Bay (51.4288° S, 57.8703° W). Little penguins were sampled at London Bridge (38.62° S, 142.93° E) and Gabo Island (37.56° S, 149.91° E).

Birds from both species were fitted with an animal-borne camera logger, GPS, and either a separate time-depth recorder (TDR) and triaxial accelerometer or dual functioning device (Table 5.1 outlines device details and sampling frequency), during ongoing studies examining their foraging ecologies (e.g., Handley and Pistorius 2015b; Sutton *et al.* 2015; Handley *et al.* 2017). Devices were attached along the midline of the back using TESA® tape (Beiersdorf, AG, GmbH, Hamburg, Germany), which limits damage to feathers on retrieval, with the ends of the tape secured by cyanoacrylate glue (Loctite 401®). Devices were orientated so that the camera filmed the birds head, followed by either the accelerometer with GPS device above and then TDR unit (gentoo penguins), or followed by the GPS then dual TDR and accelerometer (little penguins). Accelerometers were orientated to record surging (x-axis, anterior-posterior), swaying (y-axis, lateral) and heaving (z-axis, dorso-ventral). The combined weight of devices deployed on each species was 186.7g and 51.5g which accounted for  $\approx 3.10\%$  and  $3.99\%$  of an adult bird's body mass for gentoo penguins ( $6.03 \pm 0.6\text{kg}$ , mean  $\pm$  sd) and little penguins ( $1.29 \pm 0.20\text{kg}$ , mean  $\pm$  sd), respectively. Devices were  $\approx 6\%$  and  $1\%$  of each species body cross-sectional surface area.

For both species, birds were only instrumented for a single foraging trip. The cameras used on gentoo penguins did not have the option for a delayed start, therefore devices were deployed on birds as they were heading toward the sea. Devices were recovered from gentoo penguins on return from a foraging trip before they reached the colony, in order to minimize disturbance. For the little penguins, cameras recorded on a duty cycle of varied length and had a delayed start. Deployment and retrieval of devices was done when birds had returned to their burrow. The cameras used on the gentoo and little penguins were estimated to be able to record for two and three hours, respectively. Prior to each deployment, a corresponding reference time was recorded with the camera, which would later allow us to timestamp each row of annotated camera data.

Table 5.1: Details of sampling frequency and devices used on the two species of penguin sampled during my study

Species	Device	Sampling frequency	Dimensions	Manufacturer
Gentoo penguin ( <i>Pygoscelis papua</i> )	Camera: Replay XD 1080 HD	25-29.97 fps	110 x 35mm, 148g	Stable Imaging Solutions
	Accelerometer: X8m-3	25 Hz	54 x 32 x 16mm, 14g	Gulf Coast Data Concepts
	TDR: CEFAS G5	1 Hz	31 x 8mm, 2.7g	Cefas Technology Ltd
	GPS: CatTraQ	1 minute	44 x 27 x 13mm, 22g	Catnip Technologies
Little penguin ( <i>Eudyptula minor</i> )	Camera: CatCam	30 fps	25 x 45 x 15mm, 24g	Catnip Technologies
	Accelerometer: AXY-Depth	25 Hz	12 x 31 x 11mm, 7.5g	TechnoSmart
	TDR: AXY-Depth	1 Hz	12 x 31 x 11mm, 7.5g	TechnoSmart
	GPS: i-gotU GT-120	1 minute	44.5 x 28.5 x 13mm, 20g	Mobile Action Technology

## **Data processing**

An overview of the data processing and analysis steps is presented in figure 5.1. Each of the four data sources requires pre-processing, prior to interpretation and analysis. Video files were converted from the format .MOV to .AVI using MPEG Streamclip (Version 1.2), to annotate the footage using the frame based coding option in Solomon Coder (Version 16.06.26). Segments of video files were then merged using custom code in R. I developed ethograms which included bird's orientation, swimming behaviour and prey encounter events. Orientation was determined based on the bird's position in the water column with respect to physical features (sea surface or sea floor) and light intensity levels. For prey encounter events, it was not always feasible to identify definitively if prey were consumed or not. Therefore, I recorded these events as the moment a bird actively raised its head toward the prey item until the moment its head returned to a neutral position after the bird may have either been successful in capturing the item or not.

Raw accelerometer data was processed with the software CoarseTimeConverter (Version 3.0) and custom code in R. This allowed for data to be timestamped, the subsequent merging of batches of files and for converting the raw accelerometer data from each axis into units of acceleration (g). TDR data were processed using the diveMove package (Luque 2007).

Data from all devices was interpolated to the same sampling frequency as that of the accelerometers (25 Hz) using the 'interp1' function in the signal package (Signal Developers 2013). Discrepancies in the internal timers of each device caused clock drift and required us to align behaviours represented by each data source. I did this through manual inspection and correction of the data, using IGOR Pro (WaveMetrics, Inc.) with the Ethographer extension. Specifically, I converted the surge acceleration data to pitch ( $^{\circ}$ ), and then used changes in this signal to first match the TDR data at the onset of the dive, and then match the camera data using the change in bird's orientation as it began the descent of a dive.

## **Data analysis**

All data analyses were conducted in R 3.1.2 (R Core Team 2013) and data are presented as means with standard error unless otherwise stated.

I first determined the overall number of PEEs for each species. As the focus of my study was to determine whether it was possible to distinguish PEEs from all other swimming behaviour (i.e. searching for prey or commuting behaviour), I removed portions of the deployments that related to types of PEEs for which too few observations were recorded. Thus, I was left with sufficient observations to build both a two and three class model for gentoo penguins, and a two-class model for little penguins (see Results). I also removed all data above 1m depth to



reduce noise in the acceleration data associated with surface swimming and periods while birds were stationary on the surface. This removal of surface data also helped reduce the influence of the swimming class observations vs. the much fewer PEE observation classes, facilitating the development of a suitably predictive machine learning algorithm.

Similarly to Carroll et al. (2014), I did not pre-segment data into single behaviours. By not pre-segmenting data, this supports model development where the intention is for use on unclassified data derived from wild animals. Rather, I calculated 22 summary statistics from the accelerometer data using an 11-point rolling window (0.44s). Using an odd numbered rolling window size means the mode of a behavioural state could always be determined without bias to one state or the other. The window length was determined by examining histograms of the duration for a PEE (Figure 5.2), and accounting for the fact that sampling frequency in signal processing should be at least twice the frequency of the most rapid body movement essential to characterize a behavioural mode (Nathan et al. 2012, Brown et al. 2013). For each axis I calculated the mean, standard deviation, minimum, maximum, skewness and kurtosis. Furthermore, I calculated pairwise correlations between the three axes and also, overall dynamic body acceleration (Wilson et al. 2006).

I used a support vector machine algorithm (described in Carroll et al. (2014)), with the R package `e1071` (Meyer et al. 2015), to develop the following models: (1,2) a two-class classification model for each species and (3) a three-class classification model for gentoo penguins. As support vector machines were designed for binary classification problems, I used the default one-versus-one approach for the three-class model. Data were scaled to avoid attributes in greater numeric ranges dominating those in smaller numeric ranges.

Model development for an SVM requires the choice of a specific kernel and its optimum tuning parameters (Meyer 2001). To do this, I used 10-fold cross validation with data being split into a 70:30 (train:test) ratio, for each fold. As an SVM can be computationally expensive (Bennett & Campbell 2000, Meyer 2001), I did this with an iterative approach by first selecting the optimal kernel, then parameters specific to that kernel by using a grid search over all tuning parameters with the function `'tune'` (package: `e1071`). In the final model-fitting procedure I used the `'class.weights'` option in the `'svm'` function in order to use all data and avoid possibly over proportional influence of bigger classes (i.e., the many swimming vs. the fewer PEE observations) on the separating margin (Meyer 2001).

I assessed each stage of model development, and the performance of the overall model, by looking at three metrics. 1) Accuracy: the proportion of total classifications correctly made. Importantly, accuracy can give a biased indication of how well a model performs, particularly when there are unequal observations for each class as was the case for my data. 2) Sensitivity

(True positive rate): when a class is actually observed, how often is it predicted to be observed. Thus, sensitivity is a good indicator of the model's predictive performance for a given class. 3) False positive rate: The proportion of times that the model misclassifies a point as a particular class when it should be of another class.

Similar to chapter 4, example R code and data will be provided as online supplementary material once this chapter is submitted for publication.

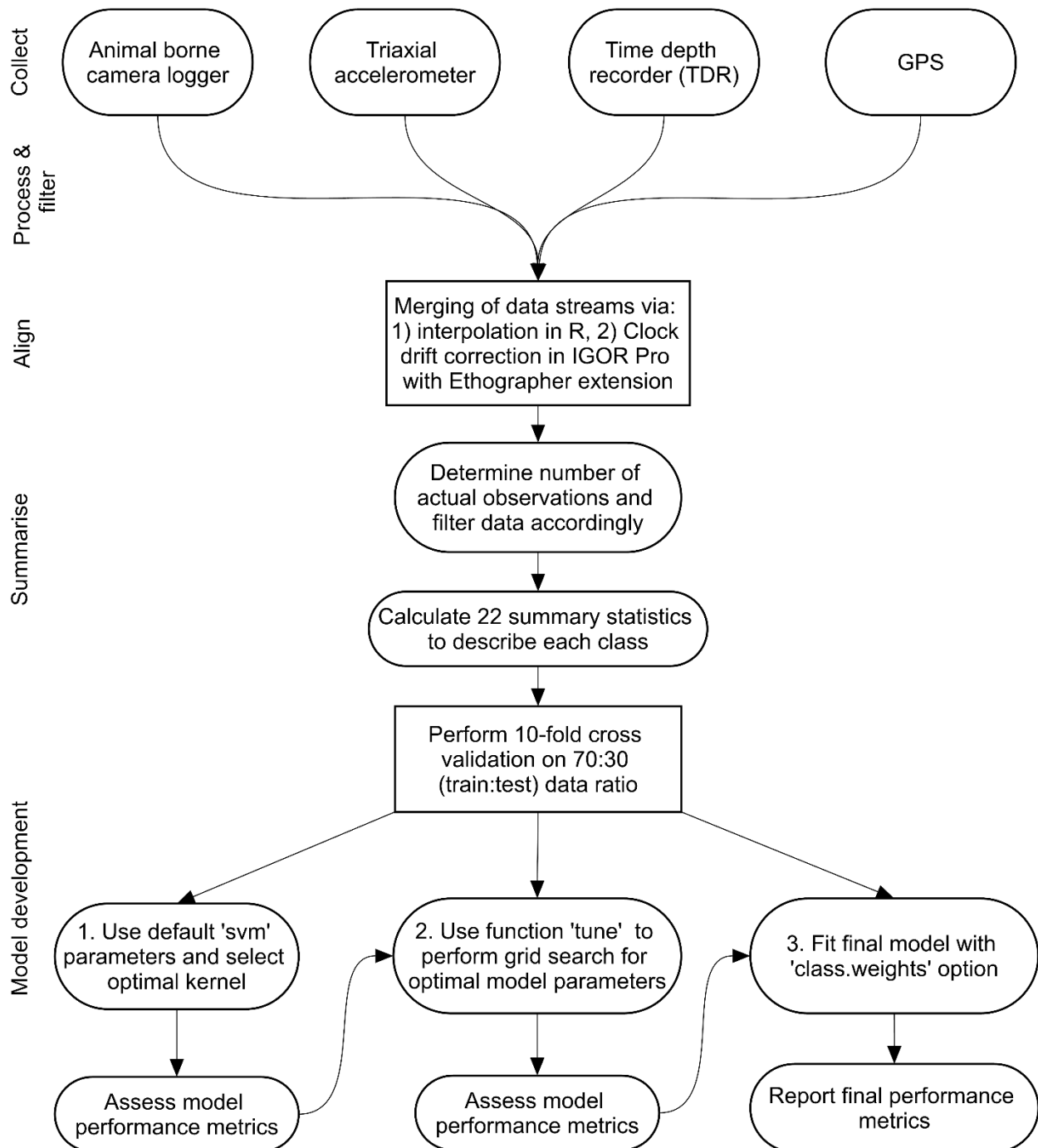


Figure 5.1: Overview of the steps required to develop a classification algorithm for identifying prey interactions by penguins as oppose to swimming, using a support vector machine

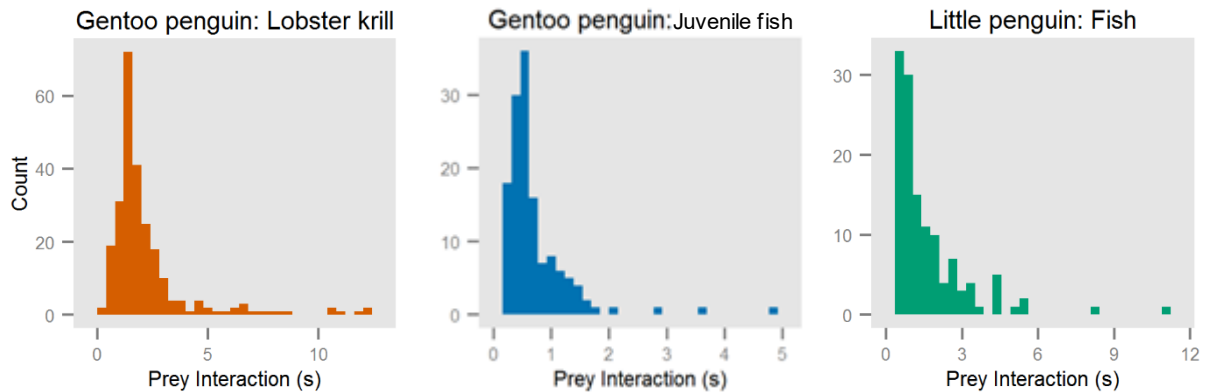


Figure 5.2: Frequency histograms denoting the duration (s) that prey encounter events lasted, for gentoo penguins attempting to feed on lobster krill and juvenile fish, and little penguins attempting to feed on fish

## Results

### Video observations

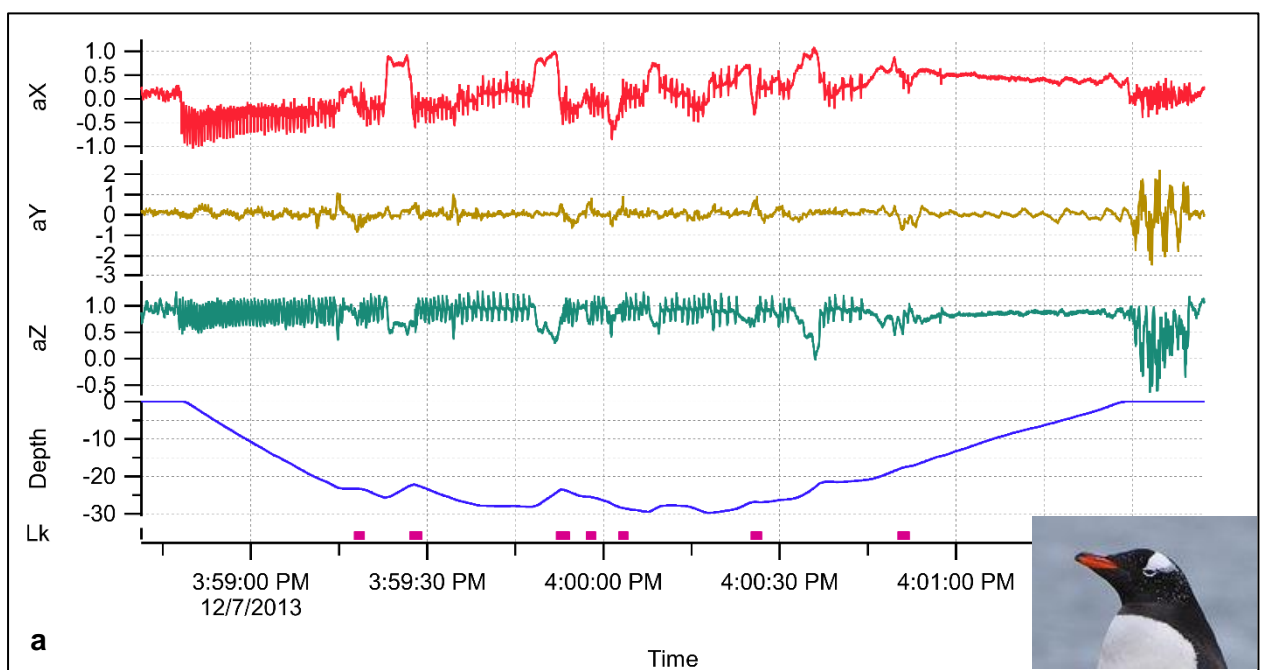
I obtained video footage and corresponding accelerometry data from six gentoo penguins at Bull Roads ( $n = 5$ ) and Cow Bay ( $n = 1$ ), and from five little penguins at London Bridge ( $n = 2$ ) and Gabo Island ( $n = 3$ ). From these, I annotated a total of 417 minutes and 189 minutes of footage at sea for gentoo and little penguins, respectively.

Please see: You Tube channel, “Handley PhD”, and search for, “Handley PhD Video 4”, for example video files.

For gentoo penguins, I identified 387 PEEs which comprised lobster krill *Munida* spp. ( $n = 250$ , Figure 5.3a) and juvenile fish ( $n = 137$ , Figure 5.3b), while for little penguins I identified 128 PEEs on fish (Figure 5.3c). Figure 5.4 shows typical accelerometry profiles of gentoo penguins encountering lobster krill (Figure 5.4a) and juvenile fish (Figure 5.4b), and little penguins encountering fish (Figure 5.4c). For both prey types targeted by gentoo penguins, there was little evidence of prey pursuit in the video footage. Rather, birds appeared to continue swimming in a uniform fashion with quick strikes of the head toward the prey. In some instances, there was no pause between strikes of the head for juvenile fish as birds appeared to rapidly target individual prey items. From the footage, it was evident that little penguins pursued the comparatively larger and more mobile fish prey.



Figure 5.3: Exemplar still images of the moment before striking at a (a) lobster krill and (b) juvenile fish by gentoo penguins, and at a (c) fish by a little penguin



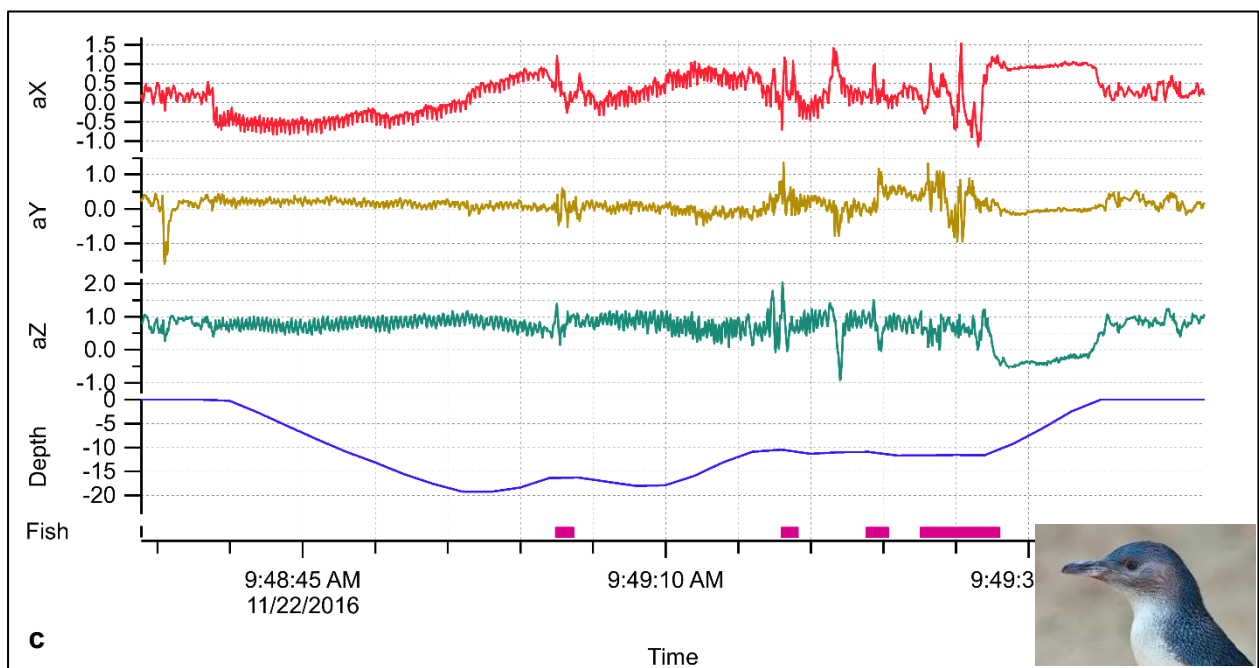
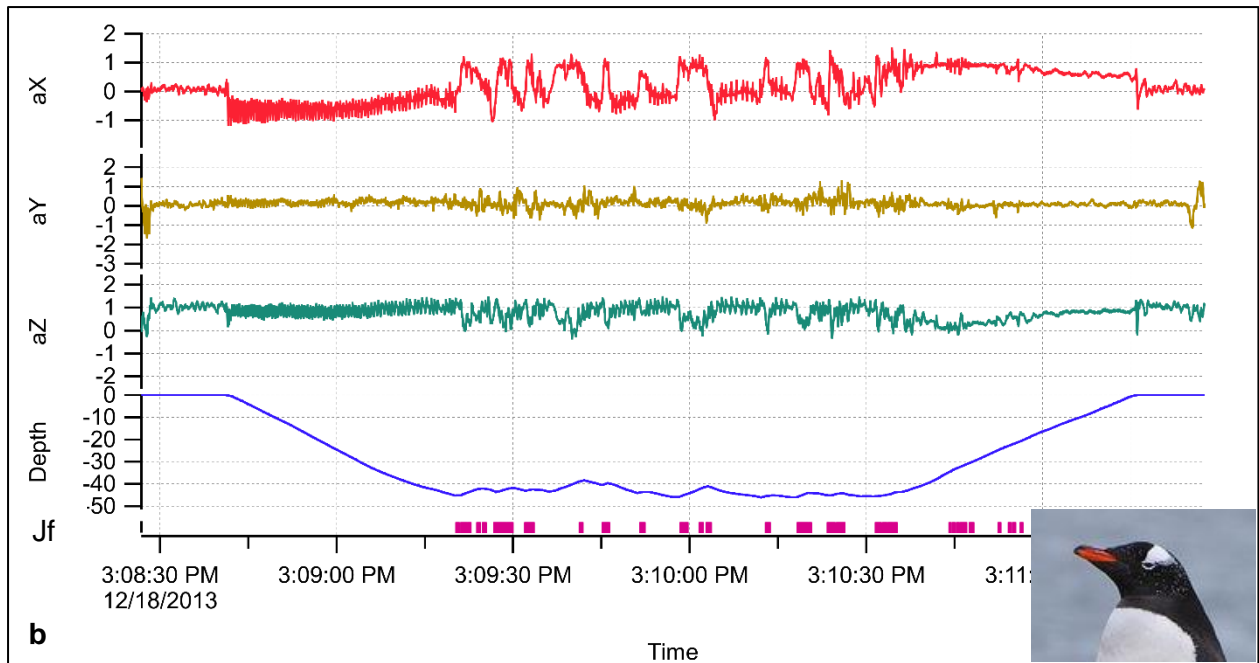


Figure 5.4: Exemplar accelerometer profiles during a single dive where gentoo penguins were feeding on (a) lobster krill and (b) juvenile fish, and where little penguins were feeding on (c) fish. Accelerometer data is in units of g. Lk = lobster krill, Jf = Juvenile fish

The average duration of prey interactions for lobster krill, juvenile fish and fish was 2.25s ( $\pm 2.00$ ), 0.72s ( $\pm 0.59$ ) and 1.62s ( $\pm 1.52$ ) (mean, sd), respectively (Figure 5.2). Following data summarization, this yielded a ratio of observations necessary for model development of

28194:1323:233 (swimming:lobster krill:juvenile fish) and 6207:384 (swimming:fish), for gentoo and little penguins, respectively.

### Model performance

The two class models for each species both had a high accuracy of > 90% (Table 5.2). However, because I had an unbalanced number of observations, it is more informative to look at sensitivity and the false positive rate. Sensitivity for PEEs in both models was > 70%, but for the gentoo penguin model it was 15.5% lower than that of the little penguin model. The false positive rate was below 10% for both species, however, the gentoo penguin model performed slightly better than the little penguin model.

Table 5.2: Performance metrics for a two-class support vector machine to classify swimming vs. prey encounter events in gentoo and little penguins. Metrics represent the mean and standard error following 10-fold cross validation

Model species	Accuracy (%)	Sensitivity (%)	False positive rate (%)
Gentoo penguin	92.2 (0.06)	72.3 (0.5)	6.7 (0.07)
Little penguin	91.6 (0.2)	87.8 (1.2)	8.1 (0.3)

The three-class model for gentoo penguins had a high overall accuracy (Table 5.3). Sensitivity for juvenile fish was 38% lower than sensitivity for lobster krill which had a reasonably high sensitivity. The false positive rate was relatively low for both prey items, but particularly so for juvenile fish compared to lobster krill. I additionally determined the proportion of PEEs which were classified as another class. Of the misclassifications of PEE's, 97.6% ( $\pm 0.1$ ) and 91.8% ( $\pm 0.7$ ) of lobster krill and juvenile fish observations, respectively, were misclassified as 'swimming'. Preying on lobster krill was only misclassified as preying on juvenile fish 2.4% ( $\pm 0.1$ ) of the time, while preying on juvenile fish was misclassified as preying on lobster krill 8.2% (0.7) of the time.

Table 5.3: Performance metrics for a three-class support vector machine to classify swimming as opposed to a lobster krill or juvenile fish prey encounter event, in gentoo penguins. Metrics show the mean and standard error following 10-fold cross validation using a 70:30 (train:test) ratio

Metric	Percentage (%)
<b>Accuracy</b>	90.2 (0.1)
<b>Sensitivity</b>	
swimming	91.2 (0.1)
lobster krill	77.5 (0.4)
juvenile fish	49.5 (1.1)
<b>False Positive Rate</b>	
lobster krill	7.3 (0.1)
juvenile fish	1.6 (0.04)

## **Discussion**

### **Device effects**

Externally attaching equipment to a marine predator can increase the drag experienced by the animal. For penguins, there are mixed results regarding the degree to which birds are affected, either neutrally or negatively (Saraux et al. 2011, Agnew et al. 2013, Wilson et al. 2015). Based on wind tunnel tests looking at drag on various species, it is clear that numerous aspects should be considered when looking at the effect of a tag on a diving marine predator, such as tag cross sectional area, average swimming speed, prey capture methods and duration of tag deployment (Todd Jones et al. 2013, Vandenabeele et al. 2015). Therefore, although gentoo penguins in my study had devices that were larger in terms of body cross sectional area compared to the little penguins, I do not expect birds of both species to have been largely impacted for the following reasons; (a) the typical prey capture method by gentoo penguins did not involve birds actively pursuing prey, (b) even when gentoo penguins did actively pursue prey, I observed them to be successful in capturing large squid (Handley, unpublished data), (c) the size of devices used on little penguins was negligible compared to body size, and (d) for both species tags were only deployed for a single foraging trip, thereby minimising possible long term effects on fitness.

### **SVM applicability to wild data**

My results show that using a machine learning approach, the SVM, on accelerometry data obtained from wild penguins it is feasible to identify PEE's. This was possible through a supervised classification approach, where animal-borne camera loggers were used to classify data obtained from back mounted accelerometers. This approach provided greater predictive ability for the two-class model of the little penguins as sensitivity toward a PEE was 87.8 % as oppose to 72.3 % for gentoo penguins (Table 5.2). This indicates that when a true prey event occurs, the little penguin model has a greater chance of predicting occurrence than the gentoo penguin model. The gentoo penguin model was also slightly more conservative than the little penguin model, having a lower false positive rate (Table 5.2). This indicates a lower chance of misclassifying an event as prey handling when it should have been swimming compared to the little penguin model. Regarding results from the three-class gentoo penguin model, my study shows that it is not only possible to distinguish between swimming and a PEE, but that even the type of PEE can be accounted for to a certain degree using the SVM approach. This is further supported by the low proportion of PEEs getting misclassified as feeding on the other prey type. Furthermore, separation of PEEs into each of their classes can, in some cases, enhance the predictive ability for that class as sensitivity for lobster krill was higher compared to just a PEE in the two-class model.

My model for little penguins developed in a wild setting marginally outperformed a two-class SVM developed for little penguins in captivity, where overall accuracy was 84.95% and the false positive rate was 9.8% (Carroll et al. 2014). The fact that the wild-developed model outperformed the captive model demonstrates that the SVM approach was robust to noise introduced by the more diverse feeding behaviours of wild animals, such as a greater range of prey types and environmental conditions. This finding suggests that where both options are possible, animal-borne video cameras may be preferable to studies performed on marine predators in captivity.

The fact that both studies achieved relatively strong predictive performance is an important result, given the small size of little penguins. Currently, their size precludes researchers from using a dual accelerometry approach, which was shown to be highly effective for recognizing prey captures by Adélie penguins foraging on pelagic prey (Watanabe & Takahashi 2013). It is clear, however, that accelerometers mounted on different parts of the body will give different signals in response to movement, which will affect the capacity to determine specific behaviours (Gleiss et al. 2011, Preston et al. 2012). For example, when using either a neckband or backpack accelerometer on Canada geese (*Branta canadensis*), the positioning of these accelerometers allowed for comparable predictive performance to recognise gross movements such as walking and resting. However, to classify more detailed movements like foraging or vigilance the neckband accelerometer performed better (Kölzsch et al. 2016). Similarly, there was a higher detection rate for prey capture events by southern elephant seals (*Mirounga leonina*) when accelerometers were placed on the head compared to the neck (Gallon et al. 2012). Therefore, future studies could benefit from a multi-accelerometer approach, as sensors placed on specific body parts will better represent those local forces as oppose to a single trunk mounted accelerometer which could rather represent a body-integrated signal (Wilson et al. 2016). Considering this benefit of a dual accelerometry approach and the recent development of minituarised accelerometers (Hammond et al. 2016), future studies on gentoo penguins, and other predators which capture prey in a more passive manner, might consider applying this method. Before doing so, however, the studies will also benefit from the use of an animal-borne camera logger, as it was only through these devices that I could get context about prey interactions for gentoo penguins and the resultant features reflective in their accelerometry profiles (Figure 5.4).

Using animal-borne camera loggers clearly enhanced the understanding of how both species interacted with prey and subsequently aided in the window length chosen during model development. When Carroll et al. (2014), used their captive trained SVM to identify prey handling for wild little penguin data, they considered that three consecutive 0.3s windows would be indicative of a prey handling event. From the video footage obtained in my study and



the duration of events (Figure 5.2) for little penguin PEE's, I corroborate their approach. However, were this approach to be used for the gentoo penguin PEE's on juvenile fish, there would likely be an underestimation of PEE's. I expect this would still have been the case if I was able to accurately identify consumption or not. Importantly though, the context in which prey presents itself clearly also needs to be considered. In some instances, gentoo penguins attempted to catch solitary juvenile fish, while in others the gentoo penguins rapidly struck at juvenile fish continuously when there were high numbers of juvenile fish present. Therefore, unless one used an extremely high sampling frequency for the accelerometers, it would be difficult to determine individual PEEs when penguins are rapidly consuming multiple prey. Thus, it would be important to consider the purpose of a specific study and whether it will be necessary to identify specific events or localized bouts of feeding.

Disentangling one behaviour from another with accelerometers can be particularly challenging when behaviours occur simultaneously, such as walking and eating (Graf et al. 2015). This is because patterns of locomotion could be inherently similar, particularly when behaviours are adopted in the same posture, making it difficult for algorithms to distinguish between different classes (Bidder et al. 2014, Fehlmann et al. 2017). This provides an additional explanation as to why the three-class model for gentoo penguins had poor performance for classifying juvenile fish observations. The size of the juvenile fish likely precludes the gentoo penguins from needing to alter their swimming kinematics to a large degree. Furthermore, considering that birds eat while swimming, this also explains why for both lobster krill and juvenile fish such a high proportion of behaviours were misclassified as swimming as opposed to the alternate prey item. One further aspect to consider regarding the poor classification of juvenile fish observations, is the lower number of actual events observed which could be used during model development. This was a recognised limitation in studies looking to classify feeding events in both cheetah (*Acinonyx jubatus*) (Broekhuis et al. 2012) and puma (*Puma concolor*) (Wang et al. 2015). However, based on the video observation where it was clear that gentoo penguins continued swimming largely uniformly while striking their head at juvenile fish, I suggest this similarity in body posture and movement is a key driver behind the poor model performance. Similarly, Watanabe and Takahashi (2013) also recognised that their model performed better for *Pagonetia borchgrevinki* as opposed to krill, because of the distinct body motions when feeding on this midwater fish.

## **Conclusion**

I have shown how a back mounted accelerometer on free ranging marine predators can serve as a valuable tool for identifying PEEs. This was made possible with the use of a powerful machine learning algorithm, the support vector machine, which allowed us to integrate

information provided by all three axes of an accelerometer into the classifier. It was clear from my study that the capacity to build a classifier was greatly enhanced by using wild observations of prey interactions. Therefore, while captive surrogates will certainly provide a good baseline, I advocate for the development of models based on wild observations. This will enhance the opportunity to account for multiple, live prey types, many of which could not feasibly be obtained for captive feeding trials. I encourage the continued exploration of the subtleties in animal movement during prey interactions and support the notion proposed by Graf et al. (2015) to build multispecies databases, which will further enhance our ability to understand the broad applicability of accelerometry data to individual species inhabiting diverse environments. I envision that with the miniaturisation of technology, a multi accelerometer tag approach will enhance the ability to identify prey interactions, especially for those predators that attempt to capture prey in a more passive manner. Finally, it is clear that a proliferation of methods are now available for classification of behaviours from accelerometry data (e.g: Nathan et al. 2012; Gao et al. 2013; Bidder et al. 2014; Fehlmann et al. 2017; Ladds et al. 2017; Sur et al. 2017). Support vector machines are often deemed to be one of the best classifiers, and the approach along with supplementary R code I will provide, offers a readily available tool for practitioners to incorporate into their toolbox. I encourage the use of my method, not only for the identification of PEEs by a predator but also for any scenario which requires a powerful tool for multiclass classification.

## Chapter 6 General Discussion

Seabirds are currently the world's most threatened avifauna owing to the numerous anthropogenic induced changes in the environment (Croxall et al. 2012). While many aspects regarding their biology have been investigated, numerous questions, both pure and applied, still remain for species inhabiting a variety of habitats (Lewison et al. 2012, Croxall et al. 2012). For conspecifics that breed over a broad range or across a variety of different habitat types, it is critically important to understand the degree of variation in a species realized niche. This can be achieved by investigating the foraging ecology of a species, which involves identifying the relationships that characterise the food web an individual is a part of (Stephens & Krebs 1986, Stephens et al. 2007). Of primary importance is to determine whether that species is a specialist or generalist in terms of the resources it requires and the manner in which those resources are obtained. This is particularly relevant in the current day, as generalist populations are believed to be more amenable to global change (Clavel et al. 2011). However, even populations which are considered generalists at a global scale, may in fact consist of locally specialised populations. Therefore, the study of a species foraging ecology across multiple locations will elucidate whether that species is a specialist at the population level, or if a generalist, consists of individuals that all have a broad realized niche (Type A) or subsets of individuals that specialise (Type B) (Van Valen 1965, Bearhop et al. 2004). One seabird group for which this knowledge is of critical value are the penguins (Spheniscids). These birds, many of which have a restricted range compared to their volant counterparts during the breeding period (Ratcliffe & Trathan 2011, Borboroglu & Boersma 2013), are sensitive to local environmental perturbation and have, therefore, been deemed as sentinels of the marine environment (Boersma 2008). Only five of the eighteen species are listed as "Least Concern" on the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species, with the remaining listed as "Near Threatened" (3), "Vulnerable" (5) and "Endangered" (5) (IUCN 2017). Therefore, understanding their foraging ecology and developing ways to improve investigations, will be critical toward the conservation and management of these birds.

In this thesis, the overarching aim was to investigate the foraging ecology of gentoo penguins (*Pygoscelis papua*) at the Falkland Islands. While these birds were recently downlisted to "Least Concern" on the IUCN Red List (Birdlife International 2016), new genetic evidence now clearly shows that these birds are a well-defined subspecies, the northern gentoo penguin (*Pygoscelis papua papua*), and are genetically distinct from those breeding at other sub-Antarctic archipelagos and the Antarctic (Dinechin et al. 2012, Levy et al. 2016, Clucas et al. 2017, Vianna et al. 2017). Furthermore, the Falkland Islands hold the world's largest population (Baylis et al. 2013, Lynch 2013), therefore, despite genetic variation, elucidating factors

influencing this population may have global relevance to the species as a whole. Specifically, in my study I aimed to determine the diet and distribution of these birds across multiple breeding colonies, which were each chosen for their unique geographic position (Chapters 2 and 3). I also investigated the fine-scale interactions between predator and prey (Chapter 4). Following the novel insight into the foraging ecology of these species, I developed a new method to identify prey encounter events (PEEs) by penguins (Chapter 5). This method can be implemented across multiple penguin species, and across many diving marine central-place foragers.

The motivation for my study at the Falkland Islands, was that much is unknown for these birds across the entire archipelago. While gentoo penguin diet has been studied in the past using stomach content (Thompson 1994, Clausen & Putz 2002, 2003, Clausen et al. 2005) and stable isotope analysis (Weiss et al. 2009, Masello et al. 2010, 2017), much of this knowledge comes from a single colony, New Island, and a revision of the diet via stomach content analysis is required considering recently recognised potential for competition with fisheries (Handley et al. 2016). This knowledge can aid in understanding ecosystem change, considering the declining gentoo penguin populations at the Kerguelen archipelago (Lescroël & Bost 2006) and Prince Edward Islands (Crawford et al. 2014), believed to be occurring due to competition with fisheries and a change in local food availability because of altered benthic production, respectively. Furthermore, there is little knowledge of the bird's distribution (Boersma et al. 2002, Clausen & Putz 2003, Masello et al. 2010, 2017) from multiple colonies at the Falkland Islands during the breeding period, a vital knowledge gap for marine spatial planning (Raymond et al. 2015, Lascelles et al. 2016, Hinke et al. 2017a), especially considering the proposed offshore hydrocarbon industry (Augé et al. 2015). Across the gentoo penguins range, there is no information which has been derived from video loggers that can help to understand how these birds interact with prey. This point is critical as previous studies highlighted the uncertainty in using seabirds as indicators of marine ecosystem status, which might arise because of basic physical and biological factors affecting how efficiently a seabird can exploit local resources (Piatt et al. 2007a, Durant et al. 2009). Identifying where and when resources are used is clearly a critical step for all penguins, hence the development of a simplified methodology.

### **Foraging plasticity in gentoo penguins**

In my study, I found that gentoo penguin diet at the Falkland Islands varies spatio-temporally and that these birds forage on a diverse array of prey items, which include benthic-demersal prey such as rock cod fish (*Patagonotothen* spp.), adult lobster krill (*Munida* spp.), Patagonian squid (*Doryteuthis gahi*) and juvenile fish (likely *Patagonotothen* spp.), and epipelagic prey

such as Falkland herring (*Sprattus fuegensis*) and southern blue whiting (*Micromesistius australis*). This diversity in prey items was further reflected in contrasting dive types seen at the different colonies, where it was clear that birds from colonies which primarily performed benthic dives consumed benthic-demersal prey, while those performing pelagic dives consumed epipelagic prey. The use of animal-borne camera loggers verified, for the first time, that not only do gentoo penguins consume a diverse array of prey items, but also the methods used to capture and pursue prey are varied. Larger prey items are actively pursued, while smaller, less mobile prey items are consumed in a more passive manner. Furthermore, prey behaviour clearly has an influence on the success of capture. Birds will even engage in intra-specific kleptoparasitism at-sea, undergoing the risk of injury, to try and secure highly profitable prey items (Handley & Pistorius 2015). The above mentioned factors lend support to these birds following optimal foraging theory (Emlen 1966, Macarthur & Pianka 1966).

By tracking gentoo penguins with GPS devices, I found that birds seldom travelled farther than 30km from any colony, and it became clear that the surrounding bathymetry plays a critical role in determining the type of prey consumed. For those birds that foraged in waters where the seabed gradually sloped away, benthic diving and benthic-demersal prey were common. However, when birds foraged in waters which rapidly became deep, pelagic diving and epipelagic prey were most common. There were exceptions to this though, most notably the guard stage of the 2013 breeding season at Cow Bay, when the epipelagic prey, southern blue whiting, formed the primary component of the diet. This indicated that birds do show flexibility in their foraging ecology. This flexibility was also well documented when looking at the degree of diet specialisation (1 = all individuals rely on different resources, 0 = all rely on the same) vs. trophic niche width (0 = entire population consumes a single prey item), which indicated that when birds from a colony foraged on a larger array of prey items, so to do did their degree of diet specialisation increase. This primarily occurred at the sites with shallow sloping seabeds. Therefore, it is not that gentoo penguins perform the deepest dives that physiology and water depth allow, rather, in shallow waters they target the bottom, whereas in deep water they target shoals in the water column. However, in shallow waters birds can also readily switch to a pelagic foraging technique, as reflected by the type and greater diversity of prey items at these sites. Both this diversity in prey items and inshore foraging nature appear to continue into the pre-molt period, as indicated by the stable isotope data. Again, at the colonies with gently sloping seabeds, measures of niche width (Bayesian estimate of the standard ellipse area,  $SEA_B$ . Isotopic richness,  $IRic$ ), were typically largest, apart from Bull Roads (with a gently sloping seabed) in 2013 when birds from the Steeple Jason colony (with waters that rapidly become deep) were unable to be sampled. Furthermore,

the values I recorded for  $\delta^{13}\text{C}$  were similar to those of the imperial cormorant (*Phalacrocorax articeps*) at New Island, an inshore foraging species (Weiss et al. 2009).

In my attempt to determine diet through stable isotopic mixing models, I was unsuccessful. Therefore, while it is clear that diet varies in diversity across different colonies during the breeding period, and likely into the pre-molt period, the type of prey consumed during the pre-molt period remains to be determined. The inshore foraging nature of these birds, and the resulting paucity of data regarding environmental characteristics, limited the ability to develop habitat distribution models, despite using dive locations to develop the response variable. The novel methodology developed to identify PEEs, and use of these to identify important areas as oppose to just location data or dive locations, along with concurrent developments in remote sensed data (Pope et al. 2017), will serve as an exciting avenue through which habitat distribution models may improve for inshore foraging species in future.

The observed flexibility in foraging behaviour of these birds at the Falkland Islands, with spatio-temporal variability in the diet and the ability to forage in both a benthic and pelagic manner while remaining in neritic waters, is in line with the historical foraging plasticity observed both at the Falkland Islands and for other subspecies across their range (Lescroël et al. 2004, Lescroël & Bost 2005, Miller et al. 2009, 2010, Masello et al. 2010, Kokubun et al. 2010, Ratcliffe & Trathan 2011, Lynch 2013). Over the course of the breeding period, it has been suggested that prey switching may be necessitated by differing demands for energy requirements during the breeding season (Williams & Rothery 1990, Le corre et al. 2003, Quillfeldt et al. 2011), which may then also be manifested in differing distributional characteristics. There was some evidence, based on the energy content of prey items (Ciancio et al. 2007), that supported this hypothesis. However, annual variation in the diet of gentoo penguins (Volkman et al. 1980, Adams & Klages 1989, Coria et al. 2000, Libertelli et al. 2004), and at different sites within an archipelago (Lescroël et al. 2004, Clausen et al. 2005, Miller et al. 2010), has been recorded when there were known differences in prey availability based on at-sea surveys. Furthermore, in a review comparing 12 species of pinnipeds and seabirds (Schreer et al. 2001), the primary determinants of dive type were water depth and preferred prey. Although in my study I was unable to perform simultaneous at-sea surveys of prey availability, animal-borne camera loggers did reveal the flexibility with which birds could capture prey. Furthermore, the distribution of the main prey items is relatively well known at the Falkland Islands, thanks to dedicated fisheries research cruises and studies relating to prey items. Therefore, I agree with other authors that prey availability appears to be the driving force shaping foraging strategies in these birds.

The observed diversity in foraging strategies by gentoo penguins might mean that certain sub-populations could fare better than others. However, when diet composition and diving patterns varied over a five-year period for gentoo penguins at the South Shetland Islands, they were still able to successfully fledge chicks at similar rates. Therefore, gentoo penguins (Miller et al. 2009), and indeed many other seabirds that forage in contrasting manners (Harding et al. 2013, Sala et al. 2014, Berlincourt & Arnould 2015), appear to be successful breeders under a range of conditions. From an evolutionary stand point, this helps answer why gentoo penguins could be faring so well compared to their specialist congeners. Across their range, including at the Falklands, gentoo penguin population numbers are increasing while the opposite is largely occurring for the Adélie and chinstrap penguin populations in Antarctica (Miller et al. 2010, Kokubun et al. 2010, Baylis et al. 2013, Borboroglu & Boersma 2013, Hinke et al. 2017b).

A key factor that could affect the fitness of gentoo penguins is food availability within close proximity to the breeding colony. The trip parameters obtained from tracking data can provide proxies of foraging success (Lewis et al. 2001, Ryan et al. 2004, Pichegru et al. 2010). Variation in these parameters can be linked to population dynamics as seen in Magellanic penguins (*Spheniscus magellanicus*), where increased foraging distance and duration decreased the chances of successful breeding (Boersma & Rebstock 2009). Reduced food availability has also been attributed to an increased foraging range for Adélie penguins (*Pygoscelis adeliae*) which was reflected by low population numbers (Ballance et al. 2009). While the distance and duration of birds sampled in my study were well within previously recorded estimates at other archipelagos (Lescroël & Bost 2005, Miller et al. 2010, Kokubun et al. 2010, Ratcliffe & Trathan 2011), they were considerably shorter compared to a colony at New Island, when birds exhibited poorer breeding success in a season which showed signs of considerably longer trip distance and duration (Masello et al. 2017), compared to conspecifics across their range (Ratcliffe & Trathan 2011). Reduced food availability is also the suggested reason for the declining populations at the Kerguelen archipelago (Lescroël & Bost 2006) and Prince Edward Islands (Crawford et al. 2014). Therefore, although these birds can forage in a diverse manner, it appears their inshore nature may be a rate limiting factor on population numbers.

### **Penguins as sentinels of the marine environment**

Penguins, and indeed many seabirds, are clearly influenced both positively and negatively when change occurs in their surrounding marine environment. The degree to which populations respond to those changes will vary, and this warrants investigation into numerous factors that may affect seabird population numbers (Piatt et al. 2007a, Durant et al. 2009). A key challenge in fully understanding a marine species though, is observing it during all aspects

of its life cycle. This is where animal-borne camera loggers used in my study provided novel insight by revealing that prey behaviour can significantly influence trophic coupling in marine systems. This should, therefore, be accounted for in studies using marine top predators as samplers of mid to lower trophic level species. Specifically, footage from my study revealed that gentoo penguins were not always able to capture lobster krill (*Munida* spp.) prey that could actively defend itself with their pincers. Furthermore, swarm density of lobster krill had a significant influence on whether birds attacked a swarm or not. This indicated that grouped prey defence and the confusion effect may be factors that limit prey capture ability. While these factors are well recognised in terrestrial systems, my study is the first to reveal their combined influence on a marine central place forager.

If we are to fully reveal the extent to which penguins can be used as marine sentinels we will need to uncover their at-sea behaviour across species in differing foraging contexts. Furthermore, we will need to recognise their distribution at sea across numerous unsampled colonies. Fortunately, with satellite technology we now have an unprecedented ability to discover the location of previously unknown penguin colonies (Fretwell & Trathan 2009, Lynch et al. 2012b). However, inferring at-sea distribution around these colonies is an area of on-going research. This challenge may be exacerbated for the generalist penguin species as the distribution of ecologically specialised species is easier to model than those tolerant to a large variety of habitats. Furthermore, ecological adaptation by sub-populations can result in different habitat preferences in discrete parts of a species' range (Hernandez et al. 2006, McPherson & Jetz 2007). These factors likely contributed to the limited ability with which habitat distribution models could be transferred across colonies in my study.

By not yet being able to accurately identify the distribution of breeding gentoo penguins at other colonies, this presents the challenge then as to how one effectively conserves or manages such a species, despite populations currently increasing. At the Falkland Islands, this is particularly important for gentoo penguins, especially those breeding at colonies in the north-east, considering the current exploration for offshore hydrocarbons and potential development of inshore fisheries (Augé et al. 2015). However, the limited range of gentoo penguins also means that they should receive adequate protection under the umbrella of the further ranging species. My data provides critical baseline information needed for multi-species studies to recognise important areas at sea which should be identified for marine spatial planning program's (Augé et al. 2015, Raymond et al. 2015, Lascelles et al. 2016, Thiers et al. 2016).

Alternate solutions to species conservation and management are also of vital importance and some of the most effective conservation approaches have sought a balance between



socioeconomic gains and species protection (Fisher et al. 2014, Oldekop et al. 2016). These approaches are often more tangible in a terrestrial setting. Yet, considering that approximately 15% of animal protein consumed by people is marine sourced (Smith et al. 2010), it is imperative we find a balance in this setting. Perhaps even more so in a region where there has been overexploitation in the past (Laptikhovsky et al. 2013). Thus, as a thought related to the tracking of animals, I propose the idea of using data to produce art (Figure 6.1) which can be used as a means of public engagement. Furthermore, while the video footage in my study revealed novel understanding of a predator-prey interaction, it will also be a powerful medium through which we can achieve species conservation (Weinstein et al. 2015, Hassan et al. 2017). These are simple, yet effective approaches of many, that may help to change actions and maximize species persistence (Mcgowan et al. 2016).

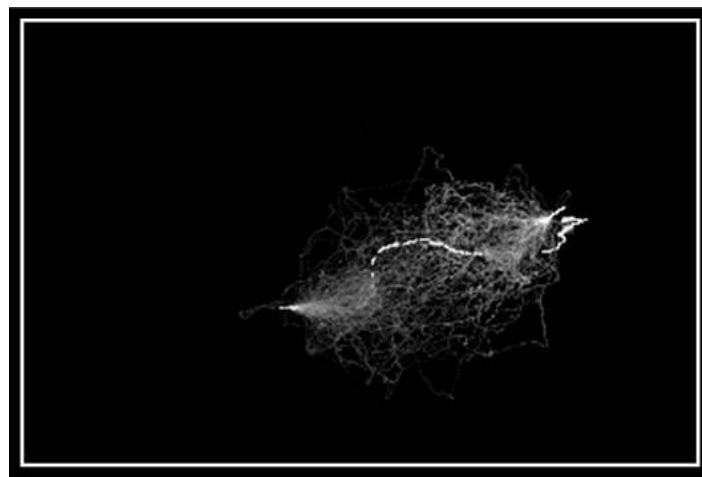


Figure 6.1: Raster image used for canvas print production. The image depicts 100 possible foraging paths used by a bird through a continuous-time correlated random walk model ('crawl' package, (Johnson et al. 2008)). Bright white colours depict areas of high use

### **Towards the future**

Understanding the foraging ecology of a species will clearly enhance our ability to make informed conservation and management decisions for that species. However, knowledge of a species foraging ecology alone will not be the only aspects one should consider. To make fully informed decisions, and to better understand the role of gentoo penguins as sentinels of the environment at the Falkland Islands, I recommend the following research questions should be addressed in future:

1. Understand disease prevalence, immunity levels, and test for potential pathogens (Tompkins et al. 2015).
2. Investigate the use of physiological markers that could be used as indicators of a populations health (Cooke et al. 2013).

3. How do sub-colonies vary with respect to foraging behaviours and demographic parameters?
4. Determine the annual breeding frequency of adult birds.
5. Understand the drivers of breeding phenology.
6. While the work of Levy et al. (2016) shows mixing among breeding populations, it would be valuable to know at what time scale this mixing occurs.
7. Further to the above, would be to extend the work of Boersma et al. (2002), and gain greater understanding of juvenile dispersal and the degree of natal philopatry.
8. Investigate the distribution of birds, and revise detailed dietary knowledge through stomach content analysis (Clausen & Putz 2003), during the nonbreeding period.
9. Tie in the gentoo distribution data collected during my study with the current multispecies investigation (Augé et al. 2015). Then, use decision support software for spatial conservation prioritization (Watts et al. 2009, Lehtomäki & Moilanen 2013) to enhance marine spatial planning efforts at the Falkland Islands.

Specifically to this thesis; with the well-established method of stomach content analysis, I can confirm that the potential interaction with fisheries at a single colony, Cow Bay, recognised by Handley *et al.* (2016), does not appear to be prevalent for the island wide population. This is because at the other colonies (Bull Roads, Bull Point and Steeple Jason), the primary diet items are not the commercially sought rock cod fish. However, whether this is the case beyond the breeding period remains to be confirmed. Therefore, as posed in the questions above, diet studies using stomach content analysis would be advantageous during the nonbreeding period, and at timely intervals in the future. Stable isotope analysis may be a solution to investigate nonbreeding period diet and to overcome the need for the more invasive stomach sampling. However, there are still underlying caveats that need to be addressed before this method can be used at the Falkland Islands. Principally, there is a need to use prey items definitively from the area where birds might have been. Obtaining the stable isotope signatures of prey items found directly around colonies would have enhanced my study as there was uncertainty relating to the effect of location source required to compare baseline isotopic values, even though I used secured fresh prey items from research cruises around the Falkland Islands. And, perhaps most importantly, further work is needed to determine the specific trophic discrimination factors between different tissues of gentoo penguins and the broad range of prey species consumed at the Falkland Islands.

This thesis reaffirms the value in using animal-borne camera loggers to gain insight into the lives of difficult to observe species. However, key caveats of this technology are the lack of ability to fully perceive the surrounding environment of the bird, and the lengthy procedure of data processing. Here is where technological and analytical innovation will be needed.

Technologically, wide angle lenses will increase the field of view permitting clarity into the immediate surrounds of the bird (Mattern et al. 2017). Furthermore, manufacturers of recreationally available cameras such as GoPro are currently developing a camera called Fusion, which will allow for spherical video capture. It is not unfeasible that this technology will soon be miniaturized to the extent that it can be used on multiple penguin species. The analysis of this data along with reproducible methods, will be the next step. Hence, the supplementary material I produced for chapter 4 is a first step in this regard. Enhancing tools for automated image analysis will also be required, and applications such as Google's TensorFlow, which use a branch of machine learning known as deep learning, appear to be a promising approach for ecologists in the future (Rampasek & Goldenberg 2016).

Clearly, the advancements in understanding a species foraging ecology made in this thesis were possible through technological advancement, and biologging devices are rapidly enhancing our ability to study a species ecology (Wilmers et al. 2015). In light of technological advancement, there has even been debate about whether tools or ideas are the drivers of science (Dyson 2012). Indeed, the unprecedented detail we can obtain now about animal movement has even led to the development of a movement ecology discipline (Nathan et al. 2008), calling for a burgeoning array of new questions to be answered (Hays et al. 2016). Some of which, such as the impact of prey distribution on foraging behaviour, have been addressed in this thesis. However, a challenge of this rapid technological innovation will be to provide the skills ecologists need to deal with such tools. Because most of these tools rely on computational innovation and fall into the realm of 'big data', there is now a pressing need to train ecologists in this discipline (López-López 2016). Thus, training in future should lead ecologists to a point where they can comprehensively use such tools, or at least to the point where they can effectively communicate and build a suitable rapport with a qualified individual(s) (Boyd et al. 2010).

### **Final thoughts**

Ultimately, my study has revealed the broad foraging capabilities of gentoo penguins at the Falkland Islands; probably a key driver in their current population increase at this archipelago and across their range. It remains to be seen though if this flexibility across all behaviours, especially those relating to movement and prey interactions, occur at an intra-individual level, considering the diet analyses in my study and others (Polito et al. 2015, Herman et al. 2017) have indicated the birds to be "Type B" generalists, which are those subsets of individuals that utilize specific prey items. Perhaps two key questions in this regard, highlighted by Hays et al. (2016), are: How do learning and memory versus innate behaviours influence movement patterns and ontogenetic changes? To what degree do social interactions influence movements? These questions are particularly key for gentoo penguins, as unlike their

congeners, there is evidence of extended parental care, which might allow them to develop foraging skills before they are completely independent (Polito & Trivelpiece 2008). Understanding if intra-individual flexibility occurs across all mechanisms, will greatly enhance our ability to understand how amenable these birds will be to potential environmental change in the Anthropocene.

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## Appendix: Chapter 2 (Figures and Tables)

**Table A2.1 (A,B):** Regression equations for relationships between hard part remain (CL = carapace length; LRL = lower rostral length; LHL = lower hood length; oto = otolith length) and cephalopod, crustacean or fish, (A) length (DML = dorsal mantle length; TCL = total carapace length; PL = pre-anal length; TL = total length) and (B) mass (M) for prey taxa found in gentoo penguin stomach contents at the Falkland Islands during a study investigating breeding period diet over the austral summers of 2011, 2012 and 2013. Note: A total of 37 prey taxa were identified during my study. Those not listed here are available in Table S3, and length and mass for these prey items were measurable directly. Reference equations developed in my study through support from the Falkland Islands Fisheries Department (FIFD). NA indicates data were not available.

**Table A2.1 (A)** Length

Species	Common Name	Code (FIFD)	Hard part		Reconstituted <sup>i</sup>		
			Range (mm)	N (measured)	Length <sup>ii</sup>	r <sup>2</sup>	Reference
Cephalopod							
<i>Doryteuthis gahi</i>	Loligo/Patagonian squid	LOL	NA	446	DML (mm): $\ln(\text{DML}) = 4.23 + (1.01 \times \ln(\text{LRL}))$	NA	Xavier & Cherel (2009)
<i>Gonatus antarcticus</i>	NA	GON	NA	NA	DML (mm): $\text{DML} = 12.82 + (19.02 \times \text{LRL})$	NA	Clarke (1986)
<i>Onykia ingens</i>	Greater hooked squid	ING	0.4 – 7.0	367	DML (cm): $\text{DML} = (\text{LRL} \times 3.1161) + 7.9934$	0.87	Clausen & Huin (2002)
<i>Semirossia patagonica</i>	Mickey mouse/Bobtail squid	SRP	1.5	1	DML (mm): $\text{DML} = \text{LHL} \times 13.45$	NA	Thesis
Crustacean							
<i>Munida gregaria</i>	Lobster krill	MUN	12.0-28.6 CL	55	TCL (mm): $\text{TCL} = 0.719 + (1.229 \times \text{CL})$	0.99	Tapella & Lovrich (2006)
<i>Munida subrugosa</i>	Lobster krill	MUU	13.6-28.2 CL	57	TCL (mm): $\text{TCL} = 0.565 + (1.293 \times \text{CL})$	0.98	Tapella & Lovrich (2006)
Fish							
<i>Champscephalus esox</i>	Icefish	CHE	1.3 - 2.5	6	TL (cm): $\text{TL} = 7.7785 + (\text{oto} \times 4.9837)$	0.97	Thesis
<i>Cottoperca gobio</i>	Frogmouth	CGO	3.1 - 6.3	52	TL (cm): $\text{TL} = 0.2092 \times (\text{oto}^{2.6871})$	0.9	Clausen & Huin (2002)
<i>Dissostichus eleginoides</i>	Patagonian toothfish	TOO	11.0 - 17.6	20	TL (cm): $\text{TL} = 3.5358 \times (\text{oto}^{1.2189})$	0.74	Thesis
<i>Genypterus blacodes</i>	Pink cusk eel	KIN	NA	45	TL (cm): $\text{TL} = -18.3696 + (\text{oto} \times 5.6394)$	0.79	Alonso et al. 2000
<i>Macruronus magellanicus</i>	Whiptail hake/Hoki	WHI	11 - 25.2	12	PL (cm): $\text{TL} = 0.4117 \times (\text{oto}^{1.4208})$	0.96	Thesis
<i>Micromesistius australis</i>	Southern blue whiting	BLU	NA	NA	TL (cm): $\text{TL} = (\text{oto} \times 2.5405) - 2.1599$	NA	Huin (2005)
<i>Patagonotothen ramsayii</i>	Rock cod	PAR	0.8 - 8.8	1131	TL (cm): $\text{TL} = (\text{oto} \times 4.2731) - 4.9164$	0.88	Clausen & Huin (2002)
<i>Patagonotothen tessellata</i>	Rock cod	PTE	NA	NA	TL (cm): $\text{TL} = \text{oto} \times 2.9174$	NA	Huin (2005)
<i>Salilota australis</i>	Red cod	BAC	1.4 - 4.9	12	TL (cm): $\text{TL} = 0.5928 \times (\text{oto}^{1.5095})$	0.87	Clausen & Huin (2002)
<i>Sprattus fugensis</i>	Falkland herring	SAR	0.7 - 4.9	649	TL (cm): $\text{TL} = 4.8981 + (\text{oto} \times 5.7029)$	0.79	Clausen & Huin (2002)

Table A2.1 (B) Mass

Species	Common Name	Code (FIFD)	Hard part		Reconstituted <sup>i</sup>		
			Range (mm)	N (measured)	Mass (g)	r <sup>2</sup>	Reference
Cephalopod							
<i>Doryteuthis gahi</i>	Loligo/Patagonian squid	LOL	NA	446	$\ln(M) = 2.25 + 2.39\ln(\text{LRL})$	NA	Xavier & Cherel (2009)
<i>Gonatus antarcticus</i>	NA	GON	NA	NA	$\ln(M) = 0.086 + 2.13\ln(\text{LRL})$	NA	Clarke (1986)
<i>Onykia ingens</i>	Greater hooked squid	ING	0.4 - 7	367	$M = (\text{LRL} \times 2.7799) \times 4.1559$	NA	Clausen & Huin (2002)
<i>Semirossia patagonica</i>	Mickey mouse/Bobtail squid	SRP	1.5	1	$M = \text{LHL} \times 1.45$	NA	Thesis
Crustacean							
<i>Munida gregaria</i>	Lobster Krill	MUN	15.4-28.1 CL	47	$\log(M) = -3.052 + (2.911 \times \log(\text{CL}))$	0.99	Tapella & Lovrich (2006)
<i>Munida subrugosa</i> (male)	Lobster Krill	MUU	13.3-28 CL	32	$\log(M) = -3.355 + (3.150 \times \log(\text{CL}))$	0.99	Tapella & Lovrich (2006)
<i>Munida subrugosa</i> (female)	Lobster Krill	MUU	14.4-24.1 CL	30	$\log(M) = -3.3034 + (2.914 \times \log(\text{CL}))$	0.98	Tapella & Lovrich (2006)
Fish							
<i>Champscephalus esox</i>	Icefish	CHE	1.3 - 2.5	6	$M = 8.8399 \times (\text{oto})^{1.604}$	0.97	Thesis
<i>Cottoperca gobio</i>	Frogmouth	CGO	3.1 - 6.3	52	$M = 3.77 \times (10^{-5} \times \text{oto})^{8.6794}$	0.9	Clausen & Huin (2002)
<i>Dissostichus eleginoides</i>	Patagonian toothfish	TOO	11.0 - 17.6	20	$M = 0.6791 \times (\text{oto})^{3.5098}$	0.86	Thesis
<i>Genypterus blacodes</i>	Pink cusk eel	KIN	NA	24	$M = (0.0016 \times \text{TL})^{3.2251}$	0.97	Alonso et al. 2000
<i>Macruronus magellanicus</i>	Whiptail hake/Hoki	WHI	11.0 - 25.2	12	$M = 0.0035 \times (\text{oto})^{4.1798}$	0.97	Thesis
<i>Micromesistius australis</i>	Southern blue whiting	BLU	NA	NA	$M = 0.0109 \times (\text{oto})^{3.9605}$	0.88	Huin (2005)
<i>Patagonotothen ramsayii</i>	Rock cod	PAR	0.8 - 8.8	1131	$M = 0.0306 \times (\text{oto})^{4.3}$	0.82	Clausen & Huin (2002)
<i>Patagonotothen tessellata</i>	Rock cod	PTE	NA	NA	$M = 0.1585 \times (\text{oto})^{3.2893}$	NA	Huin (2005)
<i>Salilota australis</i>	Red cod	BAC	1.4 - 4.9	12	$M = 0.0025 \times (\text{oto})^{4.4758}$	0.93	Clausen & Huin (2002)
<i>Sprattus fugensis</i>	Falkland herring	SAR	0.7 - 4.9	649	$M = 4.7038 \times (\text{oto})^{2.7245}$	0.78	Clausen & Huin (2002)

<sup>i</sup> = All input values are in mm.

<sup>ii</sup> = Note, units for output values of reconstituted length vary; either in millimetres or centimetres as in parentheses.

**Table A2.2:** Prey carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope values of exemplar prey items believed to be consumed by adult gentoo penguins at the Falkland Islands. Typical prey consumed by gentoo penguins was kindly collected by the Falkland Islands Fisheries Department during research cruises conducted in October 2012 and 2013 by bottom and plankton trawling close to the Falklands (P. Brewin, pers. com.). Prey tissue included fish dorsal muscle, squid dorsal mantle muscle, crustacean abdomen muscle (large crustaceans) and whole exemplar specimens of a small pelagic amphipod. Material was dried and ground to a fine powder before lipid removal using cyclohexane (Chouvelon et al. 2011). Superscripts indicate grouping of prey items used in the final mixing model. Locations of prey capture can be obtained from the author: jonorow@gmail.com

Name				Isotopic values				Length (mm)			Mass (g)		
Species	Common	Code	n	$\delta^{13}\text{C}$ (mean)	$\delta^{13}\text{C}$ (sd)	$\delta^{15}\text{N}$ (mean)	$\delta^{15}\text{N}$ (sd)	mean	min	max	mean	min	max
<sup>1</sup> <i>Munida gregaria</i>	Lobster krill	MUG	4	-17.4	0.2	12.5	0.2	24.1	21	27.4	5	2.8	6.3
<i>Munida subrugosa</i>	Lobster krill	MUU	5	-15.6	0.3	11.9	0.2	20.5	19.2	22.5	3.1	1.9	5.1
<i>Themisto gaudichaudii</i>	NA	TG	3	-21.4 <sup>a</sup>	0.4	4.2	0.8	NA	NA	NA	NA	NA	NA
<i>Champscephalus esox</i>	Icefish	CHE	2	-15.8	0.1	11.6	0.6	150	150	150	19.9	19.5	20.4
<i>Cottoperca gobio</i>	Bull blenny	CGO	4	-16.4	0.4	13.7	0.6	202	185	213	91.8	73.6	111.2
<i>Dissostichus eleginoides</i>	Patagonian toothfish	TOO	2	-16.4	0.3	14.2	0.1	232.5	222	243	111.5	108.8	114.3
<i>Genypterus blacodes</i>	Pink cusk eel	KIN	2	-17.5	0.9	16	0.1	538.5	530	547	564.4	548.7	580
<i>Ilucoetes fimbriatus</i>	Eelpout	EEL	2	-16.6	0.2	13.7	0.7	176.5	173	180	20.8	20.6	21
<i>Macruronus magellanicus</i>	Patagonian grenadier	WHI	2	-17.9	0.3	12.5	0.3	487	470	504	329.5	307	352
<i>Merluccius hubbsi</i>	Common hake	HAK	2	-18.1	0.1	15.3	0.1	401.5	376	427	594.6	434	755.3
<sup>3</sup> <i>Micromesistius australis</i>	Southern blue whiting	BLU	7	-18.6	0.4	11.2	0.5	185	160	200	31.7	23.5	38.6
<sup>2</sup> <i>Patagonotothen ramsayii</i>	Rock cod	PAR	7	-18	0.2	12.1	0.5	177.9	145	211	48.3	23.6	81
<i>Salilota australis</i>	Red cod	BAC	6	-17.1	0.3	13.8	0.5	235.2	170	292	131.9	44.6	256.7
<sup>3</sup> <i>Sprattus fuegensis</i>	Falkland herring	SAR	5	-18.4	1	11.4	0.5	168.4	165	173	29.1	28	31.5
<i>Thysanopsetta naresi</i>	Small flounder	THN	2	-17.8	0.5	10.9	0.1	126	122	130	22.5	18.7	26.3
<sup>3</sup> <i>Doryteuthis gahi</i>	Patagonian squid	LOL	12	-18.4	0.7	11.3	0.4	128.7	93	170	49.4	23.8	78.1
<i>Onykia ingens</i>	Greater hooked squid	ING	5	-19.8	0.6	10.3	0.9	141	121	159	97.6	63.2	141.7

(a) indicates lipid removal following Post et al. (2007). Raw mean value was: -23.63



**Table A2.3:** Prey species identified from stomach content analysis of gentoo penguins at the Falkland Islands. Prey are represented by their percentage index of relative importance (%IRI). In bold, represents the main prey items identified as considered by having >1% IRI. Typical habitat of prey items was determined from various sources. NA indicates data were not available.

Scientific Name	Common Name	Code	% IRI	Habitat	Source
<b>Crustacean</b>					
<b><i>Munida</i> spp.<sup>a</sup></b>	<b>Lobster krill</b>	<b>MUN</b>	<b>25.48</b>	<b>Benthic</b>	<b>Tapella &amp; Lovrich (2006)</b>
<i>Munida</i> spp. (juvenile)	Juvenile lobster krill	JM	0.31	Pelagic	Tapella & Lovrich (2006)
<i>Themisto gaudichaudii</i>	NA	TG	0.83	Pelagic	Brickle et al. (2009)
<i>Campylonotus vagans</i>	Prawn	CAV	<0.01	Benthic	Thatje et al. (2001)
Amphipoda (benthic)	Benthic amphipod	B.AMP	<0.01	Benthic	Brickle, P (pers. com.)
Amphipoda (pelagic)	Pelagic amphipod	P.AMP	<0.01	Pelagic	Brickle, P (pers. com.)
Amphipoda (unknown)	Amphipod	AMP	<0.01	NA	NA
Brachyura	Crab	Crab	<0.01	Benthic	Brickle, P (pers. com.)
<i>Euphausiid</i> spp.	Krill	EUA	0.02	Pelagic	Brickle, P (pers. com.)
Paguridae	Hermit crab	H.Crab	0.06	Benthic	Brickle, P (pers. com.)
Sphaeromatidae	Isopod	ISO	0.16	NA	NA
<b>Fish</b>					
<b><i>Patagonotothen</i> spp.<sup>b</sup></b>	<b>Rock cod</b>	<b>PATA</b>	<b>46.55</b>	<b>Benthic</b>	<b>Brickle et al. (2006)</b>
<b><i>Sprattus fuegensis</i></b>	<b>Falkland herring</b>	<b>SAR</b>	<b>11.44</b>	<b>Pelagic</b>	<b>Zenteno et al. (2015)</b>
<b>Fish (juvenile)</b>	<b>Juvenile fish</b>	<b>JF</b>	<b>2.66</b>	<b>NA</b>	<b>NA</b>
<b><i>Micromesistius australis</i></b>	<b>Southern blue whiting</b>	<b>BLU</b>	<b>1.02</b>	<b>Pelagic</b>	<b>Brickle et al. (2009)</b>
<i>Cottoperca gobio</i>	Bull blenny	CGO	0.19	Benthic	Laptikhovsky & Arkhipkin (2003)
<i>Champscephalus esox</i>	Icefish	CHE	0.14	Demersal	Hureau (1985)
<i>Agonopsis chiloensis</i>	Snail fish	AGO	0.08	Demersal	Nakamura et al. (1986)
Perciformes	NA	Perciform	0.03	NA	NA
<i>Salilota australis</i>	Red cod	BAC	0.03	Benthic	Brickle et al. (2011)
<i>Dissostichus eleginoides</i>	Patagonian toothfish	TOO	0.01	Pelagic	Laptikhovsky et al. (2006)
<i>Macruronus magellanicus</i>	Patagonian grenadier	WHI	<0.01	Demersal	Amato & Carvalho (2005)
<i>Harpagifer bispinis</i>	Magellanic spiny plunderfish	HAB	<0.01	Benthic	Gon & Heemstra (1990)
<i>Genypterus blacodes</i>	Pink cusk eel	KIN	<0.01	Benthic	Nyegaard et al. (2004)
<i>Thysanopsetta naresi</i>	Small flounder	THN	<0.01	Benthic	Nakamura et al. (1986)
<i>Ilucoetes fimbriatus</i>	Eelpout	EEL	<0.01	Benthic	Matallanas & Corbella (2012)

Scientific Name	Common Name	Code	% IRI	Habitat	Source
<b>Cephalopod</b>					
<i>Doryteuthis gahi</i>	Patagonian squid	LOL	9.87	Benthic	Arkhipkin <i>et al.</i> (2013)
<i>Onykia ingens</i>	Greater hooked squid	ING	0.47	Benthic	Jackson et al. (1998)
<i>Gonatus antarcticus</i>	NA	GON	0.23	Pelagic	Arkhipkin & Laptikhovsky (2010)
Cephalopoda (juvenile)	Juvenile squid	JC	0.22	NA	NA
<i>Mussoctopus</i> sp.	Octopus	Octo	0.11	Benthic	Cherel, Y (pers. com.)
<i>Semirossia patagonica</i>	Bobtail squid	SRP	0.08	Benthic	Rodhouse et al. (1992)
<b>Other</b>					
Gastropod	Sea snail	Gastropod	<0.01	NA	NA
Nacellid	Limpet	Limpet	<0.01	NA	NA
Mytilid	Mussel	Mussel	<0.01	NA	NA
Venerid	Clam	Clam	<0.01	NA	NA
Polychaeta	Polychaete worm	Polychaete	<0.01	NA	NA

a: Conflicting views exist on whether or not there are two separate species, *Munida gregaria* and *Munida subrugosa* (Tapella & Lovrich 2006), therefore, average data for the two morphs was used.  
b: As recognised in Handley et al. (2015) species likely from this genus are *Patagonotothen ramsayi* and *Patagonotothen tessellata*. Therefore, average length and mass data were used for *Patagonotothen* spp based on the two species.

**Table A2.4:** Median value and range of prey size for the major prey items consumed by gentoo penguins at the Falklands Islands during the 2011, 2012 and 2013 austral summers. Sampling occurred during the incubation (I), guard (G) and crèche stages (C) across four colonies: Steeple Jason (SJ), Cow Bay (CB), Bull Point (BP) and Bull Roads (BR) The major prey items were determined through the percentage index of relative importance and were (LOL) Patagonian squid *Doryteuthis gahi*, (PATA) Rock cod *Patagonotothen* spp., (SAR) Falkland herring *Sprattus fuegensis*, (BLU) southern blue whiting *Micromesistius australis* and (MUN) lobster krill *Munida* spp. Size of these prey items were determined through reconstituted length via hard part remains. Therefore, not included in this list are juvenile fish which were typically smaller than 40 mm total length (determined from the few intact specimens) but do not have associated regression equations for hard part remains.

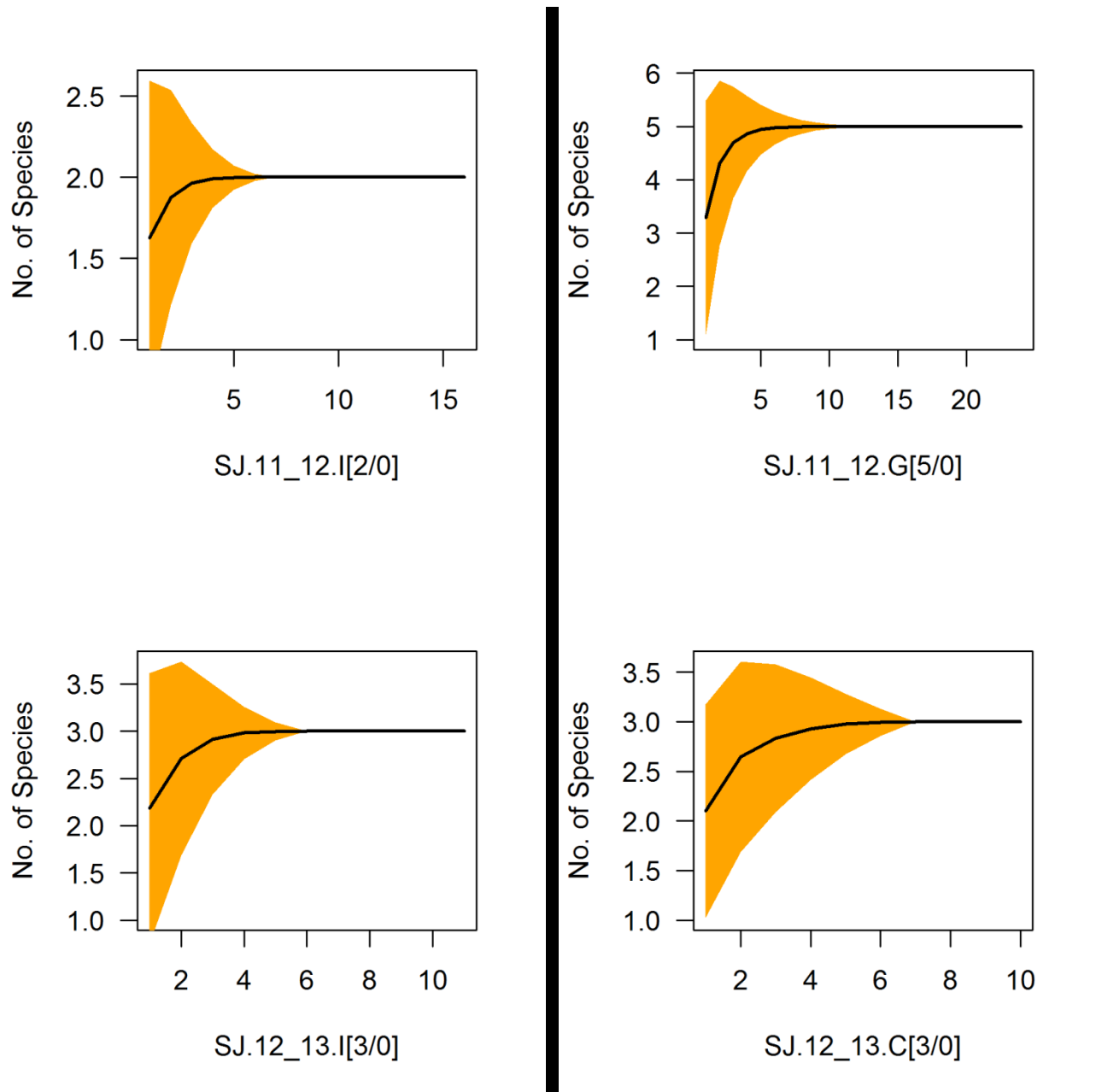
Year	Stage	Species	Colony	Median (mm)	Range (min)	Range (max)	n
2011	I	LOL	SJ	82.6	41.0	152.4	17
2011	I	PATA	SJ	176.8	94.1	230.7	6
2011	I	SAR	SJ	123.1	100.3	203	247
2011	G	BLU	BP	11.4	11.4	11.4	1
2011	G	BLU	CB	49.5	49.5	49.5	1
2011	G	LOL	BP	110.5	27.2	201.4	47
2011	G	LOL	CB	82.6	47.9	166.4	75
2011	G	LOL	SJ	68.7	27.2	110.5	13
2011	G	MUN	BP	23.5	11.9	33.8	402
2011	G	MUN	CB	26.1	20.6	31.2	8
2011	G	MUN	SJ	20.8	12.7	26.9	20
2011	G	PATA	BP	79.7	61.7	194.7	513
2011	G	PATA	CB	88.7	61.7	295.4	782
2011	G	PATA	SJ	148.0	86.9	266.6	135
2011	G	SAR	BP	103.2	88.9	117.4	2
2011	G	SAR	CB	174.4	151.6	311.3	7
2011	G	SAR	SJ	174.4	157.3	220.1	26
2011	C	BLU	CB	49.5	49.5	49.5	1
2011	C	LOL	BP	37.6	20.4	166.4	26
2011	C	LOL	CB	96.5	41.0	131.4	27
2011	C	MUN	BP	19.0	15.4	21.8	29
2011	C	PATA	BP	106.6	90.5	191.1	42
2011	C	PATA	CB	101.3	61.7	173.2	191
2011	C	SAR	BP	117.4	100.3	134.5	10
2012	I	LOL	SJ	120.9	103.5	138.4	8
2012	I	PATA	SJ	198.3	198.3	198.3	1
2012	I	SAR	SJ	168.7	128.8	191.6	19
2012	G	BLU	BR	12.7	8.9	16.5	2
2012	G	BLU	CB	20.3	14.0	29.2	6
2012	G	LOL	BP	124.4	89.6	201.4	58
2012	G	LOL	BR	124.4	89.6	166.4	75
2012	G	LOL	CB	96.5	61.8	138.4	33
2012	G	MUN	BP	25.7	18.3	31.5	118
2012	G	MUN	BR	23.4	18.3	29.5	59
2012	G	MUN	CB	23.1	18.9	26.7	16
2012	G	PATA	BP	83.3	58.1	230.7	248
2012	G	PATA	BR	76.1	58.1	166	368

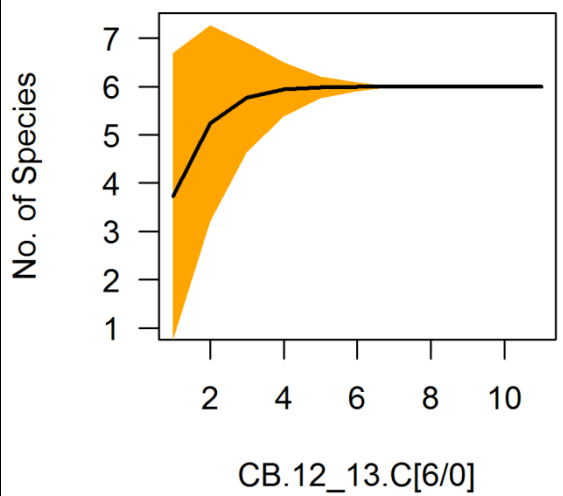
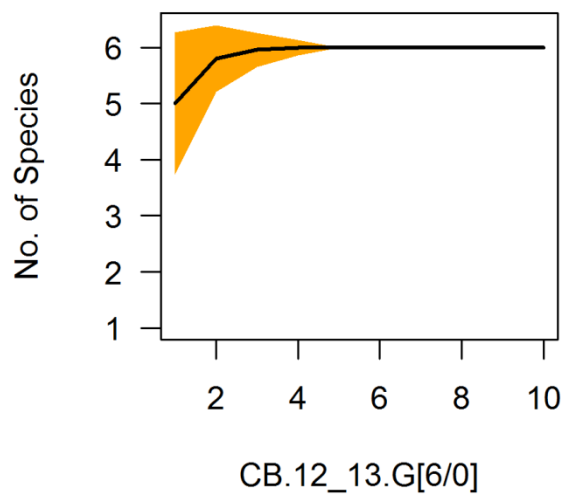
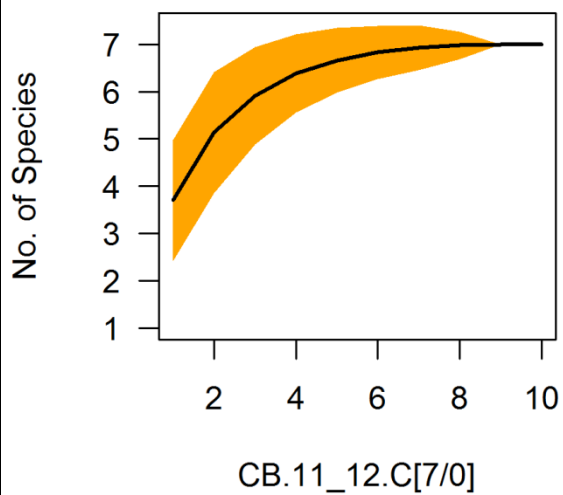
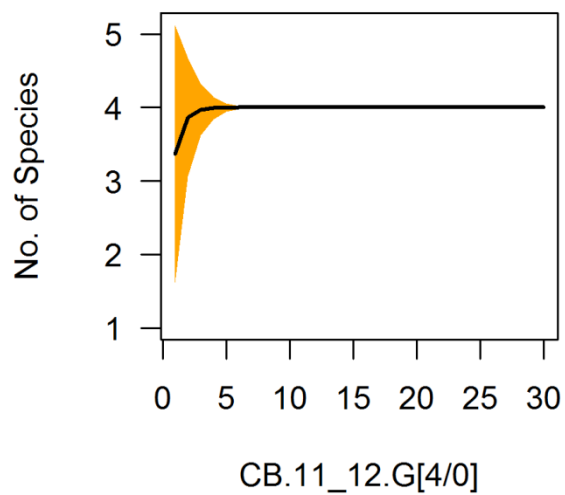
2012	G	PATA	CB	86.9	50.9	205.5	208
2012	G	SAR	BP	168.7	168.7	168.7	1
2012	G	SAR	SJ	157.3	157.3	157.3	1
2012	C	BLU	CB	39.4	21.6	52.1	15
2012	C	BLU	SJ	24.1	19.0	57.2	3
2012	C	LOL	BP	110.5	54.9	138.4	4
2012	C	LOL	BR	103.5	34.1	159.4	36
2012	C	LOL	CB	82.6	61.8	103.5	74
2012	C	LOL	SJ	68.7	54.9	110.5	9
2012	C	MUN	BP	25.2	17.9	30.7	141
2012	C	MUN	BR	24.6	17.9	30.3	208
2012	C	MUN	CB	21.1	20.4	21.8	2
2012	C	PATA	BP	94.1	25.8	173.2	86
2012	C	PATA	BR	90.5	36.5	155.2	159
2012	C	PATA	CB	86.9	72.5	119.2	58
2012	C	PATA	SJ	192.9	158.8	230.7	6
2012	C	SAR	BR	151.6	134.5	174.4	4
2012	C	SAR	CB	180.1	157.3	197.3	20
2012	C	SAR	SJ	168.7	151.6	180.1	9
2013	G	BLU	CB	31.8	14.0	54.6	539
2013	G	LOL	BR	79.1	27.2	138.4	16
2013	G	LOL	CB	75.7	20.4	159.4	47
2013	G	MUN	BR	16.5	6.4	28.3	538
2013	G	MUN	CB	13.5	9.8	19.9	106
2013	G	PATA	BR	72.5	54.5	140.8	33
2013	G	PATA	CB	94.1	65.3	198.3	90
2013	G	SAR	CB	191.6	185.9	197.3	2

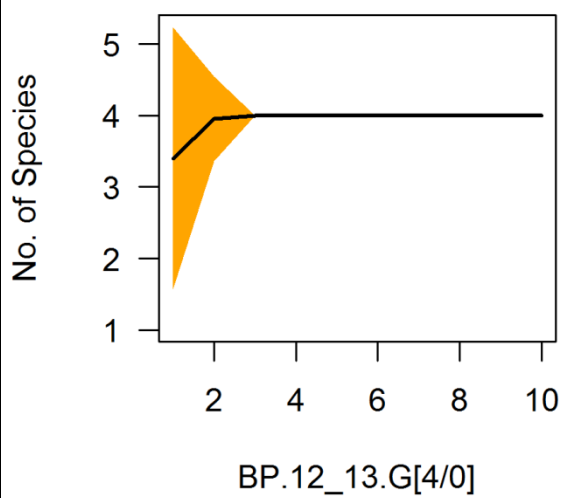
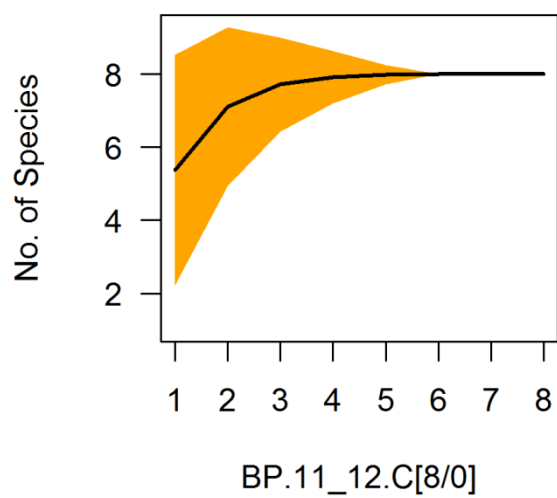
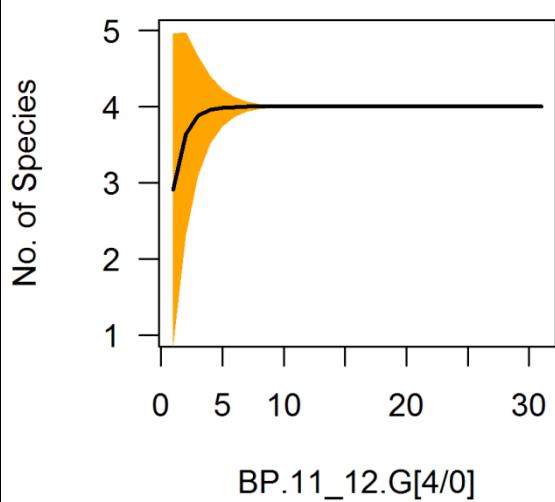
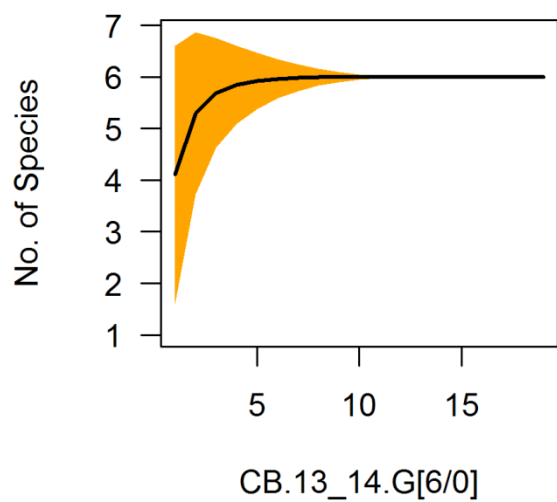
**Table A2.5:** Dietary niche metrics, trophic niche width (TNW) and degree of diet specialisation (V) determined for gentoo penguins breeding at the Falkland Islands. Stomach samples were analysed from four colonies: Bull Point (BP), Bull Roads (BR), Cow Bay (CB) and Steeple Jason (SJ), during the austral summers of 2011, 2012 and 2013, from various breeding stages: incubation (I), guard (G) and crèche (C). Refer to Table A2.3 for species abbreviations. Note, only those prey with %IRI > 1 were used for the analysis, however, the top three prey items for each sampling period are shown here for detail.

Sample Period	Diet Metrics		Prey		
	TNW	V	Primary	Secondary	Tertiary
SJ.2011.I	0.40	0.12	SAR	LOL	MUN
SJ. 2011.G	0.95	0.31	PATA	MUN	SAR
SJ.2012.I	0.65	0.20	SAR	ING	LOL
SJ. 2012.C	0.80	0.33	SAR	LOL	GON
CB. 2011.G	1.07	0.35	PATA	LOL	TG
CB. 2011.C	1.17	0.44	PATA	LOL	GON
CB. 2012.G	0.87	0.21	PATA	LOL	JC
CB. 2012.C	1.31	0.52	SAR	PATA	LOL
CB.2013.G	1.51	0.48	BLU	MUN	LOL
BP. 2011.G	1.10	0.43	MUN	PATA	LOL
BP. 2011.C	1.51	0.50	MUN	PATA	JF
BP. 2012.G	1.15	0.44	PATA	MUN	LOL
BP. 2012.C	1.27	0.41	JF	MUN	PATA
BR. 2012.G	1.15	0.33	PATA	LOL	MUN
BR. 2012.C	1.39	0.34	MUN	PATA	JF
BR.2013.G	0.36	0.10	MUN	LOL	PATA

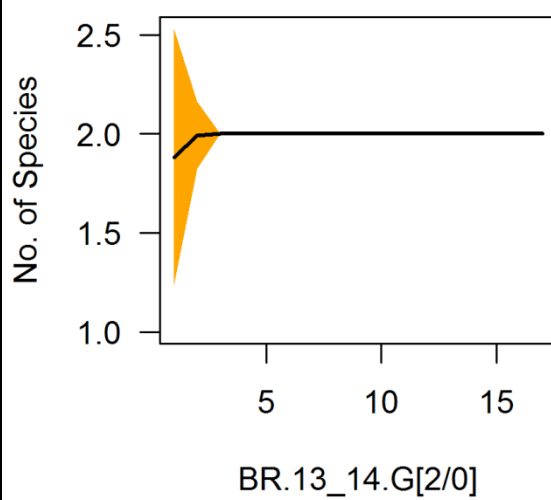
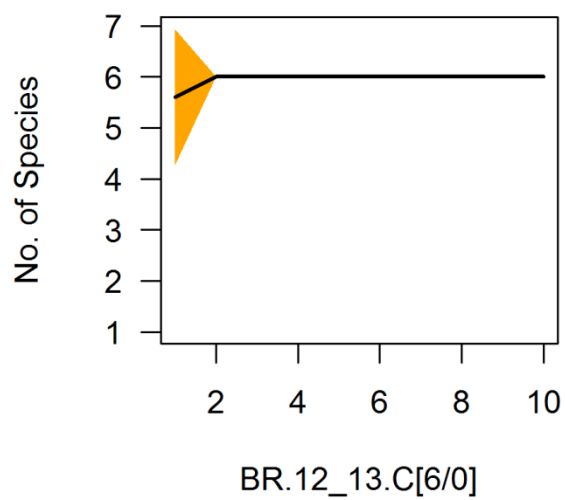
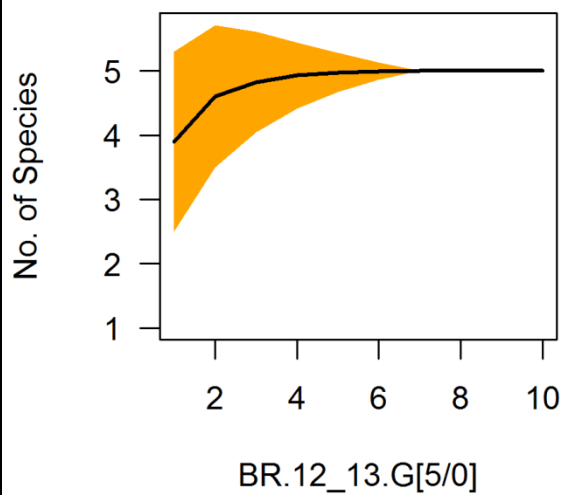
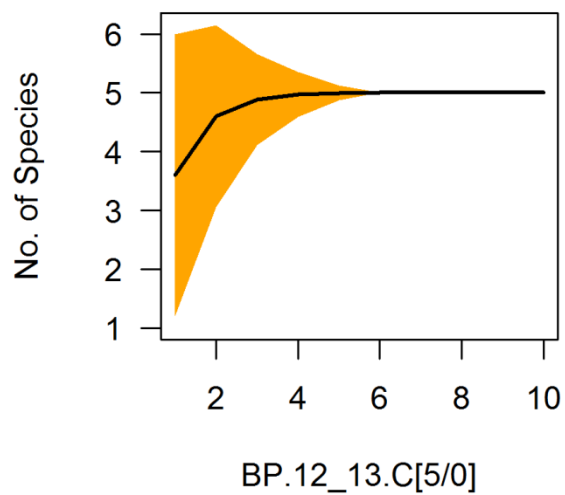
**Figure A2.1:** Prey species accumulation curves, from gentoo penguin stomach contents, for each sampling period at four colonies: Steeple Jason (SJ), Cow Bay (CB), Bull Point (BP) and Bull Roads (BR) at the Falklands Islands. Sampling occurred in the breeding season, during the austral summers of 2011 (11\_12), 2012 (12\_13) and 2013 (13\_14) over various breeding stages: incubation (I), guard (G) and crèche (C). Square brackets represent [Chao estimator/Chao standard error] (Chao 1987). The species accumulation curves are shown in bold with 95% confidence intervals represented by the shaded area. Prey item data for each plot includes those prey which had >1% IRI in the given sampling period.







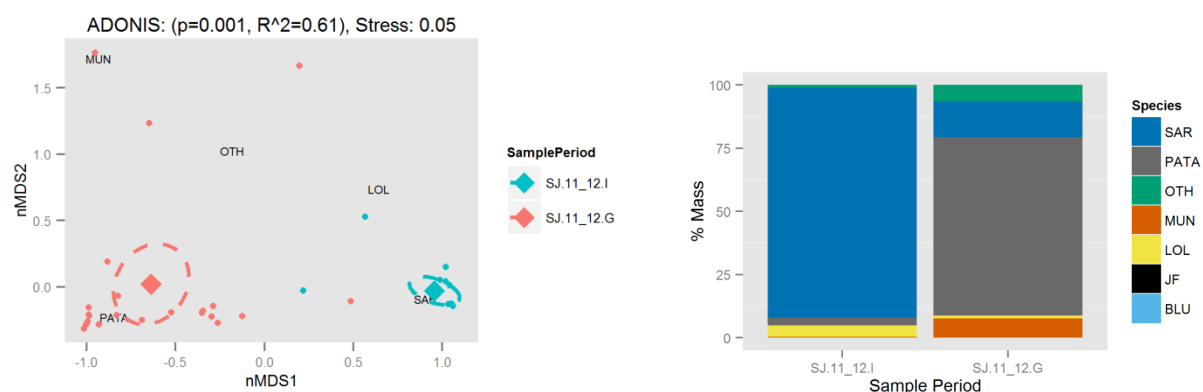




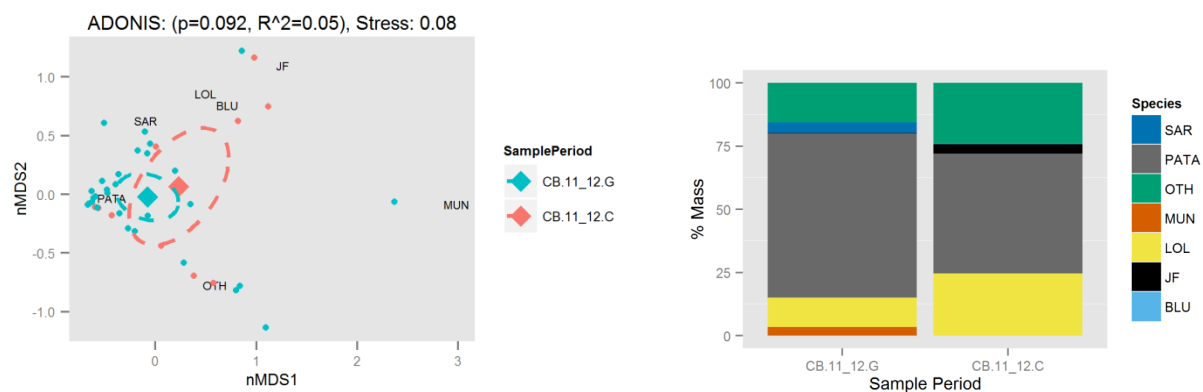
**Figure A2.2 (A-G):** Variation in diet during the breeding period depicted by two-dimensional nMDS ordination, showing grouping of diet samples, and percentage mass contribution for main prey items for gentoo penguins at the Falklands Islands. Samples were collected from four colonies: Steeple Jason (SJ), Cow Bay (CB), Bull Point (BP) and Bull Roads (BR); over two breeding seasons in the austral summer: 2011 (11\_12) and 2012 (12\_3); at different stages within the breeding period: incubation (I), guard (G) and crèche (C).

Regarding the nMDS plots: To facilitate comparison among sampling groups, 95% confidence levels (function: ordiellipse) and group centroids (diamonds) were overlaid on the nMDS plots. Additionally, the position of the major prey species is given, allowing one to identify which prey species contributes most to a given individual. Interpretation of the NMDS plot relies on how low the stress value is for a given dimension (typically 2-D or 3-D), where stress >0.2 is seen to be undesirable (Quinn & Keough 2002). The final orientation of the plot is arbitrary and only relative distances between objects are relevant for interpretation (Quinn & Keough 2002).

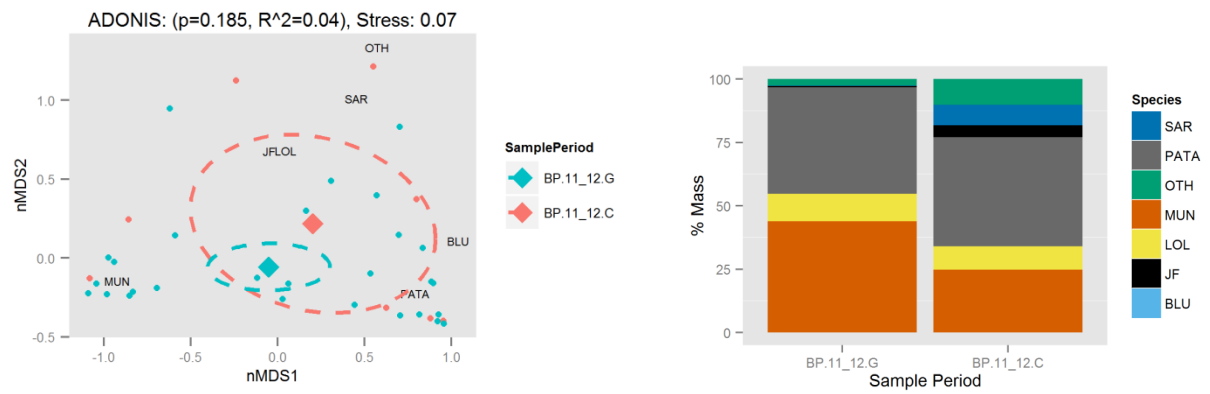
#### A: Steeple Jason, 2011/12: Incubation vs Guard



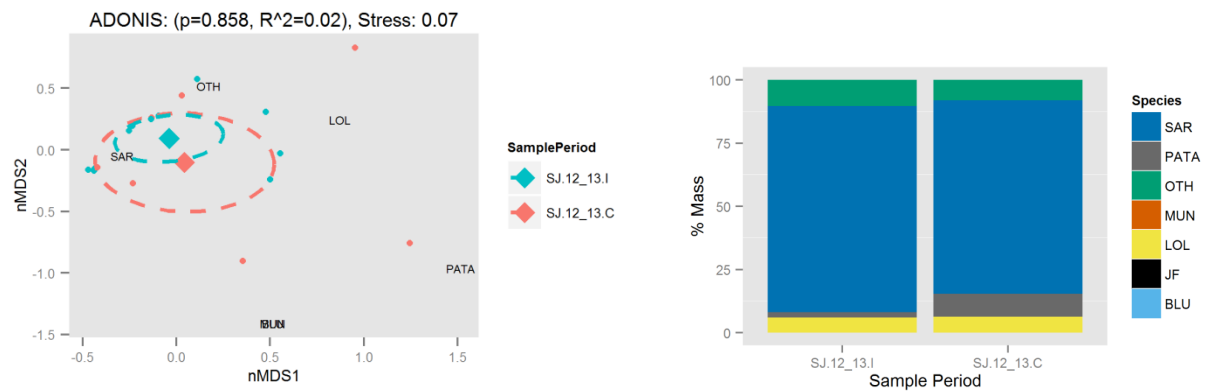
#### B: Cow Bay, 2011/12: Guard vs Crèche



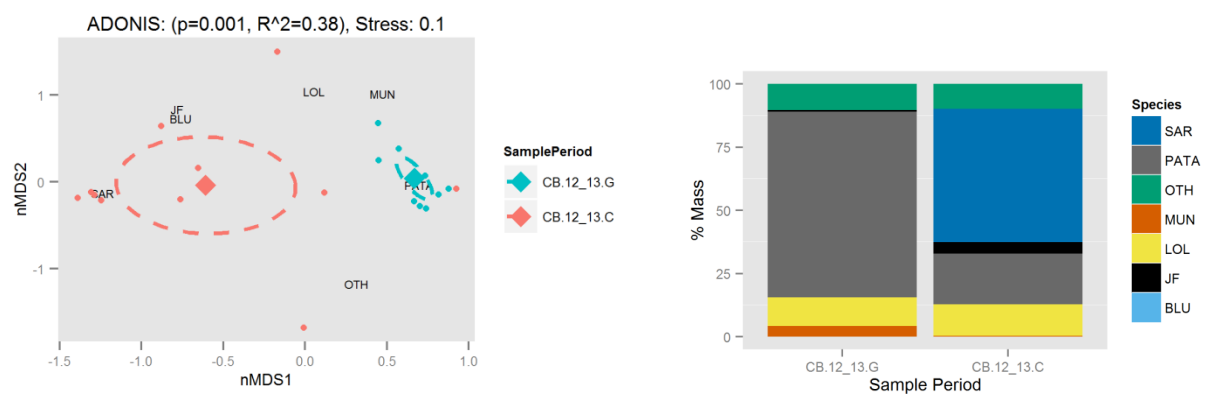
### C: Bull Point, 2011/12: Guard vs Crèche



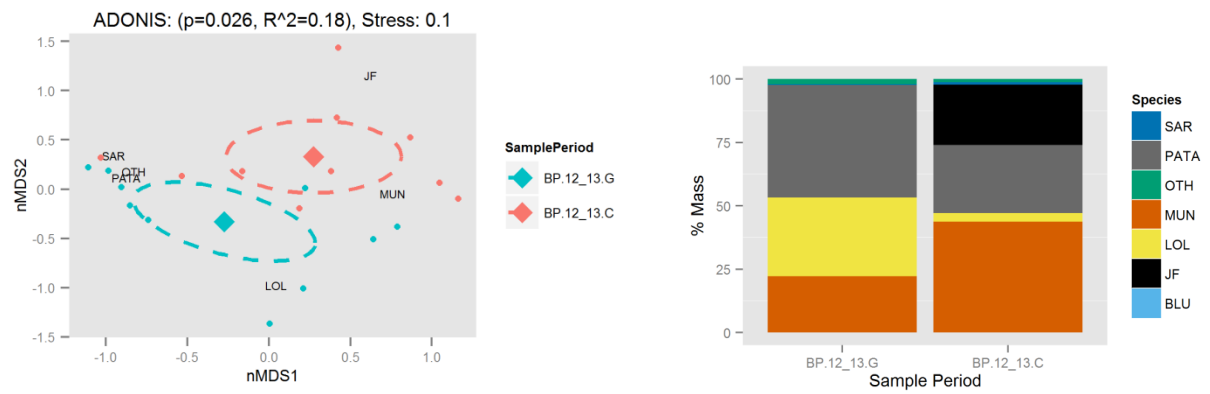
### D: Steeple Jason, 2012/13: Incubation vs Crèche



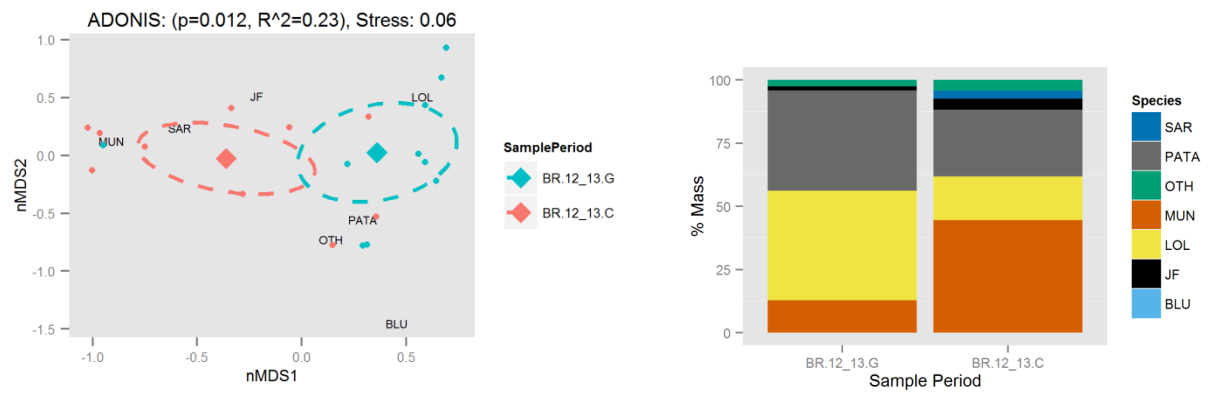
### E: Cow Bay, 2012/13: Guard vs. Crèche



# F: Bull Point, 2012/13: Guard vs. Crèche

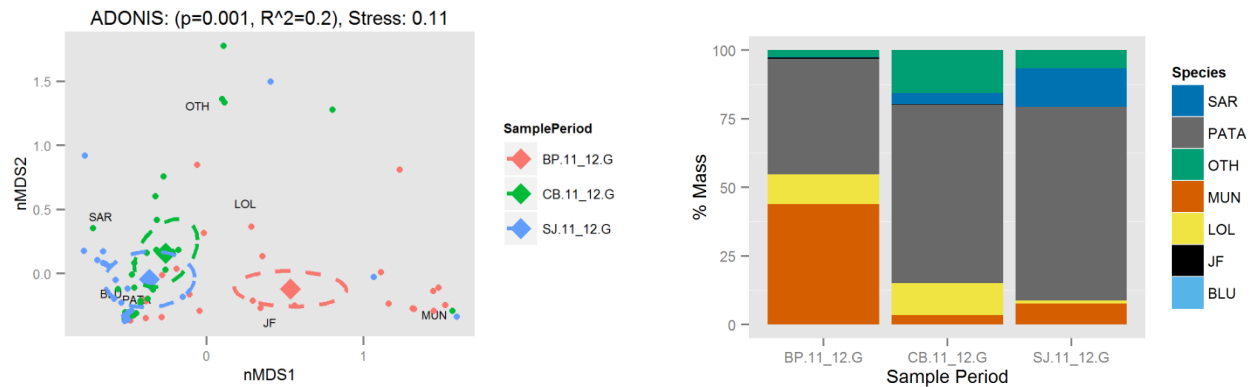


# G: Bull Roads, 2012/13: Guard vs. Crèche

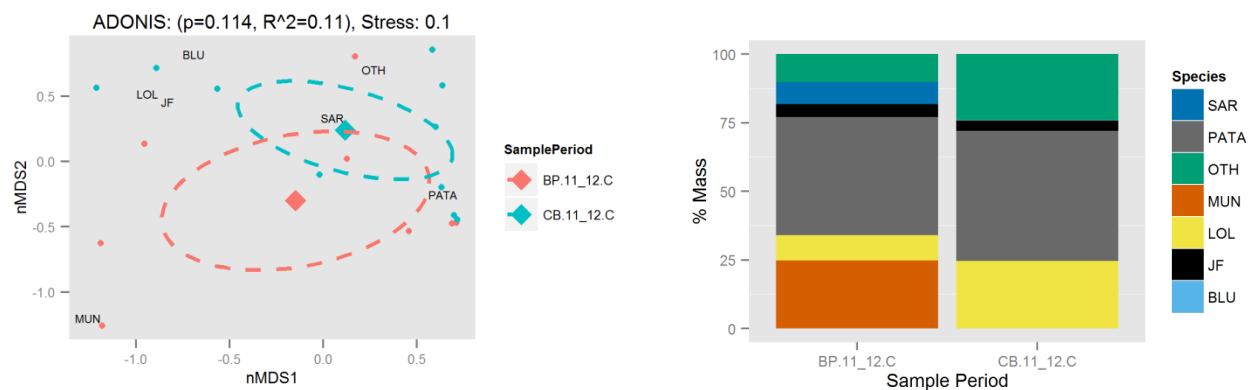


**Figure A2.3 (A-E):** Inter-colony variation in diet depicted by two-dimensional nMDS ordination, showing grouping of diet samples, and percentage mass contribution for main prey items for gentoo penguins at the Falklands Islands. Samples were collected from four colonies: Steeple Jason (SJ), Cow Bay (CB), Bull Point (BP) and Bull Roads (BR); over three breeding seasons in the austral summer: 2011 (11\_12) and 2012 (12\_13) and 2013 (13\_14); at different stages within the breeding period: guard (G) and crèche (C).

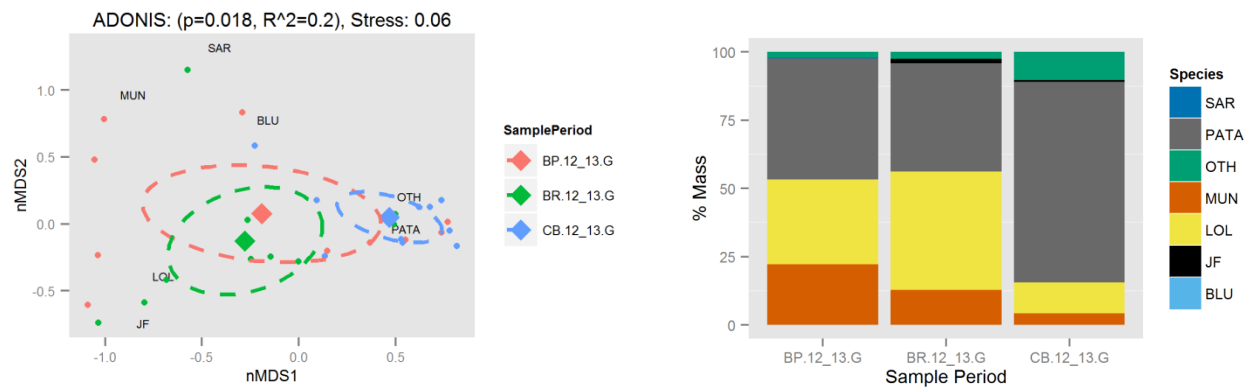
A: Guard stage of 2011/12 season, across three colonies: SJ, CB and BP.



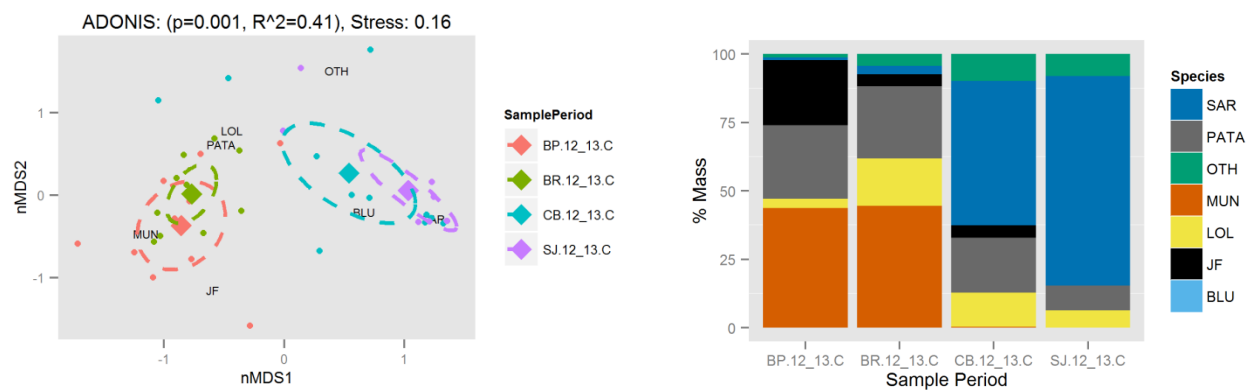
B: Crèche stage of 2011/12 season, across two colonies: CB and BP.



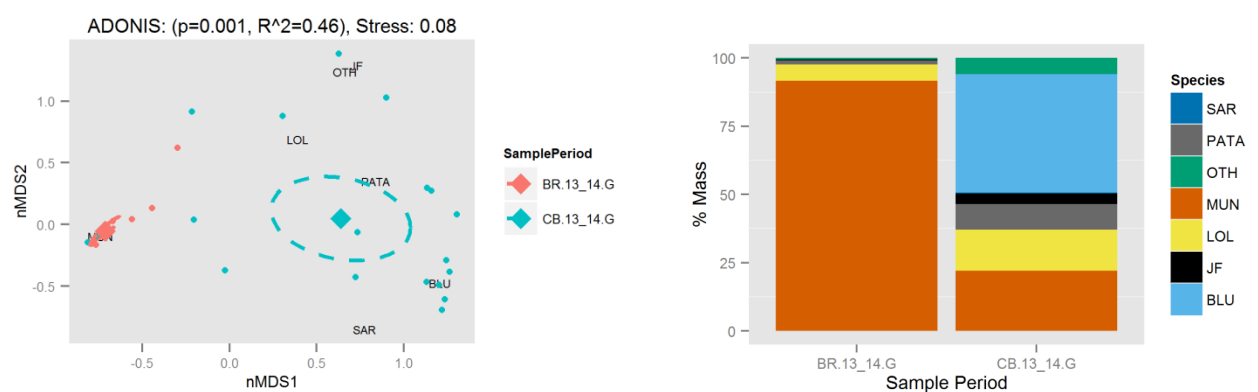
C: Guard stage of 2012/13, across three colonies: CB, BP and BR.



D: Crèche stage of 2012/13, across four colonies: SJ, CB, BP and BR.



E: Guard stage of 2013/14, across two colonies: CB and BR



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### **Appendix: Chapter 3 (Model Transferability)**

Figures A3.1-A3.4 below indicate model transferability for distribution models generated from gentoo penguin tracking data at the Falkland Islands during the guard period of breeding. The top panel of each figure represents the training data while the bottom three panels represent the test data. Within each panel the original Presence/Absence distribution data is displayed, followed by the predicted model output and then the calibration plot. Four models were developed: One for each colony (BR Bull Roads and CB Cow Bay) over two seasons (1213 = 2012/13 and 1314 = 2013/14).

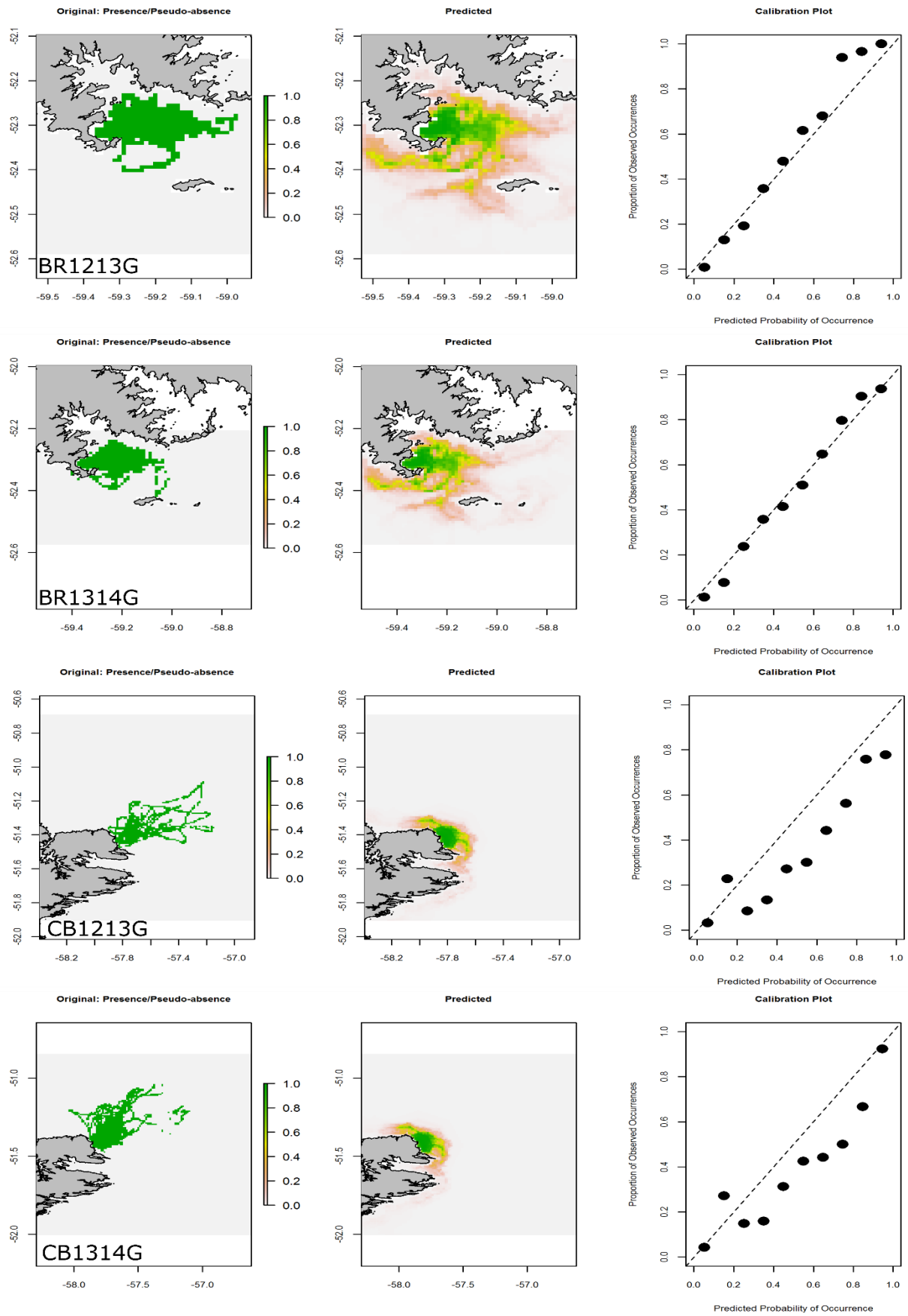


Figure A3.1: BR1213 model (training data, top panel) predicted to test data (bottom three panels)

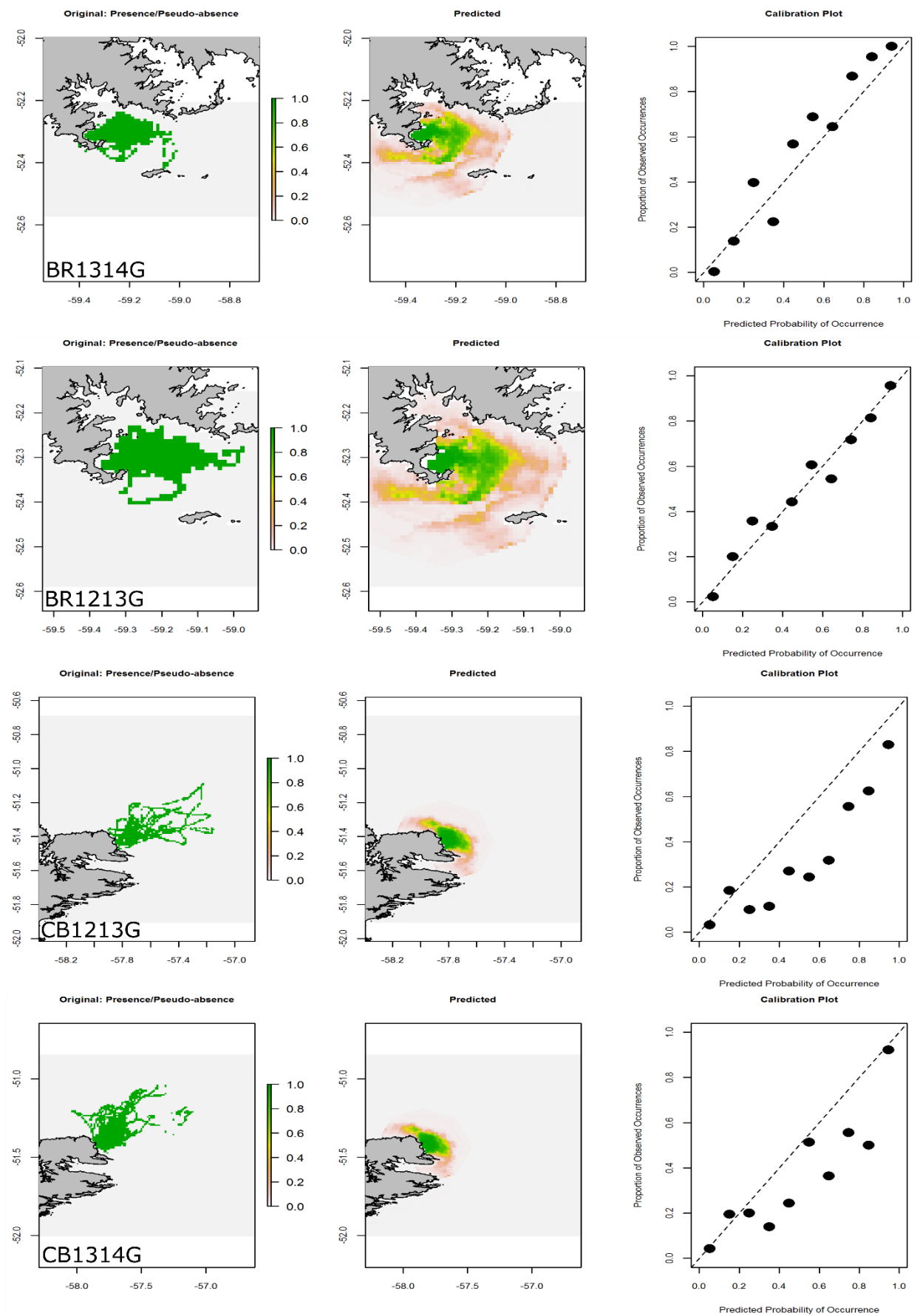


Figure A3.2: BR1314 model (training data, top panel) predicted to test data (bottom three panels)

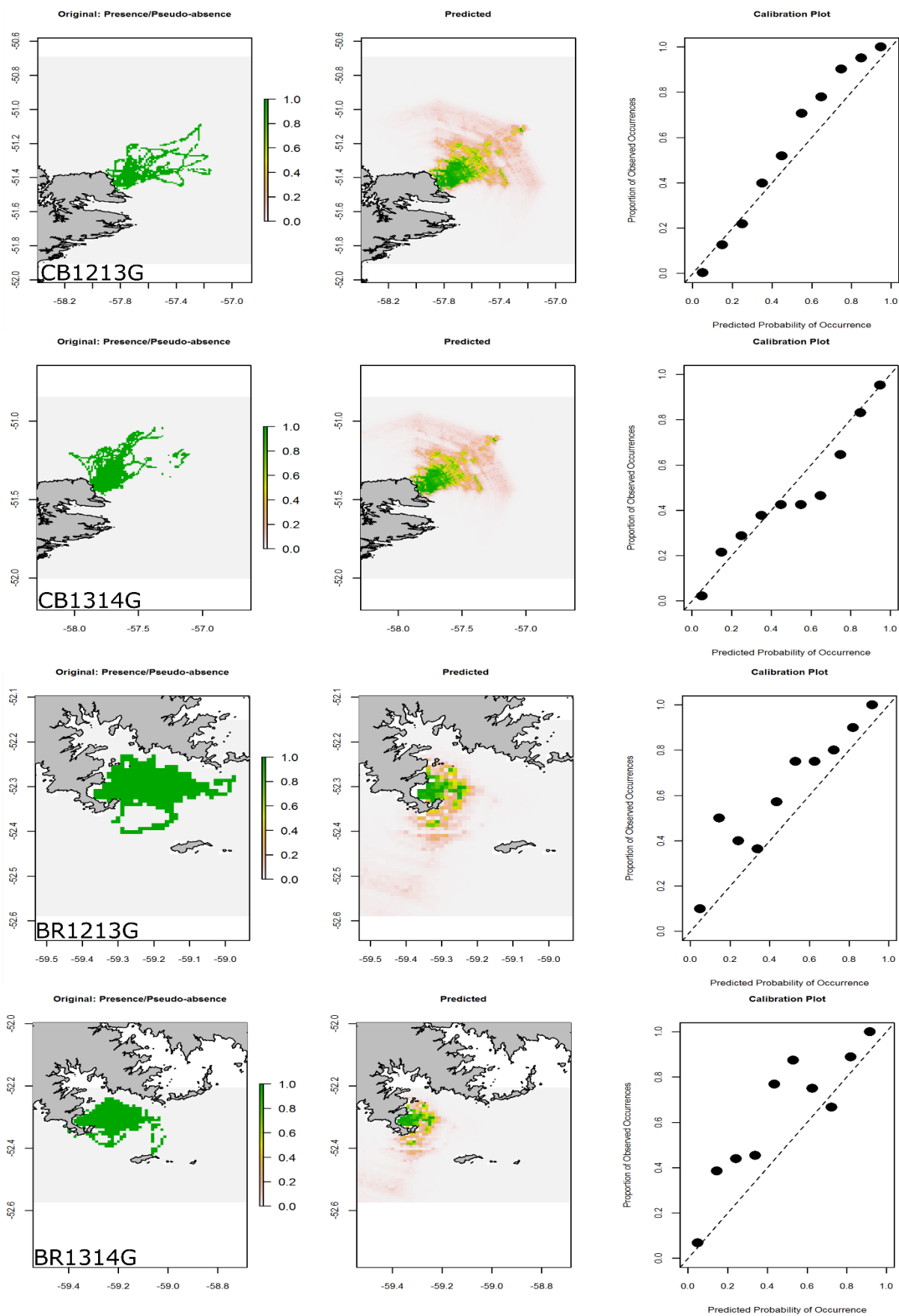


Figure A3.3: CB1213 model (training data, top panel) predicted to test data (bottom three panels)

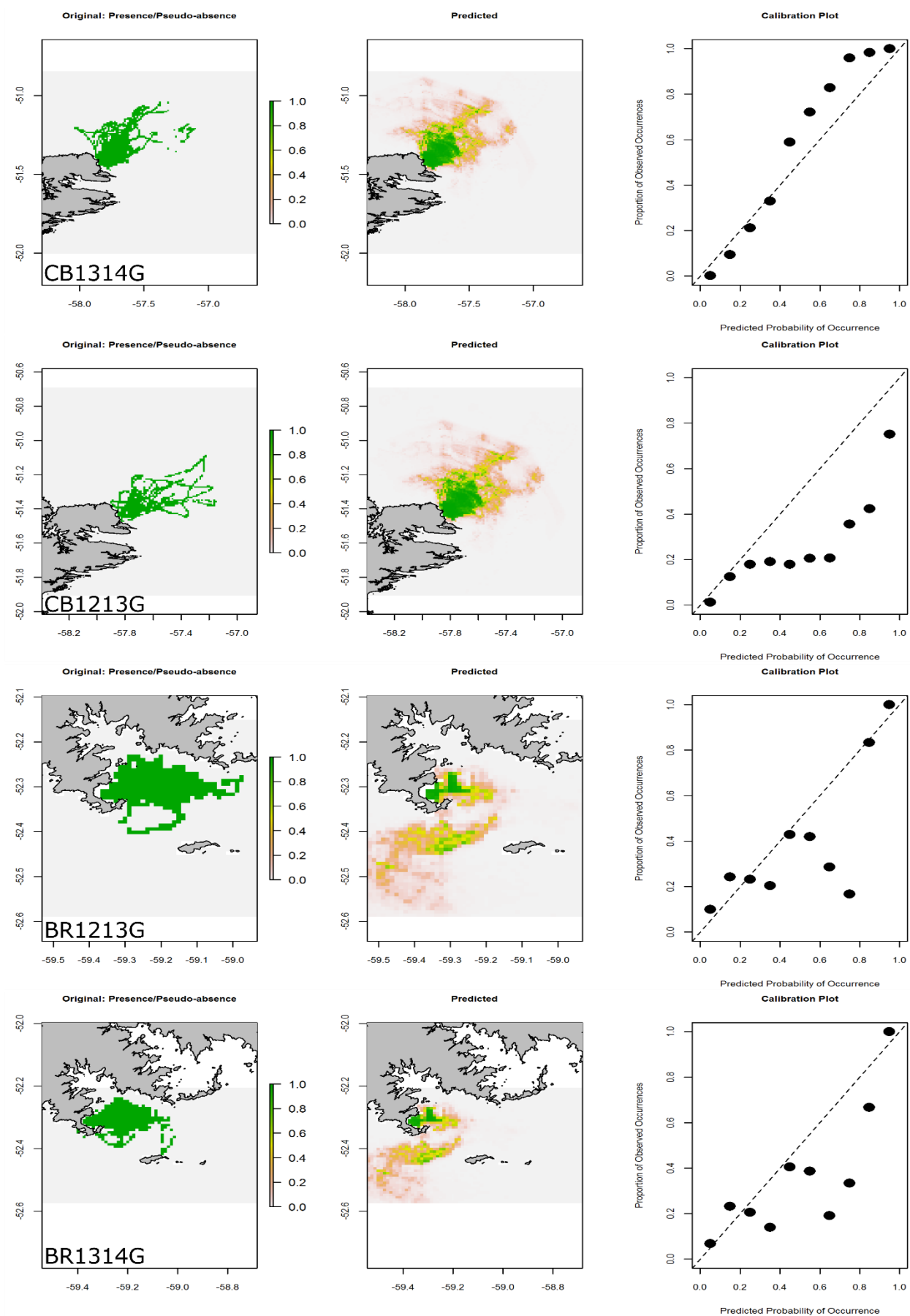


Figure A3.4: CB1314 model (training data, top panel) predicted to test data (bottom three panels)

## **Appendix: Chapter 4 (Video analysis)**

### **Video analysis and quantification of swarm density**

Cameras used in my study were Replay XD 1080 HD cameras (Stable Imaging Solutions, LLC, USA). These are commercially available action cameras which have a field of view of 135°. Various frame rate and video quality options can be chosen on the camera, however, for the purpose of my study I used the highest quality setting of 1080p at 30 frames per second. The cameras record continuously once they are turned on, hence the need to deploy on birds that were heading to the sea. Video data was analysed using a freeware approach. Specifically, video was converted from the format .MOV to .AVI using MPEG Streamclip (Version 1.2) in order to annotate the footage using the frame based coding option in Solomon Coder (Version 16.06.26). Interpolating the time from different devices and quantification of annotated video files was done with custom code in R. Unique behavioural events (still images) were then extracted by frame number, using ffmpeg (Version N-82324-g972b358).

Below outlines the detailed approach used and step by step instructions on software availability and use.

Note: Before beginning to use video data for analyses one should be aware of the many technical nuances with video data such as PAL versus NTSC, codecs, and frame rate, etc. I suggest discussion with a technically competent advisor beforehand.

### **MPEG Streamclip**

While other proprietary and freeware options exist, we suggest the use of the freeware program MPEG Streamclip (Version 1.2). This gives the user an option to batch convert multiple files from one format to many other options, and specifically to .AVI.

The following steps can be used:

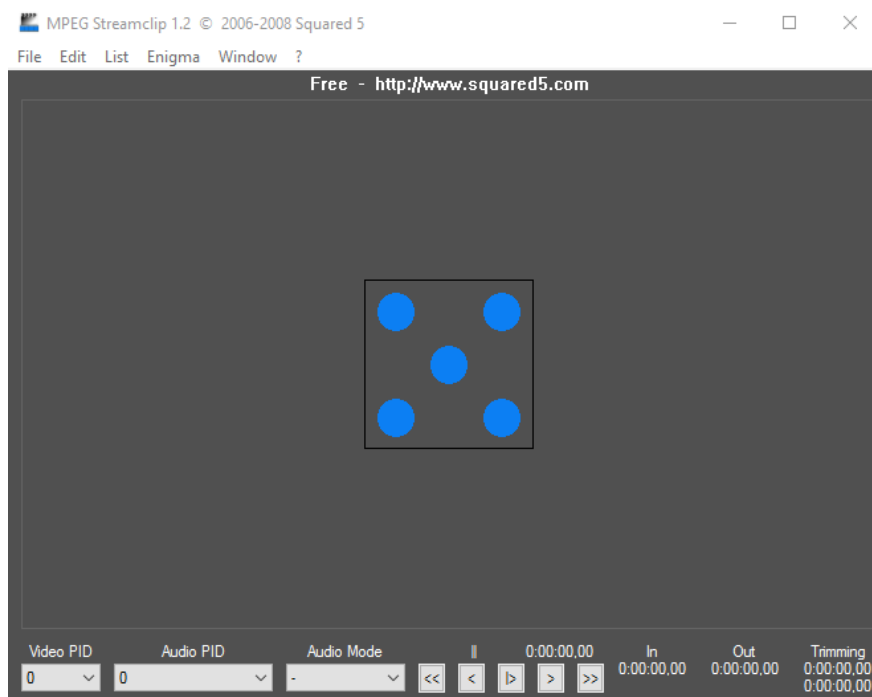
Step 1: Place all files that need to be converted into one folder. Note: I advise giving each file a unique coding.

- For example:  
Species\_Location\_DeploymentDate\_Deployment\_VideoReference\_CommonDescriptor
- CommonDescriptor refers to a common term in all files. E.g. "Vid". It often helps for sourcing files through a coding based approach.

Step 2: Install MPEG Streamclip (<http://www.squared5.com/>)

Step 3: Open





Step 4: Select: List -> Batch List

Step 5: Select: Add Files...

Step 6: Select: All files for conversion

Step 7: From the drop down menu select: Export to AVI

Step 8: Select: output file location

Step 9: Select: To Batch

- Note: You should be able to leave all settings in their default mode. If you want to compress videos you can select alternate settings.

Step 10: Select: Go

- Note: The conversion will take some time so it is well worth leaving overnight or utilising some other free time.

### **Solomon Coder**

Once your videos have been converted you will be able to use the frame based coding option in Solomon Coder, available for download from: <https://solomoncoder.com/>

Before using Solomon Coder I suggest reading all the instruction manuals. An important prerequisite is to have an understanding of what possible categories of behaviours you might

encounter in your video footage. Therefore, it is necessary to watch all your video footage prior to setting up the frame based coding option and beginning detailed annotation.

In Solomon Coder you will have the option to create event buttons (key board short cuts). I suggest the use of colour for different behavioural categories and ensure the option “display markers” is selected when creating buttons. This will make it clearer to see what you are currently coding for.

Solomon Coder offers the option for various summary statistics. While these were not used for my study I suggest future studies to consider these options as updated versions of the software are released.

## R

Quantification of video footage during my study was achieved with R version 3.2.1 (R Development Core Team). The code supplied provides the necessary starting steps for dealing with multiple deployment files and quantification(R Core Team 2013) of events.

Deployment files used in scripts 1 and 2 are small example files of hypothetical data.

Script 1: “P1\_AnimalCam\_SuppCode\_Merge Trips.R”

- This script provides an outline for merging multiple files from a single deployment, as well merging all deployments to create a single overall data frame.
- Note: There are technical nuances with video data such as PAL versus NTSC, codecs, and frame rate. Regarding frame rate specifically; some manufacturers state a recording rate of 30 frames per second (fps), while in actual fact videos are recorded at 29.97 fps. Script 1 attempts to deal with nuances of frame rate irrespective of the fps setting.

Script 2: “P2\_AnimalCam\_SuppCode\_Feeding events.R”

- This script will give reference to each unique feeding event, duration of individual events and when the first feeding event occurred.
- This script will be suitable for amendment should the user require quantification of different event types (e.g. intraspecific interactions, etc)

Script 3: “P3\_AnimalCam\_SuppCode\_MergeCAMtoTDRandGPS”

- This script provides the mechanism to interpolate data from different devices (the TDR and GPS) to the device of interest (the CAM data)
  - Users should make sure of clock alignment across different devices. Preferably with visual inspection in a preferred software. For example: IGOR Pro

(WaveMetrics, Inc.) with the Ethographer add on (Although, this is proprietary software).

- Data used in this script is an example of actual data collected during my study
- While users will need to follow the appropriate steps pre-processing TDR and GPS data this script will enable users to not only match time stamps and data, but also view cross sections of dive profiles with feeding events.
- Further sub-setting of required data can be achieved with the data frame produced in this script. Plotting of GPS data can also be easily achieved with a preferred GIS software.

## FFmpeg

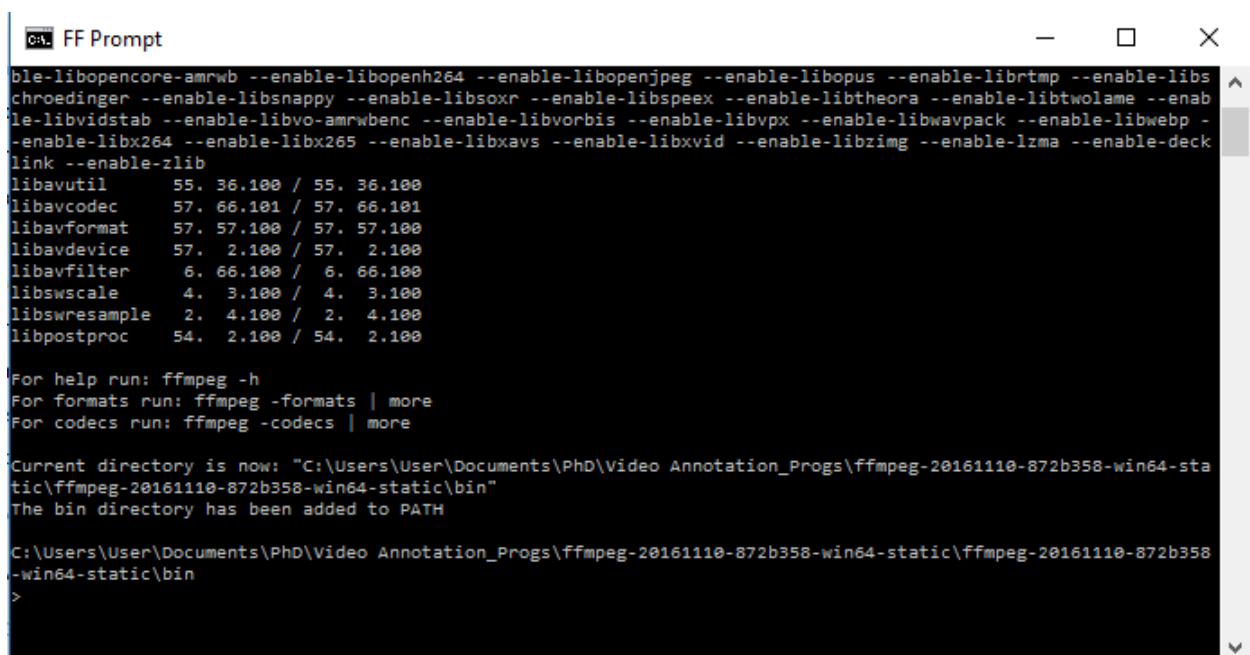
This is a free software project that produces libraries and programs for handling multimedia data. FFmpeg can be called directly with MATLAB and likely other proprietary software, however, for the purpose of keeping my approach based on freeware I used the source program.

Available for download at: <https://ffmpeg.org/download.html>

The following steps can be used to extract video frames

Step 1: Utilising your overall data frame produced in R, subset out events of interest and store this data frame in an appropriate location

Step 2: Open the FFmpeg batch file which should bring you to the following window



```
FF Prompt
ble-libopenh264 --enable-libopenh264 --enable-libopenjpeg --enable-libopus --enable-librtmp --enable-libs
chroedinger --enable-libsnappp --enable-libsoxr --enable-libspeex --enable-libtheora --enable-libtwolame --enab
le-libvidstab --enable-libvo-amrwbenc --enable-libvorbis --enable-libvpx --enable-libwavpack --enable-libwebp -
-enable-libx264 --enable-libx265 --enable-libxavs --enable-libxvid --enable-libzimg --enable-lzma --enable-deck
link --enable-zlib
libavutil      55. 36.100 / 55. 36.100
libavcodec     57. 66.101 / 57. 66.101
libavformat    57. 57.100 / 57. 57.100
libavdevice    57.  2.100 / 57.  2.100
libavfilter     6. 66.100 / 6. 66.100
libswscale     4.  3.100 / 4.  3.100
libswresample  2.  4.100 / 2.  4.100
libpostproc   54.  2.100 / 54.  2.100

For help run: ffmpeg -h
For formats run: ffmpeg -formats | more
For codecs run: ffmpeg -codecs | more

Current directory is now: "C:\Users\User\Documents\PhD\Video Annotation_Progs\ffmpeg-20161110-872b358-win64-sta
tic\ffmpeg-20161110-872b358-win64-static\bin"
The bin directory has been added to PATH

C:\Users\User\Documents\PhD\Video Annotation_Progs\ffmpeg-20161110-872b358-win64-static\ffmpeg-20161110-872b358
-win64-static\bin
>
```

Step 3: Specify the location of your video file. For this example the video is stored on the desktop in a folder called ffmpeg

```

--enable-libmodplug --enable-libmp3lame --enable-libopencore-amrnb --enable-libopencore-amrwb --enable-libopenh264 --enable-
libopenjpeg --enable-libopus --enable-librtmp --enable-libschrödinger --enable-libsnappp --enable-libsoxr --enable-libspeex
--enable-libtheora --enable-libtwolame --enable-libvidstab --enable-libvo-amrwbenc --enable-libvorbis --enable-libvpx --ena
ble-libwavpack --enable-libwebp --enable-libx264 --enable-libx265 --enable-libxavs --enable-libxvid --enable-libzimg --enabl
e-lzma --enable-decklink --enable-zlib
libavutil      55. 36.100 / 55. 36.100
libavcodec     57. 66.101 / 57. 66.101
libavformat    57. 57.100 / 57. 57.100
libavdevice    57.  2.100 / 57.  2.100
libavfilter     6. 66.100 /  6. 66.100
libswscale     4.  3.100 /  4.  3.100
libswresample  2.  4.100 /  2.  4.100
libpostproc   54.  2.100 / 54.  2.100

For help run: ffmpeg -h
For formats run: ffmpeg -formats | more
For codecs run: ffmpeg -codecs | more

Current directory is now: "C:\Users\User\Documents\PhD\Video Annotation_Progs\ffmpeg-20161110-872b358-win64-static\ffmpeg-20
161110-872b358-win64-static\bin"
The bin directory has been added to PATH

C:\Users\User\Documents\PhD\Video Annotation_Progs\ffmpeg-20161110-872b358-win64-static\ffmpeg-20161110-872b358-win64-static
\bin
>cd "C:\Users\User\Desktop\ffmpeg"
C:\Users\User\Desktop\ffmpeg
>

```

Step 4: Utilise the following code to extract video frames

- **(Original)** `ffmpeg -i in.mp4 -vf select='between(n,x,y)' -vsync 0 -start_number x frames%d.png`
- **(Example)** `ffmpeg -i RPXD0002AVI.avi -vf select='between(n,200,210)' -vsync 0 -start_number 200 frames%d.png`
  - Using this example code you can **change the parts in red** for your specific files
  - **RPXD0002AVI.avi** – the name of your video
  - **(n,200,210)** – the frame number to start and end on
  - **200** – the frame number from which your images will be labelled
- For example, utilising in FFmpeg

```

C:\Users\User\Desktop\ffmpeg
>ffmpeg -i RPXD0002AVI.avi -vf select='between(n,200,210)' -vsync 0 -start_number
r 200 frames%d.png

```

Step 5: Run the code.

- Note: It can take a while to start running if you are extracting frames towards the end of the video.
- You will see the code continue to run. Push “Q” to stop once your images have been extracted

- They will be extracted to the same location as your video

## ImageJ

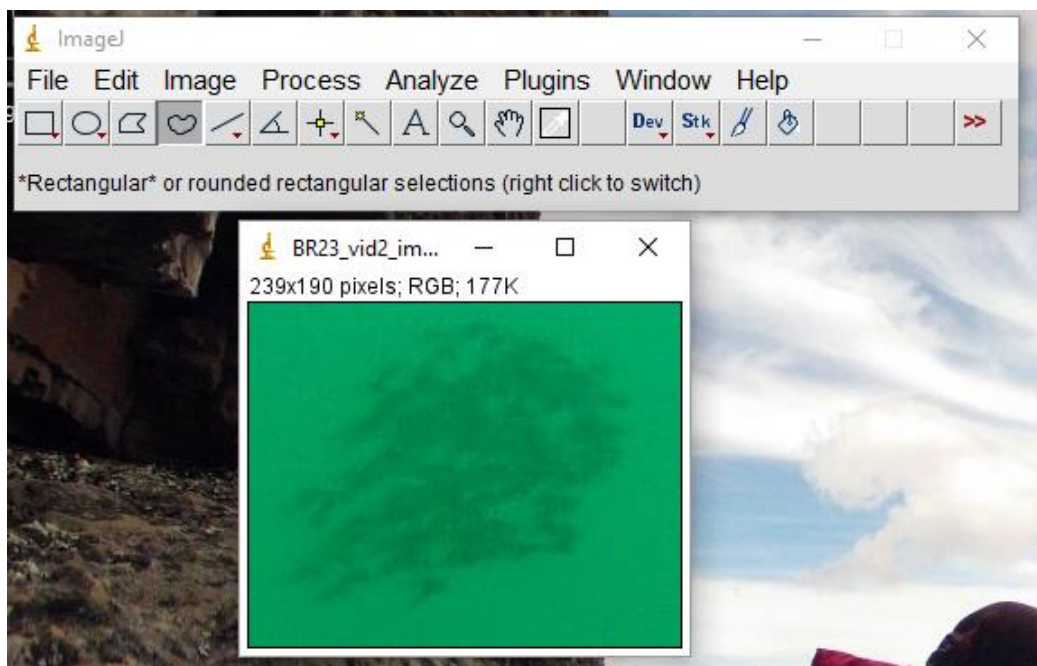
ImageJ is a powerful, open source, image analysis software utilised across a broad range of disciplines (Abràmoff et al. 2004). **Note: As of 30 October 2017, this method still needs to be tested thoroughly to assess its reproducibility.**

Determining lobster krill swarm density was achieved using the following steps:

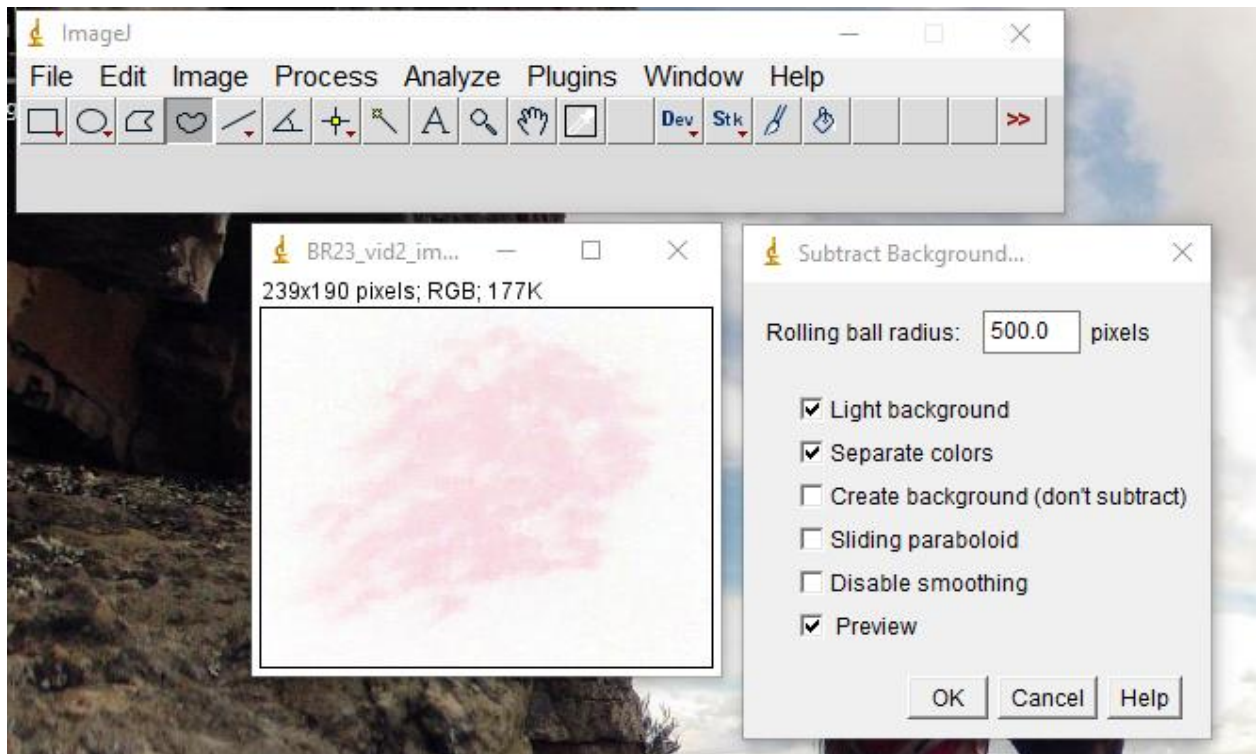
Step 1: Download and install ImageJ from: <https://imagej.nih.gov/ij/index.html>

Step 2: Open ImageJ and open your chosen extracted image

- Note extracted images were also cropped so that the majority of the image reflected just the swarm



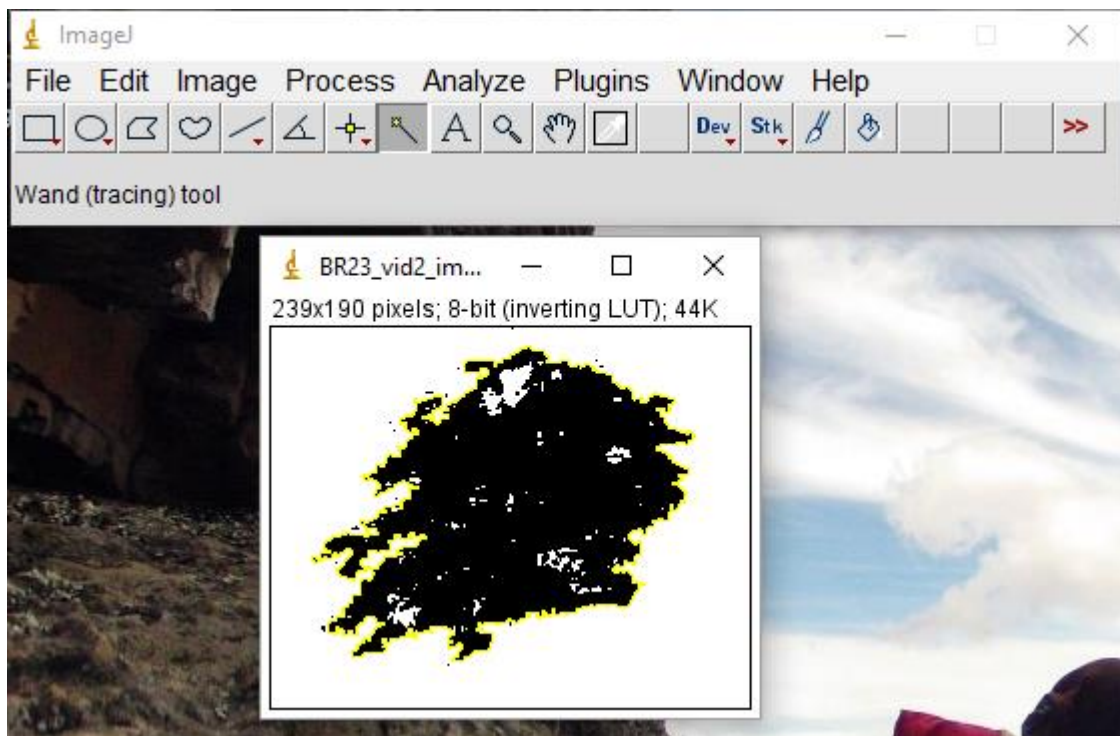
Step 3: Select: Process -> Subtract background



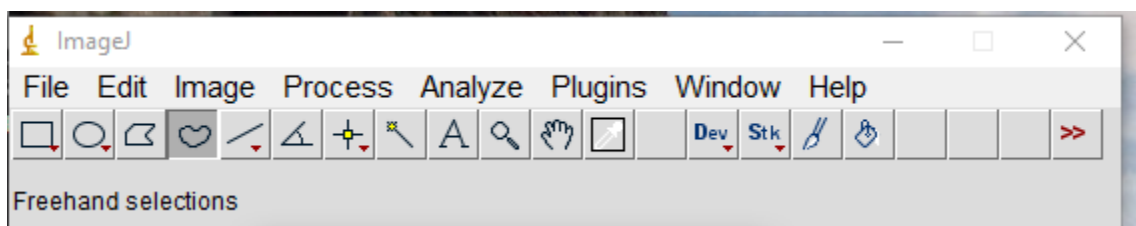
- Images may need to be adjusted by selecting
  - Rolling ball radius option and manipulating as necessary
  - Light background on or off
- Select Preview to preview images -> Then OK

Step 4: Select: Process -> Binary -> Make Binary

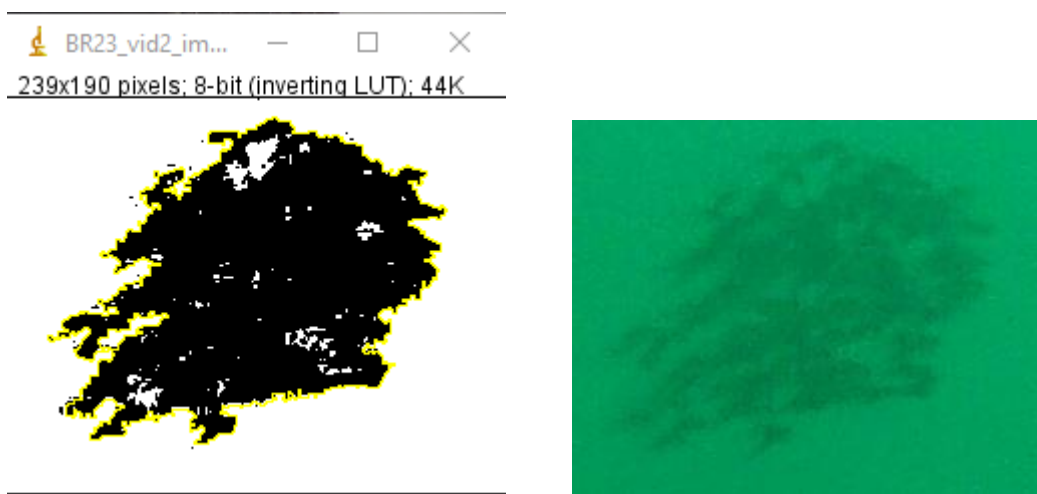
Step 5: Define the region of interest by utilising the Wand tool and then clicking on the black pixels. This should select the perimeter of your region of interest



Step 6: Alternately, one can select a region of interest using the Freehand selection tool to trace around a region of interest.



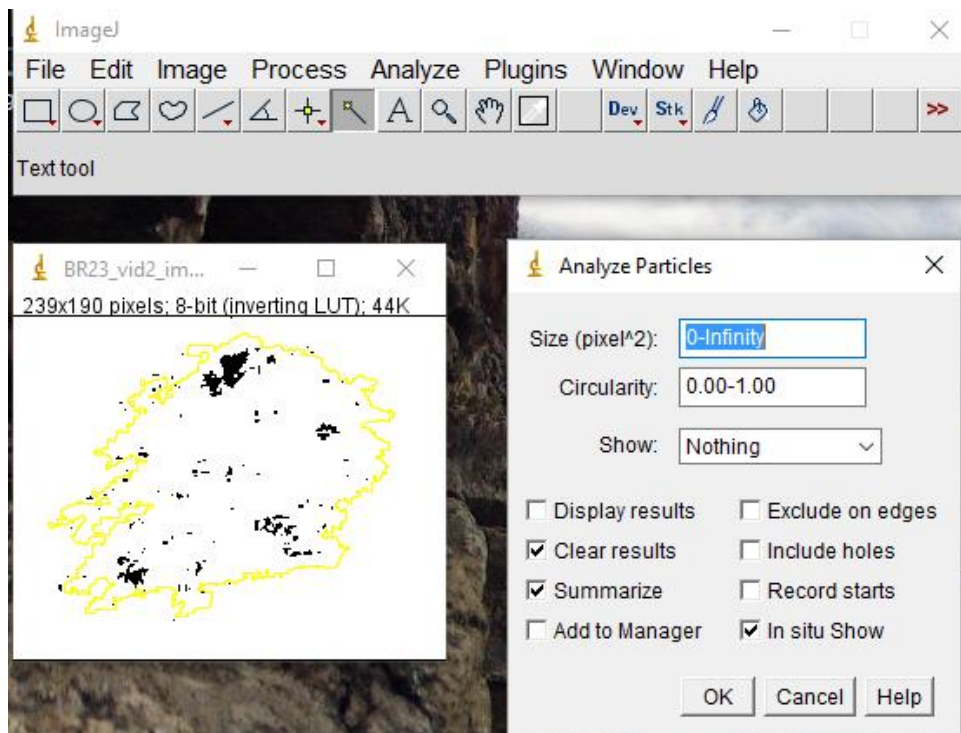
Step 7: Compare with the original image



Step 8: Determine area of pixels that make up the background. Therefore, you need to switch selection within your region of interest



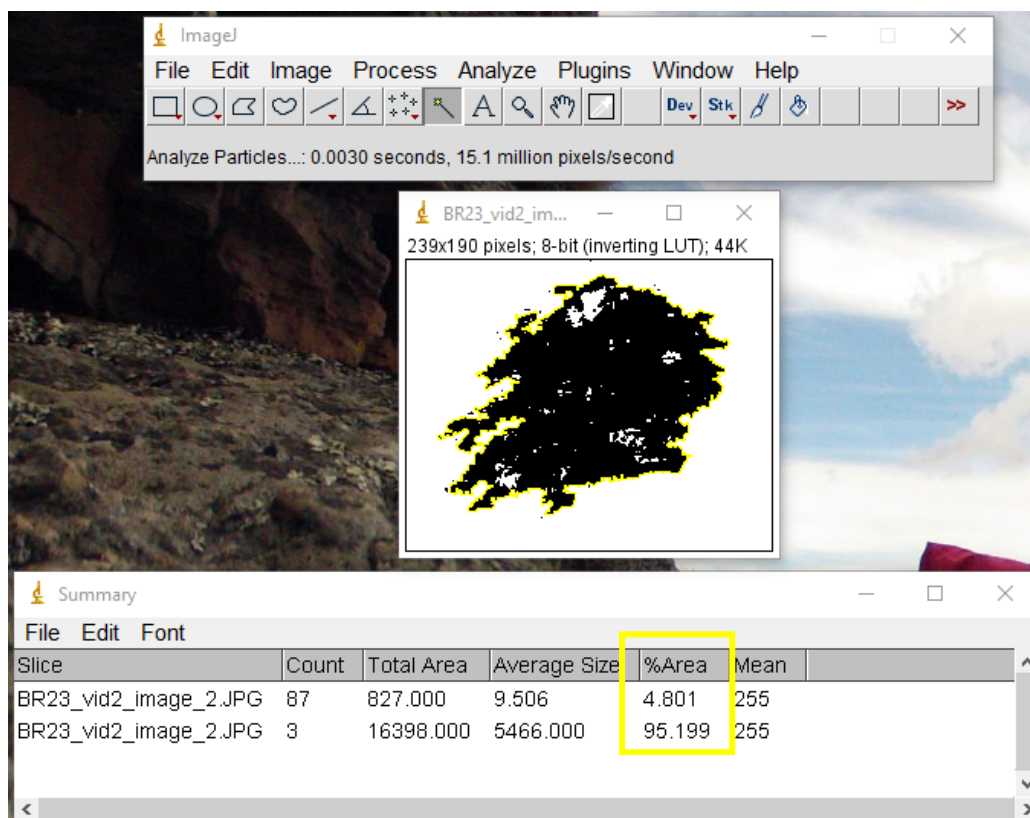
- Select: Edit -> Invert (Switches selection)
- Select: Analyze -> Analyze particles (see settings below)



Step 9: Determine area of pixels that make up the lobster krill (subject item)

- Repeat step 8.
- Record results from the summary table produced





#### Appendix references: Chapter 4

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R CORE T (2013) R: A language and environment for statistical computing.

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